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OBSERVATIONS ON SEMON'S LAW.

DERIVED FROM EVIDENCES OF COMPARATIVE ANATOMY AND PHYSIOLOGY.*

By V. E. NEGUS, M.S., F.R.C.S.

Introduction.

THE larynx is situated at the entrance of the pulmonary airway, and although its musculature in Man is complicated, it is easily separated into a sphincteric girdle, consisting of various adductor muscles—which close it—and a pair of dilator or abductor muscles—the posterior crico-arytenoids—which open it. Sir Felix Semon, as a result of prolonged observation, aided also by experimental work, contributed an article to the *Archives of Laryngology* for 1st July 1881, entitled "Clinical Remarks."

"On the proclivity of the abductor fibres of the recurrent laryngeal nerve to become affected sooner than the adductor fibres, or even exclusively, in cases of undoubted central or peripheral injury or disease of the roots or trunks of the pneumogastric, spinal accessory, or recurrent nerves."

This observation demonstrates that if the recurrent laryngeal nerves, which supply the intrinsic laryngeal muscles, are pressed on, or in any other way partially disarranged in their function, the individual may be able to carry on movements of closure but not movements of dilatation on one or both sides

* The Semon Lecture, 1930, of the University of London, delivered on Thursday, 6th November, at the Royal Society of Medicine, London.

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of the larynx according to whether one or both nerves are affected. There has been in the past some dispute as to priority for this observation, and with some it is usual to speak of Rosenbach's Law; by others reference is made to Semon-Rosenbach's Law. I do not propose to go into any discussion of this matter now because it is quite immaterial to the subject, and it is sufficient to know that the observations were fully established and carefully described by Sir Felix Semon. Objections have been brought forward disputing the truth of Semon's Law, notably by Grossman. Here, again, I will not enter into any discussion because in my limited experience Semon's Law has appeared to be a true one, and I propose to take it as a basis of this lecture.

The evidence of comparative anatomy is strongly in favour of its truth.

In choosing a subject it seems to me highly appropriate that I should if possible make some observations connected with the outstanding work of the founder of this lecture. I am afraid that they will not be of practical utility, but there may be in them some points of interest, because the subject lends itself to interesting contemplation and carries investigations beyond the immediate limits of the larynx and beyond the purely clinical aspects. Semon himself, although in no doubt as to the truth of his law, invited evidence from others which would throw additional light on the subject. He writes in the paper already referred to:—

"In the face of the comparative novelty of the subject and of all the difficulties connected with this question, I would rather believe that the time has not yet come when we can venture to give an *explanation*, but that, before all, by numerous further contributions, the *fact* should receive further corroborative evidence, that: *There is a proclivity of the ABductor fibres of the recurrent nerve to succumb to pathological influences affecting the roots and trunks of the motor nerves of the larynx.*"

It is necessary first to realise the importance of Semon's Law; it has given rise to a great deal of discussion in the past because of its immense bearing on clinical matters. If both the muscles which open the larynx are paralysed, the individual affected has the greatest difficulty in breathing and may die of asphyxia. This is sufficient reason for devoting attention to the factors concerned with paralysis of the dilator muscles; it seems necessary to start at the very beginning and to work

