THE

EPARTERIAL BRONCHIAL SYSTEM

OF THE MAMMALIA.

GEO. S. HUNTINGTON.

[ANNALS N. Y. ACAD. SCI., XI, May 17, 1898.]

LANCASTER, PA.
THE NEW ERA PRINTING COMPANY.
1898.

[ANNALS N. Y. ACAD. SCI., XI, No. 8. pp. 127–176, May 17, 1898.]

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(Read February 14, 1898.)

[PLATES XV–XXVIII.]

INTRODUCTION.

DURING the past five years I have devoted much time to the examination of the mammalian lung in reference to the structure of the bronchial system and the distribution of the pulmonary vascular supply. In presenting, as a preliminary communication, some of our more important results to the Section at this meeting, I may state that the research is by no means completed, although it comprises the detailed examination of over two hundred lungs from all orders and many families of the mammalia. Some of the facts established appear to me so conclusive that I do not hesitate to direct your attention to the same, especially because they render my interpretation of the mammalian type of bronchial distribution and pulmonary vascular supply different from the one presented by Ch. Aeby in his valuable monograph "Der Bronchialbaum der Säugethiere und des Menschen." Inasmuch as Professor Aeby's views have been adopted, almost without exception, by the authors of current anatomical textbooks and incorporated more or less extensively in these volumes, the matter appears to me one of more than common interest and importance.

The preparations upon which the conclusions stated in this paper are based were obtained almost invariably by corrosion of the injected bronchial system and pulmonary artery, the only methods which I believe can be relied upon to give absolute and satisfactory results.

I have appended to this paper a nearly complete bibliographical list of articles on the subject which have appeared since the publication of Professor Aeby's book in 1880.

Before proceeding to details, I may briefly recapitulate the main facts and conclusions which Professor Aeby's work contains on the mammalian lung.

1. Aeby recognizes in each lung a main or "stem"-bronchus which can be followed caudad and dorsad throughout the entire lung, diminishing in size gradually by giving off lateral branches, capable of being separated into a dorsal and ventral set. Aeby defines this as the monopodic type of division.

2. The pulmonary artery follows the same general plan of distribution, the main trunk of each side crossing the bronchus ventro-dorsad and continuing caudad on the dorsal aspect of the stem-bronchus, between the ventral and dorsal lateral branches, which are separated from each other by the vessel.

3. In the human lung and in the lungs of most mammalia the lateral branches on the left side are all given off from the stem-bronchus caudad of the point of intersection of the same with the artery. They constitute, therefore, a group of "Hyparterial bronchi." On the right side in man and in most mammalia a bronchus is given off from the stem-bronchus cephalad of its intersection with the pulmonary artery. Aeby distinguishes this bronchus, which in man supplies the upper lobe of the right lung, as the "Eparterial" bronchus.

4. Inasmuch as the upper lobe of the left and the middle lobe of the right lung is supplied by the first "ventral hyparterial bronchus," Aeby considers them homologous, regarding the "eparterial" bronchus and its resulting lobe (upper right) as an entirely new structure confined to the right lung, and morphologically not represented on the left side.

5. While this arrangement obtains in man and most mammalia, Aeby's researches revealed the fact that certain forms are aberrant in reference to the bronchial and pulmonary vascular distribution.

Aeby classifies the various types determined by himself as follows, the list being completed by the forms examined subsequently by M. Weber:

I. Bronchial Tree with bilateral Eparterial Bronchus.
   a. Eparterial Bronchus on both sides bronchial in derivation: *Bradypus, Equus, Elephas, Phoca.*
   b. Eparterial Bronchus bronchial in derivation on left side, tracheal on right: *Phocæna communis, Delphinus delphis, Auchenia.*

II. Bronchial tree with Eparterial Bronchus only on right side.
   a. Eparterial Bronchus bronchial in derivation: *Monotremata, Marsupalia, Edentata* (except *Bradypus*), *Rodentia* (except *Hystrix*), *Carnivora, Insectivora, Chiroptera, Prosimiæ, Primates.*
   b. Eparterial Bronchus tracheal in derivation: *Artiodactyla* (except *Camelus* and *Auchenia*), many *Cetaceans* (*Epiodon australe, Hyperoodon rostratus, Balænoptera rostrata* and *sibbaldii*).

III. Bronchial tree without Eparterial Bronchus. Bilateral hyparterial system: *Hystrix cristata, Balæna mysticetus* and *antipodum.*

IV. Bronchial tree with triple division of Trachea into three unequal Bronchi: *Pontoporia blainvillei.* (Isolated type—not found in any other mammal.)

The above postulates comprise, I believe, the main results of Aeby's research as far as they concern the subject of the present communication. They have been, as already stated, almost universally adopted and have found place, as recognized anatomical facts, in the majority of current text-books on human and comparative anatomy.

Among the subsequent contributions to the morphology of the bronchial tree one deserves special mention, on account of its importance and because it appears to me that it has not received the attention which it deserves. Albert Narath, in 1892, presented a communication to the "Anatomische Gesellschaft," entitled "Vergleichende Anatomie des Bronchialbaumes," published in the "Verhandlungen d. Anat. Gesell. VI. Versammlung, 1892." In this paper Narath controverts a number of Aeby's conclusions very forcibly.

Narath establishes the following propositions, based on extensive comparative and human material:

1. The pulmonary artery in the greater part of its course is placed *laterad* of the stem-bronchus, and does not *cross* the same in Aeby's sense.

2. The pulmonary artery does not influence the structure of the bronchial tree.

3. There is no fundamental difference between the "eparterial" and "hyparterial" bronchi of Aeby.

4. The "eparterial" bronchus is a dorsal (first dorsal) branch, probably originally a lateral branch of the first ventral bronchus shifted upwards on the stem-bronchus.

5. The right eparterial bronchus (when alone present as in man) is represented by an "apical" bronchus on the left side, derived as a lateral branch from the first ventral bronchus.

These important conclusions of Narath will be subsequently again referred to in comparing them with the results obtained by our investigations.

If we now, carefully and without prejudice, examine a large number of corrosion preparations of mammalian lungs, in which the bronchial system and pulmonary artery have been injected, the following facts will reveal themselves:

1. A unity of ground plan can be discerned in all, modified in various forms by:
   - *a.* Migration of one or more secondary bronchi cephalad on the main bronchus, or even on the trachea.
   - *b.* Corresponding changes in the branching of the pulmonary artery.
   - *c.* The appearance, in many forms, of a right accessory (cardiac or azygos) bronchus.
2. If asymmetry exists the right lung is in general the one favored by the greater development and increased calibre and number of the bronchial branches. This physiological precedence of the right over the left lung is characterized by the following facts:

a. The "eparterial" bronchus, if unilateral, is always on the right side.

b. The "cardiac" bronchus is always on the right side.

EXAMINATION OF TYPES.