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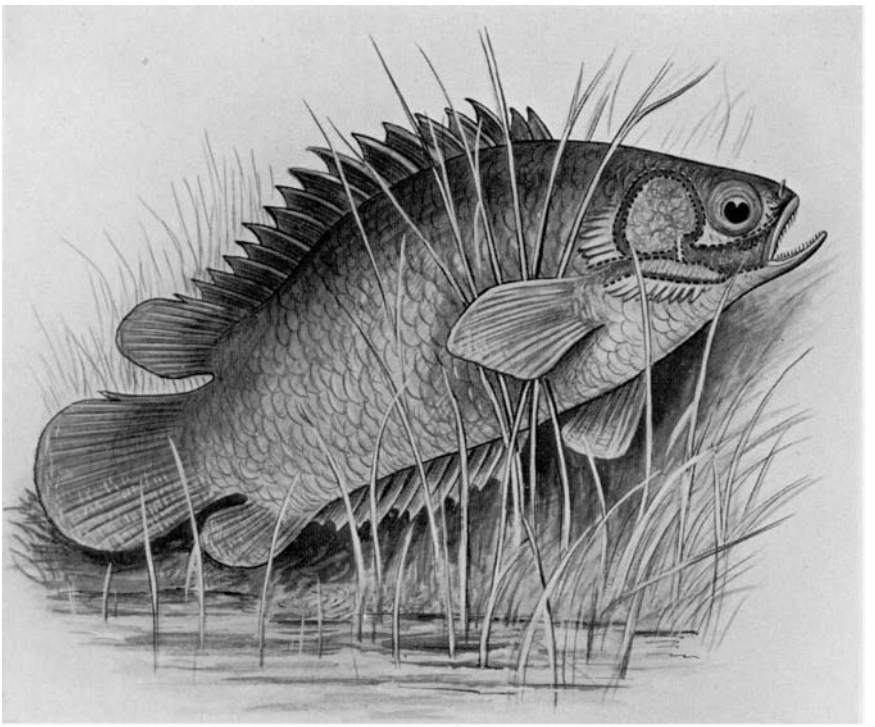


Fig. 1.—A Climbing Perch (*Anabas scandens*) progressing by means of its fins. The respiratory diverticulum is illustrated, lying above one of the gills.



Fig. 2.—Amazon Mud Fish (*Lepidosiren*).
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upwards with unbiassed judgment rather than to concentrate attention on the larynx of man, an organ which has passed through very great and prolonged phases of evolution and has therein suffered extensive modifications.

Reasons for Presence of Lungs.

To go back to the very beginnings of the larynx, it is necessary to inquire why the organ became necessary. The most primitive type of larynx is to be found in Dipnoi or Lung Fish, and by comparing the habits of these fish with those of other species, we may gain some knowledge of the evolution of the organ. The majority of fish breathe air dissolved in water. Only a small percentage of air can go into solution, and of the dissolved air only one-quarter consists of oxygen. Therefore a very large amount of water has to pass through the gills to enable sufficient oxygen to be absorbed to satisfy the requirements of the individual. If the amount of oxygen reaching the respiratory epithelium can be raised, it will confer an obvious advantage on the species. A simple method is seen in many fish which come to the surface and take a mouthful of air. This is added to the water passing through the gills, and throws into solution a certain proportion, from which oxygen can be absorbed. Gold Fish living in a glass bowl devoid of vegetation carry out this means of increased oxygenation because the water contains less than the requisite amount of dissolved air. Some fish can obtain oxygen from the air if the gills are moist, even when they are out of water. They will do this more easily if specialised epithelium be present capable of taking up oxygen in the absence of water. A notable example is the Climbing Perch (*Anabas scandens*) (Fig. 1). This fish can travel long distances on land and can sustain life for prolonged periods out of water. It has three or more concentrically arranged bony laminæ attached to the upper extremity of the fourth branchial arch; the vascular membrane which invests the laminæ can act as respiratory epithelium. There is this disadvantage, however, that the mechanism is out of action under water, as there is no means of storing air; it is satisfactory for use out of water and a mechanism of this type might serve the purpose of terrestrial species, although it is not sufficient for an animal which wishes to stay under the surface for a long time. Some fresh-water fish of India are drowned if prevented from reaching the surface, and fishermen

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avail themselves of this fact by watching for them to come up to breathe and then catching them. Some of the Loaches (e.g. *Misgurnus fossilis*) come into this category. They swallow air and pass it right through the intestine, from which absorption of oxygen takes place and excretion of CO_2 is carried on. In them, as in the Climbing Perch, there is no store of air; this difficulty is found to be partially overcome in an Indian Siluroid Fish (*Saccobranchus*) in which a long diverticulum from the branchial cavity acts as a reservoir. There is, however, no valve to prevent escape of air or entrance of water.

We now come to a further stage in evolution, namely, a fish with an air-bladder shut off from the alimentary canal by a valve consisting of a muscular sphincter. This valve represents the larynx and is to be found in the Bichir (*Polypterus*); it is doubtful, however, whether this air-bladder carries on a respiratory function. There is no doubt, however, about true air-breathing when we come to the Lung Fish, of which there are three examples, namely, the African Mud Fish (*Protopterus*), the Australian Lung Fish or Barramundi (*Neoceratodus*), and the Mud Fish of the Amazons (*Lepidosiren*) (Fig. 2). Under certain conditions these fish breathe air only and are drowned if they are deprived of the source. The African and Amazon Mud Fish breathe air mainly when torpid, and in part only at other times. They have long lungs which act as big reservoirs; there is a valve at the mouth of the trachea taking the form of a larynx. In the Australian Lung Fish air-breathing goes on at more active times, even when the fish is swimming about. It is of the greatest importance to these species that they should have some mechanism for breathing air, as otherwise they would die. They all inhabit rivers which are liable to dry up, and they are left stranded in stagnant pools in which the vegetation decays, thus cutting off the supply of oxygen (Fig. 3). They have gills with which they can breathe oxygen dissolved in water at ordinary times, and it is because of their habitat that they are not able to carry on this method of respiration at all times, as in the case of fish inhabiting deep rivers or the open sea.

We find in them a great advantage, namely, the capacity of storing in their lungs a supply of air for use under the surface, in addition to the benefit gained from being able to breathe when out of the water.

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Fig. 3.—African Mud Fish (*Protopterus annectans*) in its mud case or cocoon, in which it lies dormant when the water has dried up.
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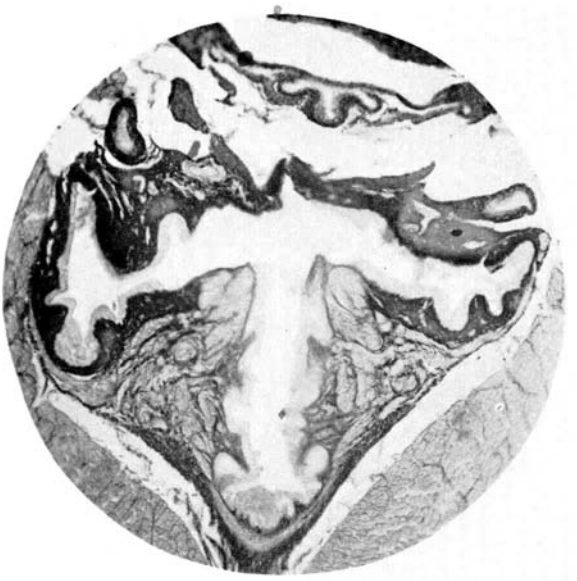


Fig. 4.—Transverse section of pharynx of South American Lung Fish (*Lepidosiren*). The big transverse cavity is the gut. The vertical fissure is the larynx, with upstanding margins and sphincteric muscle fibres. No cartilages. (Serial sections cut by Mr Steward.) (Reproduced from *The Mechanism of the Larynx*, Negus, by permission of Messrs Heinemann.)