We may profitably begin our consideration of the mammalian bronchial tree by examining seriatim a number of selected types, subsequently comparing the members of the entire series, in their probable phylogenetic relation to each other, and draw our general conclusions from such comparison.

For reasons, which will be stated later, and which induce us to regard the form as the representative of the primitive mammalian lung, we begin with the type described by Aeby as "Bronchial Tree without Eparterial Bronchus," the complete bilateral hyparterial type.

I. Hystrix cristata—European Porcupine.

Corrosion of bronchial system and pulmonary artery. Columbia University Museum, No. 413. Pl. XV.

The caudal end of the trachea enlarges to a capacious pentagonal bulla or lacuna, slightly compressed dorso-ventrally.

The bronchi, hyparterial in their derivation on both sides and perfectly symmetrical, arise from the tracheal bulla as two main trunks, cephalic and caudal (Pl. XV, *A*, *A*, *B*, *B*). Each trunk divides, in a nearly dichotomous manner, into two nearly equal secondary branches (Pl. XV, *A'*, *A''*, *B'*, *B''*), which in turn give off, by monopodic division, tertiary branches.

1. Cephalic Trunk (Pl. XV, *A*, *A*).
   a. Apical Branch (*A'*) passes to the anterior portion of each lung.
   b. Lateral Branch (*A''*) supplies the central (middle) portion of each lung.
2. Caudal Trunk (Pl. XV, *B*, *B*). Both medial and lateral secondary branches (*B'* and *B''*) ramify in the posterior portion of the lung.

II. a. Taxidea Americana—American Badger.

First specimen; juvenile animal.

Corrosion of bronchial system and pulmonary artery. Columbia University Museum, No. 1254. Pl. XVI.

The tracheal lacuna is large, bullous, rounded, projecting caudad with a blunt rounded terminal cupola between the caudal bronchial trunks.

The primary trunks of right and left side, two in number (Pl. XVI, *A*, *A*, *B*, *B*), arise directly from the expanded tracheal bud. They are, however, compared with those of *Hystrix*, no longer quite symmetrical.

1. Left Lung.

a. Cephalic Trunk (*A*).

Large, directed cephalo-laterad, distributing by monopodic division, secondary branches cephalad and caudad.

b. Caudal Trunk (*B*).

A short wide stem, directed caudo-laterad. It divides, dichotomously, into two main secondary branches, a medial and a lateral (*B'*, *B''*), each of which again divides in a nearly dichotomous manner, the main secondary and the resulting tertiary branches giving off monopodic lateral twigs. (Mixed dichotomous and monopodic type of division.)

2. Right Lung.

a. Cephalic Trunk (*A*).

A short wide stem, directed cephalo-laterad, divides into secondary branches as follows:

α. A slightly smaller apical branch directed cephalo-laterad (*A'*).

β. A somewhat larger lateral branch, directed latero-caudad (Pl. XVI, *A''*). Each secondary branch gives off monopodic tertiary branches.

b. Caudal Trunk. (*B*).

Very short, sessile, directed caudo-laterad. Divides almost immediately into two secondary branches of nearly equal size (*B'*, *B''*), the lateral branch (*B'*) being slightly the larger. Each of

these, as on the left side, gives off two terminal tertiary branches, which are studded with monopodic lateral twigs.

The two tertiary branches resulting from the division of the medial secondary bronchus (*B''*) are characterized by obtaining their arterial supply through a large trunk passing from the main pulmonary artery ventro-caudad between the cephalic and caudal trunks (angle between *A* and *B*), and inclining mesad across the secondary lateral branch of the caudal trunk (*B'*) to reach the terminal divisions of the medial branch of the same trunk (*B''*). The topography of this arterial vessel (Pl. XVI, *C*) is entirely characteristic of the usual blood-supply to the infracardiac, or Azygos lobe in other Mammalia (*cf. infra*).

II b. Taxidea Americana—American Badger.

Second specimen, large full-grown male. Corrosion preparation of bronchial system and pulmonary artery. Columbia University Museum, No. 1255. Pl. XVII.

Presents the same characters as the first specimen as regards the tracheal bulla, and the derivation of the cephalic and caudal primary trunks (*A* and *B*). The tertiary branches are more fully developed and give off more numerous and larger monopodic lateral twigs.

The main interest, compared with the first specimen, centers around the cephalic trunk (*A*) of the left lung. The trunk is only slightly smaller than the one of the right side. It divides into a large cephalic or apical branch (*A'*) and a very much smaller lateral branch (*A''*), while on the right side the primary cephalic trunk *A* divides into two nearly equal secondary branches (*A'* and *A''*). We may, therefore, assume that the large left cephalic bronchus of the younger specimen (Pl. XVI, *A*) corresponds in the main to *A'* of the older animal, and that one of the proximal lateral branches develops into branch *A''* of the adult.

The asymmetry of the right lung compared with the left is well marked. The main secondary branches (*A'*, *A''*) derived from the right cephalic trunk (*A*) exhibit a tendency toward complete separation and individual independence. The arterial

supply of the medial secondary branch (B'') derived from the right caudal trunk (B) presents the same typographical peculiarity found in the younger specimen.

General Consideration of the "Bilateral Hyparterial Type," as Shown in the Preceding Preparations.

1. *Taxidea americana* is a new form, presenting the bilateral hyparterial type, now described in detail for the first time, although I called attention to the peculiarities of the pulmonary structure of this animal in the "Cartwright Lectures," delivered in April 1896.

2. Comparison with the remaining mammalian forms leads me to regard the bilateral hyparterial type as the *primitive condition* of the mammalian lung, whereas Aeby (1) and Wiedersheim (Vergl. Anat. Lehrb., p. 262–266) consider it a complete reduction form, resulting from the bilateral suppression of the "eparterial" bronchus. The reasons for the opinion expressed are as follows:

a. The tracheal lacuna or bulla corresponds to the condition presented by the tracheal bud during the early stages of pulmonary development in mammalian embryos.[1]

b. During the early developmental stages the pulmonary artery passes caudad on each side of the tracheal stalk to the point of division. The subsequent descent of the heart turns the pulmonary trunk ventrad and caudad into the position which it later occupies in relation to the tracheal bifurcation. Hence the original position of the tracheal buds is "hyparterial.

The appearance, therefore, both of the bronchial system and of the pulmonary artery in *Hystrix* and *Taxidea* represents a persistent embryonal type.

3. We may add that this type appears as an exceedingly exceptional one in the mammalian series. In obedience to an

[1] Robinson, Arthur, "Observations on the earlier stages in the development of the Lungs of Rats and Mice," Jour. Anat. and Phys., Vol. xxiii, Pt. ii, January 1889, p. 224.

almost universal law, extension of the bronchial system by migration cephalad of some of the secondary branches brings about asymmetry of the tree and a changed relation of the cephalic primary bronchus to the pulmonary artery.