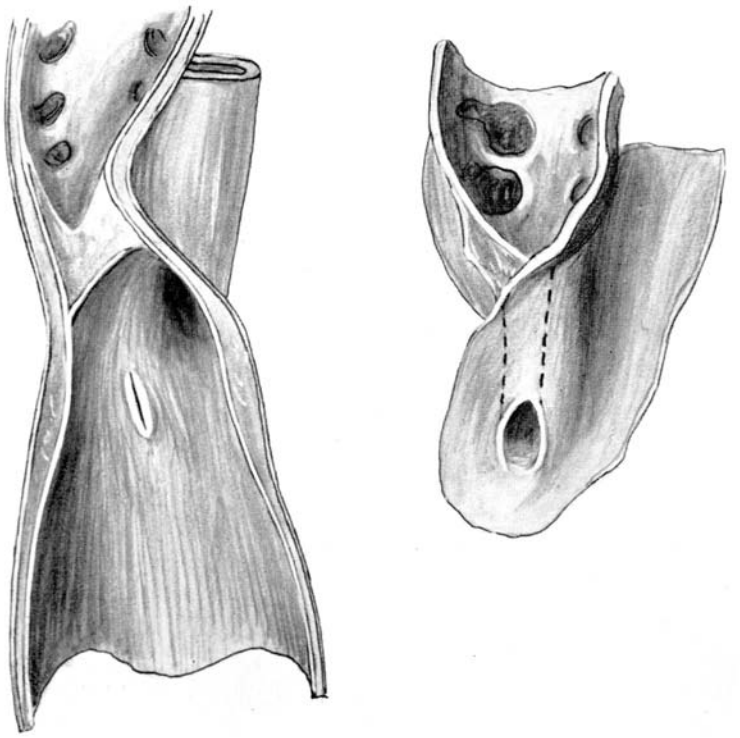


Fig. 5.—Larynx of Australian Lung Fish (*Ceratodus*) closed on the left and open on the right. It lies flat in the floor of the pharynx. The œsophagus is seen passing up to the right and the lung to the left in each drawing.

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Observations on Semon's Law

In terrestrial animals, including mammals, there is no object for storing up of air as far as the source of supply is concerned, because there is always plenty of the medium surrounding the individual. But it is of advantage to the metabolism of the body that gas exchanges should go on continuously and evenly from a reservoir of air and not in spasms, as would happen if there were no means of storage. Furthermore, it adds to efficiency if respiratory movements can be suspended during short intervals. Because of the constant store of air, the blood is always saturated with oxygen, and the arterial blood is enabled to contain a fixed percentage of CO_2. The tissues therefore receive a medium of almost unchanging consistency.

Primary Function of Sphincteric Muscle of Larynx.

Protection of Respiratory Epithelium.—In the Lung Fish there has been evolved a sac-like lung with specialised epithelium capable of carrying on gas exchanges from the air, and it is of vital importance that it should be protected from the entrance of water or food. Otherwise it will be seriously disarranged. For this reason there must be some means of closing the mouth of the air-sac at all times, except when air is passing in, to prevent swamping of the lung and drowning of the fish. The means of closure is provided by a specialised band of sphincteric muscle surrounding the opening of the lung from the food passage; it is derived from the musculature of the pharyngeal wall, but is distinct from it (Fig. 4). This band of muscle, supporting the margins of the glottic lips, is the important constituent of the most primitive form of larynx. It will be referred to throughout this paper as the sphincteric muscle, and not as the adductor group; the latter term is applicable only to higher species and lays undue stress on the vocal function of the larynx. The larynx forms a protective valve for the pulmonary air-tract and is not evolved as an organ of phonation.

In my opinion, the sphincteric muscle, because of its protective origin and vital importance, retains its function when other functions of the larynx are lost. This, I think, provides the reasons underlying Semon's Law, and I consider that in Man the same factors hold good, and find it according to supposition that the function of the sphincteric musculature should survive that of the dilator muscles if studied from this simple aspect.

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Difficulty has arisen in obtaining a clear view of the subject, because the larynx has generally been studied in its complicated human form and also because it has been looked on as primarily a vocal organ. Semon himself discusses the question rather from this point of view.

Another fallacy has arisen, namely, a belief that the action of the dilator muscles is more automatic than that of the sphincteric group. Semon had this opinion when he wrote that the explanation might perhaps "be found in the fact that the activity of the abductors, although, I believe, not *entirely* beyond the control of the will, is certainly much more automatic than that of the antagonists, and that, hence, perhaps its power of resistance against disease-producing causes is less."