The only forms in which the bilateral hyparterial type is known to exist are:

Hystrix cristata (Aeby),
Balæna mysticetus and *antipodum* (M. Weber),
Taxidea americana (Huntington).

Turning now to the conditions presented by the remaining mammalia, I have selected the following series of typical modifications, and will present them in the order in which the subsequent general phylogenetic comparison will be made.

III. Canis familiaris—Dog, ♀.

Corrosion preparation of bronchial system and pulmonary artery. Columbia University Museum, No. 1256. Pl. XVIII.

The type presented is the one followed by the vast majority of mammalia, and is defined by Aeby as "bronchial tree with eparterial bronchus only on the right side, bronchial in derivation." There is a well-developed cardiac bronchus (*C*) supplying the Azygos lobe.

Even a cursory examination of this preparation reveals the fact that, with the exception of the cardiac bronchus, a strict equivalence of bronchial elements exists on the right and left sides, but that their relation to the primary bronchus and the main trunk of the pulmonary artery differs on the two sides.

a. *Left Side.*

The first bronchus is a short, thick stem, hyparterial in position (*A*), which divides into an apical and a lateral branch (*A'*, *A''*). Compared with *Hystrix* and *Taxidea*, it is not difficult to recognize in the former the cephalic trunk (*A*) and in the latter the two secondary branches (*A'* and *A''*). The caudal portion of the bronchial tree below the origin of *A* appears as the

"stem-bronchus" of Aeby, from which the remaining secondary branches are derived. Compared with *Hystrix* and *Taxidea*, we recognize the element *B*, between the origin of the first hyparterial trunk *A*, and the origin of the lateral branch *B'*, corresponding to the caudal trunk *B* of *Hystrix* and *Taxidea*. The lateral branch *B'* corresponds to the same element in the bronchial system of *Taxidea* and *Hystrix*.

The continuation caudad of the stem-bronchus occupies the site of the secondary caudal branch *B''* in *Hystrix* and *Taxidea*, and, like this branch, divides into two nearly equal segments, a medial and a lateral, each of which gives off monopodic dorso-medial and ventro-lateral twigs.

The general comparison, therefore, of the left bronchial system of *Canis* with the bilateral hyparterial type of *Hystrix* and *Taxidea* results as follows:

Hystrix and Taxidea.		*Canis.*
A	=	*A*
A'	=	*A'*
A''	=	*A''*
B	=	*B*
B'	=	*B'*
B''	=	*B''*

Aeby's "stem-bronchus" appears as the result of the following rearrangement and further development:

1. The proximal part, between the bifurcation and the origin of the cephalic trunk *A* ("primary left bronchus") results from the segmentation and division of the tracheal bulla.

2. The second segment of the stem-bronchus is formed by the element *B* (caudal trunk) between the origin of *A* and the derivation of *B'*.

3. The third segment is continued caudad as the representative of *B''* (medial secondary caudal branch), while the lateral branch (*B'*) appears as its secondary derivative. Hence we may regard the typical "stem-bronchus" as it appears in the majority of mammalia in the following light:

"Stem-bronchus" = segmented tracheal bulla + *B* + *B''*, medial division.

A and its two secondary divisions *A'* and *A''*, *B'*, as well

as the lateral division of *B''*, appear as lateral (secondary) branches derived from the parent-stem. We have the dichotomous type of division of the primitive form replaced by the monopodic origin of lateral branches from a main parent or stem-bronchus, which condition characterizes the lung of the higher mammalia.

b. *Right Side.*

The first fact noticed is the complete separation of the branches *A* and *A'* and the consequent elimination of the primary cephalic trunk *A*. *A'* has migrated slightly dorsad and cephalad, so as to arise from the stem-bronchus near the bifurcation. *A''* has shifted ventrad and slightly caudad on the stem-bronchus. The interval thus opened between them by the elimination of the trunk *A* is utilized by the right pulmonary artery to gain the dorso-lateral aspect of the stem-bronchus.

In general there can be no question as to the morphological equivalence, regarding direction, size and lung area supplied, of the branches *A'* and *A''* on right and left sides. The same is true regarding the corresponding branches of the pulmonary artery. To be noted is the early derivation of the arterial trunk accompanying *A'* on the right side; also the somewhat more pronounced independent character of *A'*, revealed by the greater number and size of its lateral secondary and tertiary derivatives, all facts accentuating the physiological importance which the apical portion of the right lung has assumed.

The caudal segment follows in the main the type presented by the left side. We recognize the same character and derivation of the stem-bronchus.

A new element, not represented on the left side, appears as the cardiac bronchus (*C*), derived from the stem-bronchus (segment *B*) caudad and mesad to the separate origin of *A''*. Comparison with the bronchial tree of *Taxidea* shows that the large artery, accompanying the cardiac bronchus and supplying the Azygos lobe, corresponds topographically to the arterial branch which in *Taxidea* is seen to course ventro-mesad between *A* and *A'* and *B* to reach the bronchi derived from *B'*.

The cardiac bronchus appears as a secondary structure im-

planted, at somewhat varying levels as we shall see, upon the stem-bronchus of the right side, its appearance being fore-shadowed by the arrangement of the arterial branch (*C*) of the bilateral hyparterial tree of *Taxidea*.

IV. Dicotyles torquatus—Collared Peccary.

Corrosion of bronchial system and pulmonary artery. Columbia University Museum, No. 1258. Pl. XIX.

This preparation exhibits a good type of the further modifications encountered among the Artiodactyla.

On the left side the entire bronchial distribution is hyparterial, the cephalic trunk *A* dividing into an apical (*A'*) and a lateral (*A''*) branch.

On the right side, as in *Canis*, the trunk *A* disappears by complete segmentation of its secondary branches, and the pulmonary artery crosses dorso-laterad, cephalad of the origin of *A''* from the stem-bronchus.

A' has shifted its point of origin, compared with *Canis*, further cephalad and appears as a lateral branch derived from the right side of the trachea.

The distribution of the caudal trunk in symmetrical. The stem-bronchus appears as an especially distinct structure, gradually diminishing in calibre in descent. *B'* appears as its first lateral branch caudad of the origin of *A* on the left and *A''* on the right side.

The cardiac bronchus and corresponding artery occupy the same position as in *Canis*.

V. Myrmecophaga jubata—Great Ant-Eater.

Corrosion preparation of bronchial system and pulmonary artery. Columbia University Museum, No. 479. Pl. XX.

A further advance in the migration cephalad of the right cephalic trunk *A* is noted in this preparation.

The entire right trunk, carrying its secondary branches A' and A'', has shifted cephalad on the stem-bronchus, becoming "eparterial," while on the left side the trunk maintains its original position below the artery.

The secondary branch B' on the left side appears reduced.

The cardiac bronchus is large, arising below the origin of B' from the medial margin of the stem-bronchus. The corresponding artery reaches the ventral surface of the cardiac bronchus by crossing obliquely meso-caudad over the stem-bronchus below the origin B'.

VI. Auchenia glama-pacos—Llama-Alpaca.

Corrosion of bronchial system and pulmonary artery. Columbia University Museum, No. 585. Pl. XXI.

The arrangement of the bronchial system on the right side follows in the main the artiodactyl type as represented by *Dicotyles*, with certain minor exceptions to be presently mentioned. The same number and disposition of the main branches is to be noted.

On the left side further extension cephalad of the apical portion of the lung has led to a division of the cephalic trunk A, repeating the one found on the right side.

The lateral branch A'' occupies the position corresponding to the same branch on the right side, below the pulmonary artery. The apical branch A' has migrated cephalad, appearing as an "eparterial" bronchus arising close to the tracheal bifurcation from the left primary bronchus.

The arterial distribution is symmetrical; the vessels accompanying the branch A' are on both sides derived from the beginning of the pulmonary artery, coursing on the ventral aspect of the corresponding bronchus.

This form, noted already by Aeby, constitutes the type which he describes as "bilateral eparterial bronchus, tracheal on right, bronchial on left side."

The cardiac bronchus is also shifted cephalad, arising from

the ventro-mesal aspect of the stem-bronchus, opposite the origin of *A''* from the ventro-lateral surface.

The corresponding artery occupies a peculiar position. Instead of winding around the angle between stem-bronchus and *A''* caudad of the latter (see preceding types), the artery is derived from the caudal surface of the main pulmonary artery opposite the point where from the cephalic margin the apical vessel accompanying *A'* takes its origin. The artery descends on the ventral aspect of its bronchus. A similar bronchus is found on the left side, but the corresponding arterial branches are short trunks passing to their distribution from the main pulmonary artery dorsad of the stem-bronchus.

VII. Cebus capucinus—Capuchin Monkey.

Corrosion of bronchial system and pulmonary artery. Columbia University Museum, No. 488. Pl. XXII, Ventral view. Pl. XXIII, Dorsal view.

This type presents a somewhat peculiar arrangement of the cephalic trunks on both sides.

On the right side the separation of the two branches *A'* and *A''* is complete, the pulmonary artery occupying the interval between them. *A'* has migrated cephalad on the stem-bronchus, becoming "eparterial," and corresponding to the usual mammalian type of the right side.

On the left side the migration of the cephalic trunk *A* is complete compared with the preceding form (*Auchenia*). It is placed cephalad and dorsad of the point of accession of the main pulmonary artery to the stem-bronchus, and divides into the two secondary branches *A'* and *A''*.

We have, therefore, to follow Aeby's nomenclature for the moment, a "bilateral eparterial system." The eparterial bronchus of the right side, as usual, being furnished by the divorced and migrated apical branch *A'*, whereas, on the left side the entire cephalic trunk *A*, with its secondary branches *A'* and *A''*, becomes "eparterial."

This arrangement is exceptional, as the "bilateral eparterial type" is usually symmetrical. It leads, however, directly up to the condition presented by the two following forms, *Cebus niger* and *Phoca*.

The cardiac bronchus is well developed, derived from the right stem-bronchus between *A''* and *B'*.

The artery passes to the cardiac bronchus from the ventral aspect of the main pulmonary artery, before the same has crossed to the lateral aspect of the stem-bronchus, resembling the arterial arrangement noted in *Auchenia*, although a secondary branch (*C''*) is seen, in the dorsal view, winding around the stem-bronchus in the usual situation of the main artery of the Azygos lobe (Pl. XXIII).

VIII. Cebus niger—Capuchin Monkey.

Corrosion preparation of the bronchial system and pulmonary artery. Columbia University Museum, No. 484. Pl. XXIV, Dorsal view. Pl. XXV, Ventral view.

This type appears as the direct result of further development cephalad of the preceding form.

The cephalic trunks, *A*, of both sides appear as "eparterial bronchi," each dividing into the characteristic secondary branches *A'* and *A''*. On the right side the trunk *A* has shifted a little further cephalad, nearer to the tracheal bifurcation, than on the left side.

The main caudal branches and the cardiac bronchus are arranged as in the preceding form.

IX. Phoca vitulina—Harbor Seal.

Corrosion of bronchial system and pulmonary artery. Columbia University Museum, No. 584. Pl. XXVI, Ventral view.

This final type presents the complete "bilateral eparterial system," perfectly symmetrical; each cephalic trunk (*A*) is situated on the stem-bronchus close to the tracheal bifurcation, cephalad of the main pulmonary artery, and divides sym-

metrically into the secondary branches A' and A''. The corresponding arteries are situated ventrad, derived from the pulmonary artery close to its division into right and left main trunks.

In conformity with the complete bilateral symmetry of the tree a cardiac bronchus is not present.

SUMMARY.

If we briefly sum up the main facts just deduced from the examination of these specimens we find that a complete consecutive series can be established, leading from the symmetrical "bilateral hyparterial type" without cardiac bronchus (*Hystrix*), through gradual modifications, to the complete symmetrical "bilateral eparterial type" without cardiac bronchus (*Phoca*).

This series, to obtain a comprehensive view of the main features, may be schematically represented in Pl. XXVII.

Based on this comparison we may incorporate our conclusions in the following propositions:

1. The right and left lung agree, morphologically, in the type of their bronchial distribution.

2. The asymmetry—when observed—is apparent, not real, depending usually upon complete separation of the right cephalic trunk A into its two components A' and A'', and migration of A' cephalad, changing its original relation to bronchial stem and pulmonary artery; more rarely the asymmetry depends upon the complete migration cephalad of the entire trunk A, carrying the secondary branches A' and A'' (*Myrmecophaga*).

3. Aeby's hypothesis of the morphological equivalence of the middle right and upper left lobe of the human lung is, therefore, incorrect.

The proposition should read:

Right side.		Left side.
Upper + middle lobe	=	upper lobe.
Lower + cardiac lobe	=	lower lobe.

4. The active principle in changing and modifying the architecture of the lung is *not* the pulmonary artery (Aeby), but *mi-*

gration of the cephalic trunk *A*, or of its secondary branch *A'*, usually only on the right side, producing apparent asymmetry. This migration affords an opportunity for more complete development of the resulting terminal bronchial system, and for consequent increase in respiratory area.

5. In the majority of mammals this greater development of respiratory surface is confined to the right side, resulting in the formation of the so-called "eparterial bronchus," and also indicated by the development of a special accessory cardiac bronchus of the right side.

This physiological preponderance of right over left lung is especially well shown by the arrangement of the right lung in artiodactyls (*e.g.*, antelope), where the migration of the cephalic right bronchus has carried the same cephalad, beyond the bifurcation, to the trachea, and where the resulting voluminous upper lobe of the right lung at times extends completely across the mid-line to cap the apex of the more rudimentary left lung.