In cases of functional aphonia, automatic closure of the ary-epiglottic folds during swallowing, and of the vocal cords during fixation of the thorax, may be observed when the power of voluntary approximation of the glottic margins on attempted phonation has been lost; the automatic functions—of major importance—remain unaffected when the more recent and less vital function is temporarily lost.

This view disagrees with that of Semon, but if it is true, it is an argument in favour of the truth of his law; that is to say, the very fact of automaticity is associated with enduring vitality. Nothing could be more automatic than the protective closure of the laryngeal sphincter, added to which, as a reason for longer survival, is its primitive origin.

The importance of the sphincteric muscle is very marked in aquatic animals, such as Lung Fish, which have no other means of protection for their lungs (Fig. 5). There are no cartilages forming a scaffold of the larynx and none supporting the margins of the glottis. Nor is there any need for them, as the simple respiratory needs of the species are carried on with this primitive mechanism. The margins of the glottis are not raised, and the larynx is seen as a small sagittal fissure lying flat in the floor of the œsophagus. The appearance is very similar to that seen in the human embryo of 5 millimetres (Fig. 6).

In carnivorous Lung Fish the food is torn to pieces and is swallowed in lumps. The diet is mainly of a carnivorous type in the Amazon and African species; the Australian Lung Fish, however, is said to eat vegetation. There is nothing to divert food into the air-tract as there is no upraising of the glottic margins, the orifice of the larynx being scarcely noticeable.

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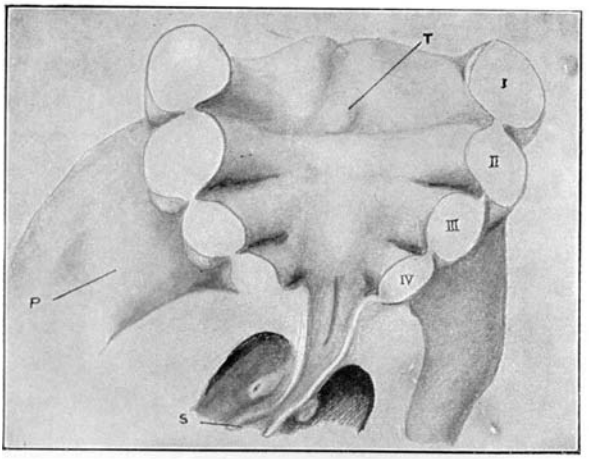


FIG. 6.—Pulmonary outgrowth in Human Embryo of 5 mm. Reconstruction model showing the pharyngeal floor. (Reproduced from Buchanan's *Manual of Anatomy*, 1925, by permission of Ballière, Tindall & Cox.)

P = Pericardium. T = Tuberculum Impar. S = Stomach. The slit-like fissure of the larynx is seen lying flat in the floor of the pharynx.