6. Except, therefore, for purposes of topography we should abandon the distinction of eparterial and hyparterial bronchi, at least to the extent of clearly recognizing the fact that in asymmetrical lungs every right "eparterial" bronchus finds its morphological equivalent among the "hyparterial" bronchi of the left side.

7. The impropriety of ascribing any morphological significance to the number of pulmonary lobes is apparent. The division into lobes is an entirely secondary character, not dependent upon the type of the bronchial distribution, but probably connected with unequal mobility in different segments of the thoracic walls. Lobe-formation is also subject to a considerable range of variation.

8. For the reasons above detailed the primitive type of the mammalian lung is the symmetrical "bilateral hyparterial form," the symmetrical "bilateral eparterial form" representing the *end-stage* in the process of evolution, not the *beginning* (Aeby, Wiedersheim).

9. The primitive type of division is practically dichotomous (*Hystrix*, *Taxidea*).

We can recognize two main trunks on each side, one cephalic, the other caudal. The cephalic trunk supplies the anterior and middle portion of the lung, the main migratory modifications in the different types taking place within its region of distribution.

The caudal trunk supplies the posterior and larger portion of the lung.

In the subsequent development of the stem-bronchus and its monopodic type of branching, characteristic of the majority of mammalian lungs, the following factors are active :

a. Complete segmentation of the tracheal bulla, producing the usual bifurcation. This establishes the proximal portion of the "stem-bronchus," and gives to the cephalic primary trunk *A* the position of a lateral branch derived from the same.

b. The caudal continuation of the stem-bronchus is composed of the primary caudal trunk *B* and its medial secondary branch *B''*, the lateral branch *B'* and subsequently developing lateral accessory branches appearing as the "ventral branches of the stem-bronchus" (Aeby).

c. The cardiac bronchus usually appears as a special accessory branch derived from the stem-bronchus of the right side only (exception *vide supra, Auchenia*).

10. In the majority of forms examined the pulmonary artery is not dorsal to the stem-bronchus, except in the terminal part. The position, as Narath has pointed out, is lateral or dorso-lateral.

11. Hence, the distinction into "dorsal" and "ventral" branches, separated by the pulmonary artery, should be abandoned.

12. It will be seen that our results agree with the conclusions reached by Narath in regard to the equivalence of the anterior or cephalic branches of right and left side in a symmetrical lungs. We differ from him in our interpretation of the derivation of the "apical bronchus" which he regards as the dorsal branch of the first ventral bronchus.

We differ also as regards the above outlined phylogenetic development of the "stem-bronchus" and its monopodic system of branching.

If we seek for an explanation of the *cause* which leads to the migratory changes of the cephalic bronchus, I admit that we enter the realm of pure hypothesis. At the same time, the very general development throughout the mammalia of this type, with the resulting greater respiratory area of the right lung, may, I think, not improbably be referred to the development of the mammalian form of the systemic and pulmonary arteries. The fact which seems to me to be most significant in this respect is the development of the fourth and fifth embryonic arterial arches (Pl. XXVIII).

We know that with the septal division of the arterial trunk into systemic aorta and pulmonary artery the fifth arches on each side are assigned to the development of the latter vessel,[1] while the remaining arches are partially used in the elaboration of the adult arterial system.

If we consider the significance of the fœtal pulmonary inculation it will appear at once that the conditions differ on the right and left sides.

On the left side the greater quantity of the blood thrown from the right ventricle into the left pulmonary artery passes through the Botallian duct directly into the aorta, only a small portion traversing the left pulmonary circulation.

On the right side, however, with the early obliteration of the dorsal segment of the fifth arch, all the blood entering the right pulmonary artery is forced to traverse the entire pulmonary circulation, returning to the left auricle by the pulmonary veins.

I believe that we may properly ascribe to this fœtal circulatory condition a great share in the more marked development of the right as compared with the left lung.

This view is further supported by the conditions found in cases of "situs inversus," where the left lung develops the "eparterial" bronchus (Lit. 6, 8, 9).

[1] It seems preferable, in general considerations, to disregard the existence of the sixth arch, demonstrated by Boas and Zimmerman, on account of the extremely temporary and evanescent character of the interpolated arch.

CONCLUSION.

I have brought this question to the attention of the Academy because I think it is high time to correct the erroneous views founded on Aeby's work. This is the more important, because his theories have been extensively transcribed and his diagrams reproduced in such of the anatomical text-books as deal with the matter at all. I subjoin a list of the anatomical handbooks most commonly in use with a brief statement of their expressions on the subject.

1. **Quain,** "Anatomy," Vol. III, Pt. IV, p. 176-179, follows Aeby's description, giving reproductions or reconstructions of three figures (195, 196, 197) and a somewhat extensive abstract of the text, stating that the right eparterial bronchus in man is not represented on the left side, and that accordingly the lobe which it supplies is also absent, making the upper left the homologue of the middle right lobe.

2. **Morris, Henry,** "Human Anatomy," Phila., 1893, p. 939–940, gives a very indifferent diagram of the ventral view of lungs, heart and pulmonary root, indicating on the right side bronchus, pulmonary artery, and pulmonary vein in the order named cephalocaudad; on the left side in the same order pulmonary artery, bronchus, pulmonary vein.

The text merely repeats this information in a brief statement.

3. **Gray, Henry,** "Anatomy, Descriptive and Surgical." New American Edition from the 13th English Edition, Philadelphia, 1897. P. 1109 gives a diagram (Fig. 706) of the human bronchial tree after Aeby and a brief description founded on Aeby's work. P. 1117 gives in Fig. 710 a faulty view of the ventral aspect of the pulmonary roots, follows it (p. 1118) with the stereotyped description of the order of relations of the structures at the root of the lungs, and concludes (p. 1121) with a xylographic horror purporting to present the roots of the lungs from behind (Fig. 711).

4. **Wiedersheim, Robert,** "Lehrbuch der Vergleichenden Anatomie der Wirbelthiere," 2te Auflage, Jena, 1886, p. 262–266, gives in extenso Aeby's diagrams and conclusions, amplified by the investigations of M. Weber.

5. **Wiedersheim, Robert,** "Elements of the Comparative Anatomy of the Vertebrates" adapted from the 3d German edition, by W. N. Parker, London, 1897, p. 269.

Reproduces Aeby's diagram (Fig. 239), gives a brief resumé of Aeby's conclusions and asserts directly that the anterior lobes of the right and left lung are not homologous, but that the middle right lobe corresponds to the anterior left, and that a want of symmetry is thus created between right and left side, the right lung retaining one more element than the left. This statement is further emphasized by the lettering on fig. 240[a] representing a ventral view of the human lungs.

6. **Joessel, G.,** "Lehrbuch, der topographisch-chirurgischen Anatomie," II, 1. Thorax. Bonn, 1890, p. 60. Gives Aeby's diagram and repeats his conclusions quite fully.

7. **Merkel, Fr.,** "Handbuch der Topographischen Anatomie," Bd. II, Lief. 2, p. 398 and 399, gives Aeby's main conclusions, but also refers to Narath's investigations and gives a schematic figure based on the latter's work. This is the only author who does not accept Aeby's views entirely.

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2. **Aeby, Ch.** "Die Gestalt des Bronchialbaums und die Homologie der Lungenlappen beim Menschen." *Centralbl. f. d. Med. Wissensch,* 1878. No. 16.

3. **Narath, Albert.** "Vergleichende Anatomie des Bronchialbaumes." *Verhandl. d. Anat. Gesellschaft.* VI. Versamml. 1892. Pp. 168–175.

4. **Hasse, C.** "Bemerkungen über die Athmung und den Bau der Lungen und über die Form des Brustkorbes bei den Menschen und Säugethieren." *Archiv. f. Anat. u. Entw.* Jahrg. 1893. Heft 5/6. Pp. 293–307.

5. **Hasse, C.** "Ueber den Bau der Menschlichen Lungen." *Ibid.,* Jahrg. 1892. Heft 5/6. Pp. 324–345.

6. **Aeby, Ch.** "Der Bronchialbaum des Menschen bei Situs inversus." *Arch. f. Anat. u. Phys.,* 1882.

7. **Zumstein, J.,** "Ueber den Bronchialbaum des Menschen und einiger Säugethiere." *Sitzber. d. Ges. z. Beförd. d. gesammten Naturwissenschaften zu Marburg,* 1889–92.

8. **Weber, Max,** "Ueber das Verhalten des Bronchialbaumes beim Menschen, bei Situs inversus." *Zoolog. Anzeiger*, 1881, No. 76.

9. **Leboucq, H.,** "Ein Fall von 'Situs inversus' beim Menschen, mit Rücksicht auf die Bronchialarchitectur," *Zool. Anz.*, 1881, No. 82.

10. **Ewart, William,** "The Bronchi and Pulmonary Blood-vessels, their Anatomy and Nomenclature; with a criticism of Professor Aeby's views on the Bronchial Tree of Mammalia and of Man." London, 1889.

PLATE XV.

PLATE XV.

Hystrix cristata—European Porcupine.

Corrosion of bronchial system and pulmonary artery. Ventral view.
Columbia University Museum, No. 413.

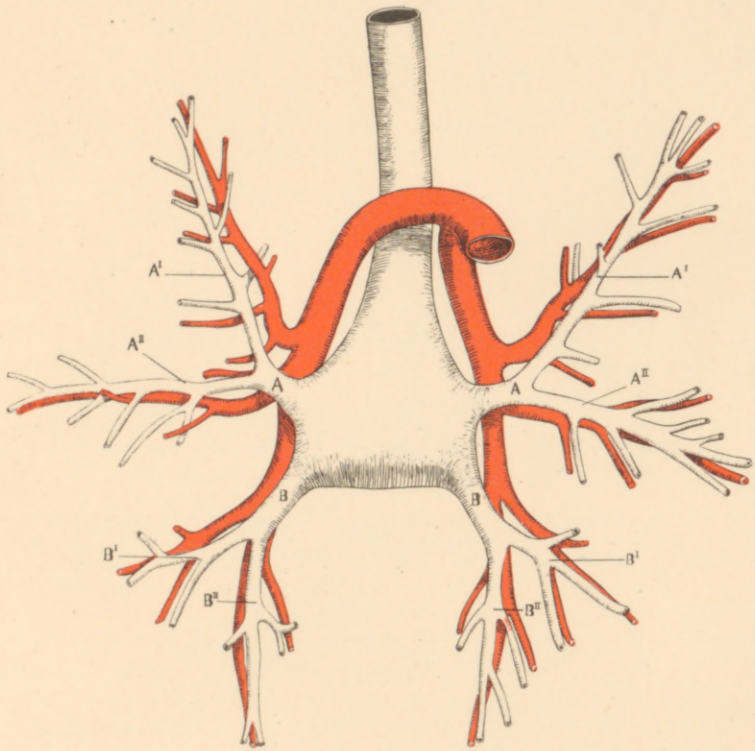
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PLATE XVI.

PLATE XVI.

Taxidea americana—American Badger.

Young animal. Corrosion of bronchial system and pulmonary artery. Ventral view.

Columbia University Museum, No. 1254.

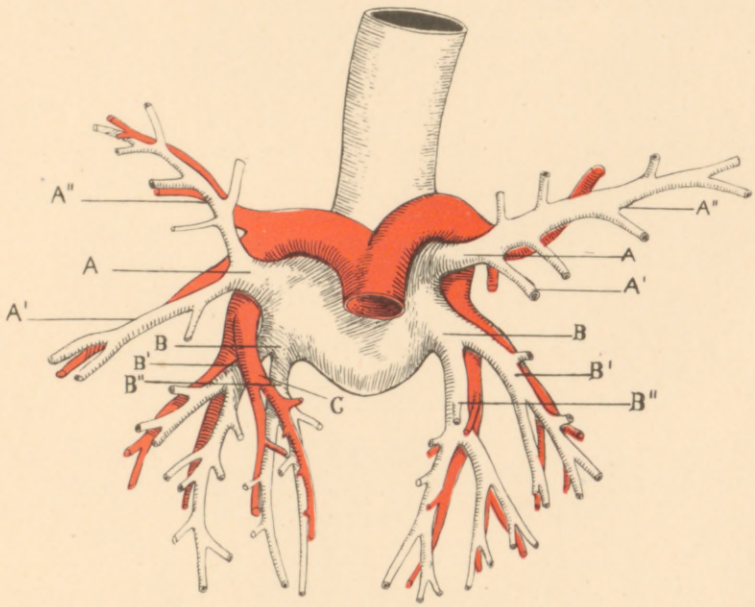
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PLATE XVII

PLATE XVII.

Taxidea americana—American Badger.

Adult ♂. Corrosion of bronchial system and pulmonary artery. Ventral view.

Columbia University Museum, No. 1255.