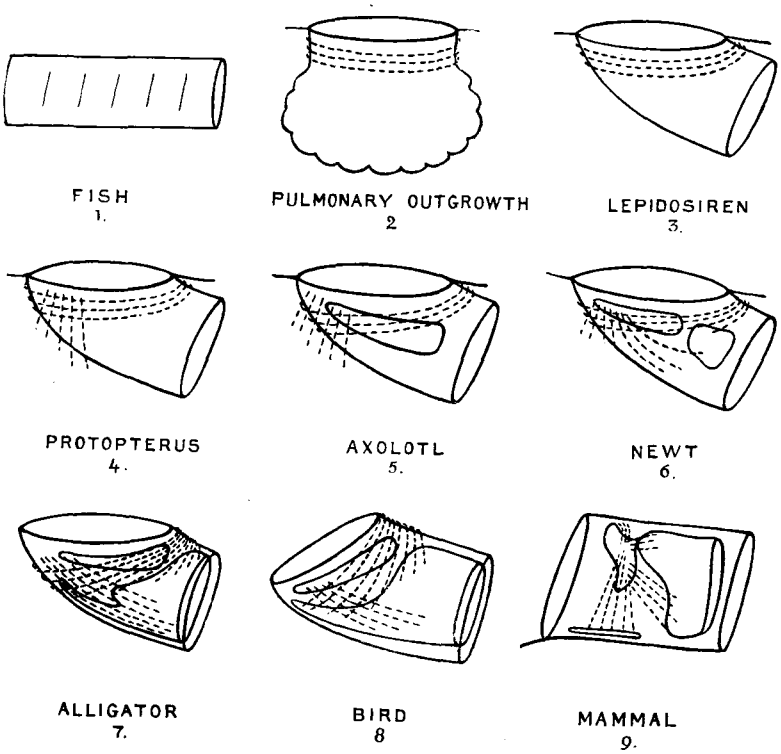


FIG. 7.—Diagram to illustrate the evolution of Lateral Cartilages. (Reproduced from the *Lancet*, 17th May 1924.)

1. Pharynx of fish with gill slits. 2. Commencing outgrowth from floor of pharynx. 3. Elongated trachea turning off towards thorax. 4. Primitive dilator mechanism. 5. Appearance of lateral cartilages. 6. Separation of cartilage into arytenoid and half of cricoid. 7 and 8. Fusion of thyroid elements with cricoid. 9. Separation of thyroid from cricoid. Shortening of arytenoid. Tilting of laryngeal aperture. Division of sphincteric muscle into components.

Interrupted lines: sphincteric muscle and dilator muscle.

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The glottis must be tightly shut during deglutition, however, because food is swallowed under water.

In the African Lung Fish (*Protopterus*) there is a little plate of cartilage in front of the anterior end of the larynx. It has no relation to an epiglottis, as has been suggested, but is a condensation of the pharyngeal floor just below the mucous membrane. Its function will be referred to later. The Australian Lung Fish (*Neoceratodus*) has a similar cartilage, but in the Amazon Mud Fish (*Lepidosiren*) I cannot find a trace of any cartilage whatsoever.

In examining the larynx of fish a peculiar modification is to be found in the Bony Pike (*Lepidosteus*) and also in the Bichir (*Polypterus*). In these fish the larynx opens on the dorsal wall of the food passage, the reason being that the lung has got to as high a position as possible against the vertebral column in order not to capsize the fish when under water, and for this reason food does not pass over it but under it. Water however would enter the glottis, and therefore the latter must be kept shut when food is swallowed because this is done when the fish is submerged.

Changes due to Presence of Lateral Cartilages. — In animals with a more highly evolved larynx lateral cartilages make their presence in the margins of the glottis; these are first seen in Axolotls (*Amblystoma*) and are found to be divided in Newts (*Molge*), the anterior part representing the arytenoid, while the posterior half fuses with its neighbour of the opposite side to form a cricoid ring (Fig. 7). When lateral cartilages are present the edges of the glottis do not so readily tend to fall in when water exerts pressure on the upper surface, even if the muscular sphincter be partially relaxed.

In amphibians the larynx is very minute, and there would be little danger of the lumps of food—which are taken without mastication—entering the air-tract. As the food is, however, in most species, swallowed under water, the glottis must, of course, be tightly shut. The sphincteric muscle is of great importance to the existence of the animal as it has the function of bringing together the lateral or arytenoid cartilages and of holding them in firm apposition, although it need not contract so powerfully as in Lung Fish in order to close the glottis.

In some reptiles, such as Monitor Lizards, the glottis is found on section to take the shape of a gothic arch, the glottic margin being bounded by long rod-like cartilages. In aquatic

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reptiles, such as Crocodiles and Alligators, the larynx is slightly domed; it lies almost flat in the floor of the pharynx as a longitudinal fissure with low margins, not impeding the passage of food (Fig. 8). Birds show the same structure, the arytenoids being long rods. In these reptiles and in aquatic birds the mouth must sometimes be opened under water to catch fish or other prey, and the pressure of the water in the pharynx and œsophagus must be considerable (Fig. 9). It is of advantage to the individual to have this domed type of larynx as it keeps shut mechanically without the exertion of great muscular effort; the sphincteric muscle is still, however, of importance, as it is required to hold the relatively large glottis closed during deglutition, whether under the water or above it. As food is not masticated by amphibians, reptiles, and birds, the bolus is generally of large size, and is not so liable to enter the glottis as in the case of mammals.