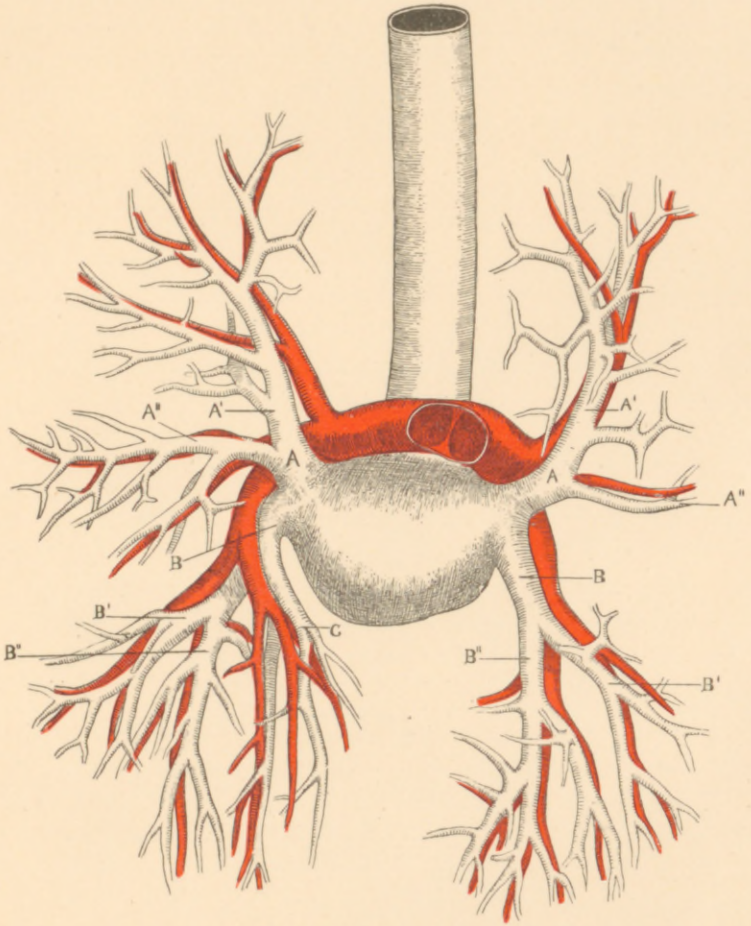
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PLATE XVIII.

PLATE XVIII.

Canis familiaris—Dog.

Corrosion of bronchial system and pulmonary artery. Ventral view.
Columbia University Museum, No. 1256.


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PLATE XIX

PLATE XIX.

Dicotyles torquatus—Collared Peccary.

Corrosion of bronchial system and pulmonary artery. Ventral view.
Columbia University Museum, No. 1258.


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PLATE XX.

PLATE XX.

Myrmecophaga jubata—Great Ant-Eater

Corrosion of bronchial system and pulmonary artery. Ventral view.
Columbia University Museum, No. 479.


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PLATE XXI

PLATE XXI.

Auchenia glama-pacos—Llama-Alpaca.

Corrosion of bronchial system and pulmonary artery. Ventral view. Columbia University Museum, No. 585.


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PLATE XXII.

PLATE XXII.

Cebus capucinus—Capuchin monkey.

Corrosion of bronchial system and pulmonary artery. Ventral view.
Columbia University Museum, No. 488.

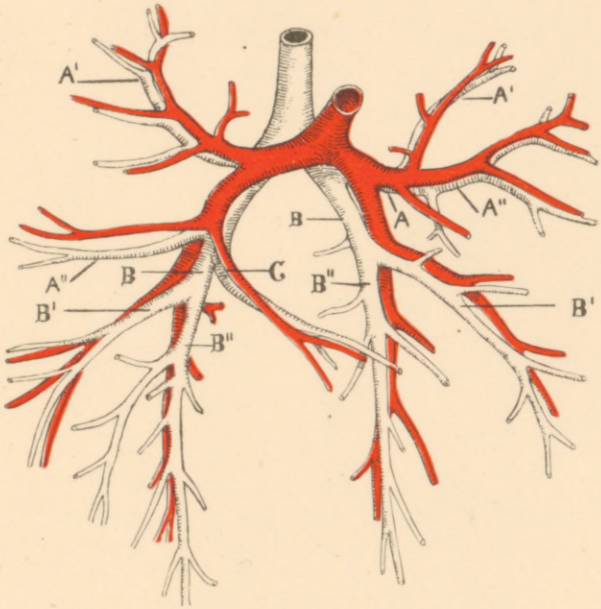
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PLATE XXIII

ANNALS N. Y. ACAD. SCI., XI, May 20, 1898—12.

PLATE XXIII.

Cebus capucinus—Capuchin monkey.

Corrosion of bronchial system and pulmonary artery. Dorsal view.
Columbia University Museum, No. 488.

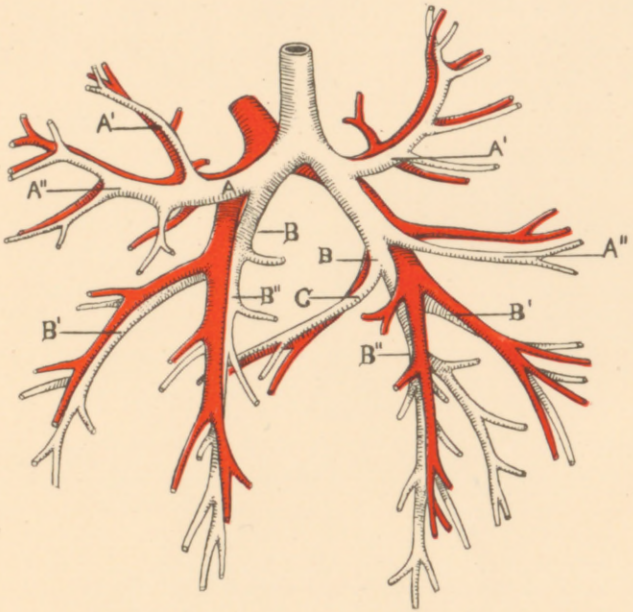
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PLATE XXIV.

PLATE XXIV.

Cebus niger—Capuchin monkey.

Corrosion of bronchial system and pulmonary artery. Dorsal view.
Columbia University Museum, No. 484.


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PLATE XXV.

PLATE XXV.

Cebus niger—Capuchin monkey.

Corrosion of bronchial system and pulmonary artery. Ventral view.
Columbia University Museum, No. 484.

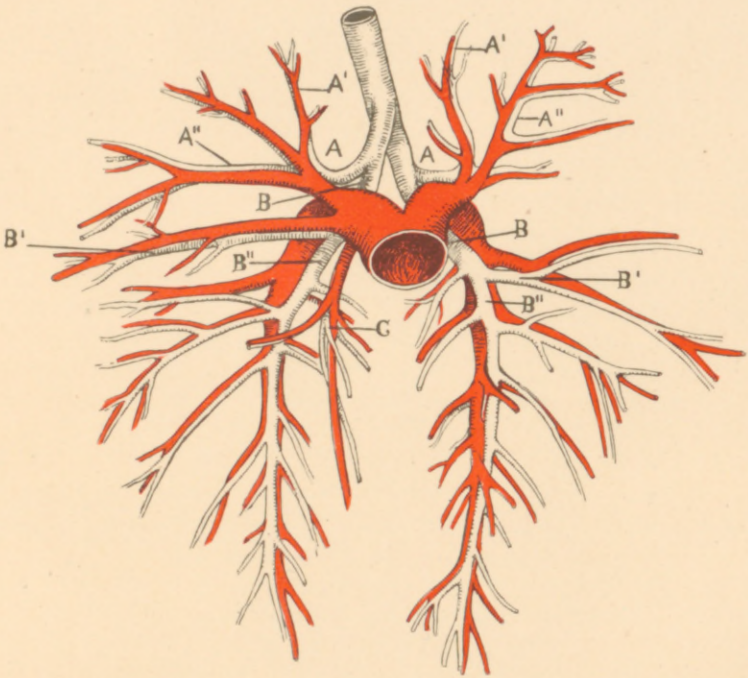
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PLATE XXVI.

PLATE XXVI.

Phoca vitulina—Harbor Seal.

Corrosion of bronchial system and pulmonary artery. Ventral view.
Columbia University Museum, No. 584.

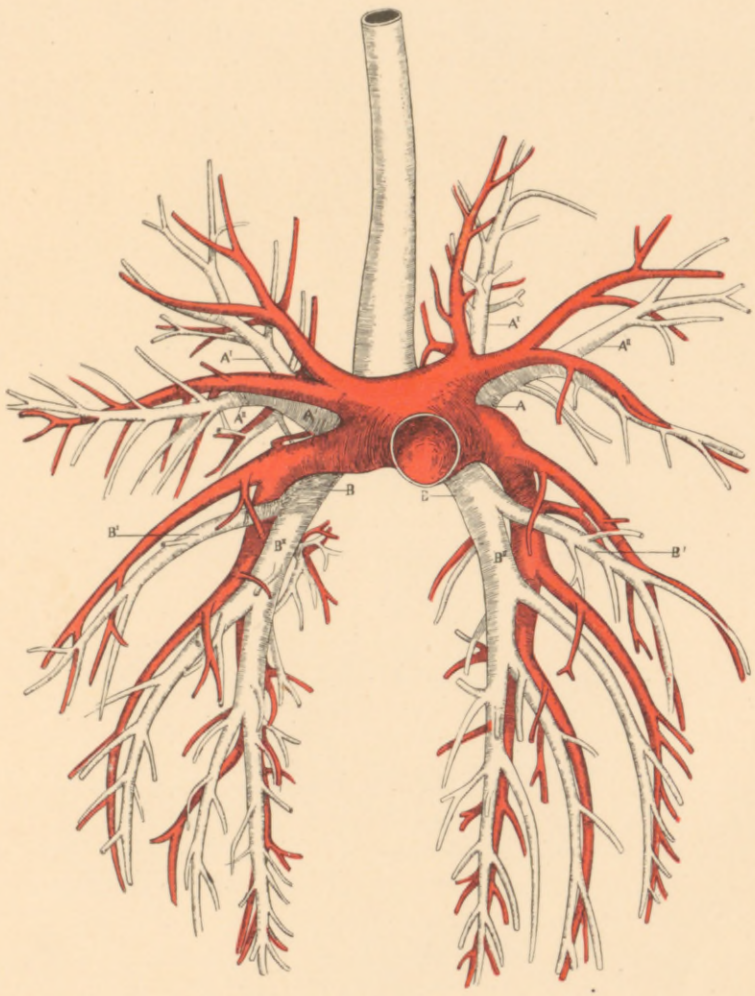
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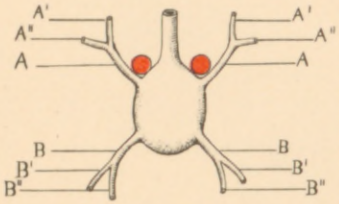
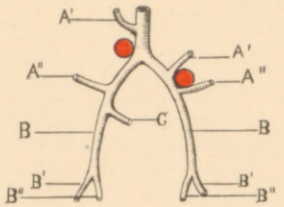
PLATE XXVII.

PLATE XXVII.

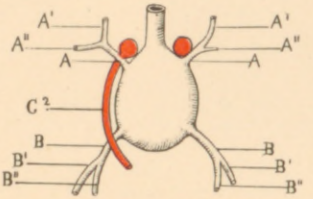
Schematic series, based on preparations described, showing types of mammalian bronchial tree and pulmonary artery.



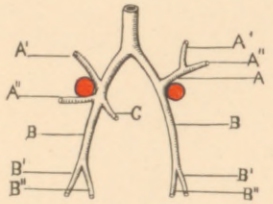
Hystrix cristata.



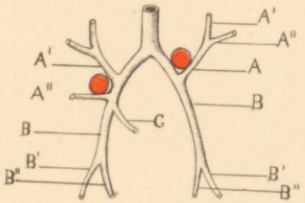
Auchenia glama-pacos.



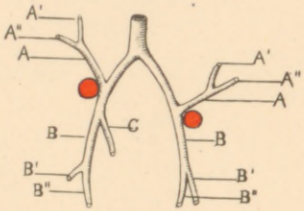
Taxidea Americana.



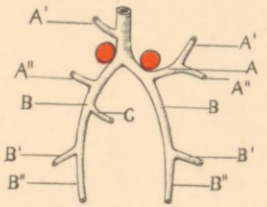
Cebus capucinus.



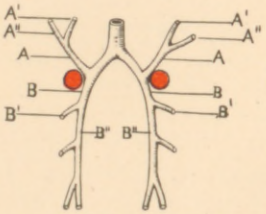
Canis familiaris.



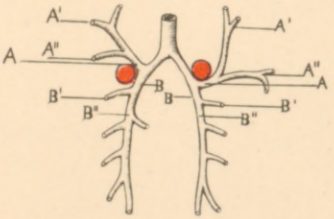
Cebus niger.



Dicotyles torquatus.



Phoca vitulina.

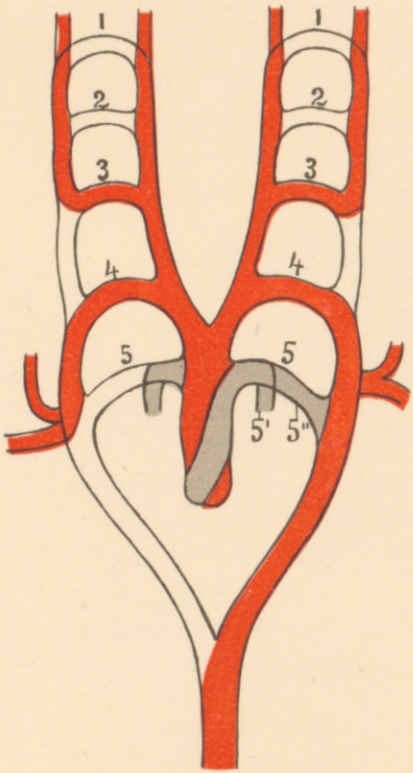


Myrmecophaga jubata.

PLATE XXVIII.

PLATE XXVIII.

Schema showing development of mammalian arterial system.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