In aquatic reptiles and amphibians the glottis is opened only for a very brief period, during which expiration and inspiration take place; for the greater time it is tightly shut, as may be seen in Alligators. In these animals a complete muscular sphincter embraces the arytenoid cartilages; its inclination to the axis of the pharynx is slightly oblique, unlike the organ of Lung Fish, in which the sphincteric fibres run close beneath the floor of the pharynx.

An interesting modification is seen in crocodilians in the form of a mouth flap (Fig. 10). The raised base of the tongue can be brought into firm contact with a fold at the posterior end of the palate, thus preventing water from reaching the larynx. Air is carried from the nostrils along a lengthy nasal passage to the orifice of the glottis so that the animal can breathe with its mouth open under water, provided the tip of the snout is above the surface.

When mammals are examined the arytenoid cartilages are seen to be shortened and a certain length of the margins of the glottis is made up of membranous folds. These folds and the cartilages must be approximated to prevent entrance of food or water, the mechanism being carried out by action of the sphincteric muscles, which are of even greater importance than when the arytenoids form the major part of the glottic margins.

Of terrestrial animals the carnivorous cat tribe has a simple type of larynx which must be shut by sphincteric action during deglutition because all food has to pass over its opening, there

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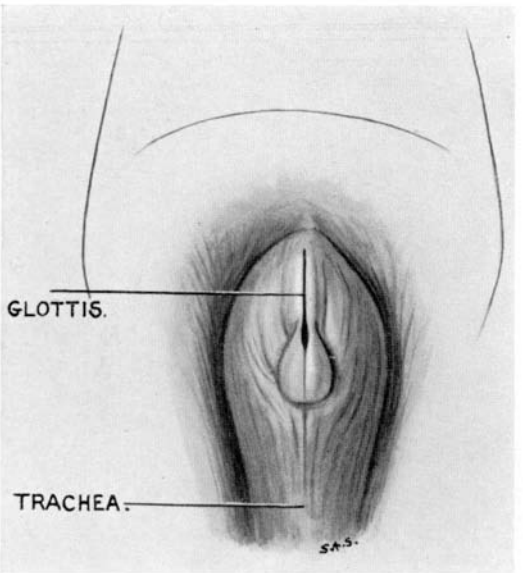


FIG. 8.—Simple type of larynx of an Alligator. (Previously produced in *Journal of Anatomy*, October 1927.)

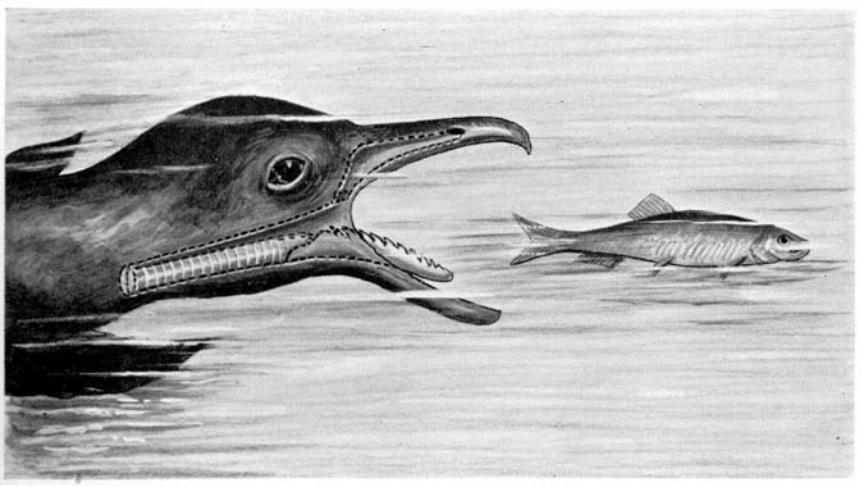


FIG. 9.—A Penguin (*Spheniscus demersus*) pursuing a fish under water. Several fish may be swallowed under the surface, necessitating firm closure of the larynx. The nasal passage and the trachea are shown in outline.

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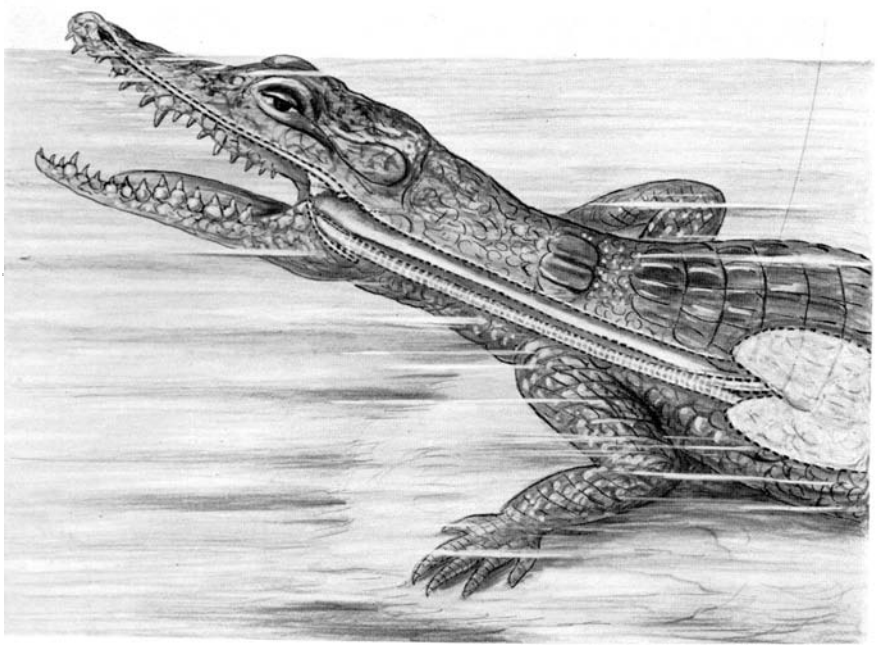


FIG. 10.—A Crocodile resting on a sand-bank with its snout above water. Air is carried to the larynx along a lengthy nasal passage; the larynx is protected against inundation by a mouth flap.

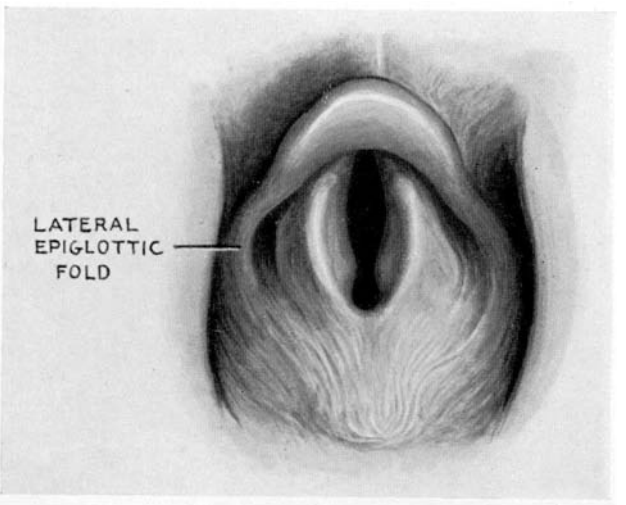


FIG. 11.—Dorsal view of larynx of a Black Leopard (*Felis pardus*) to illustrate the absence of a lateral food channel. (Previously produced in *The Mechanism of the Larynx*, Heinemann.)

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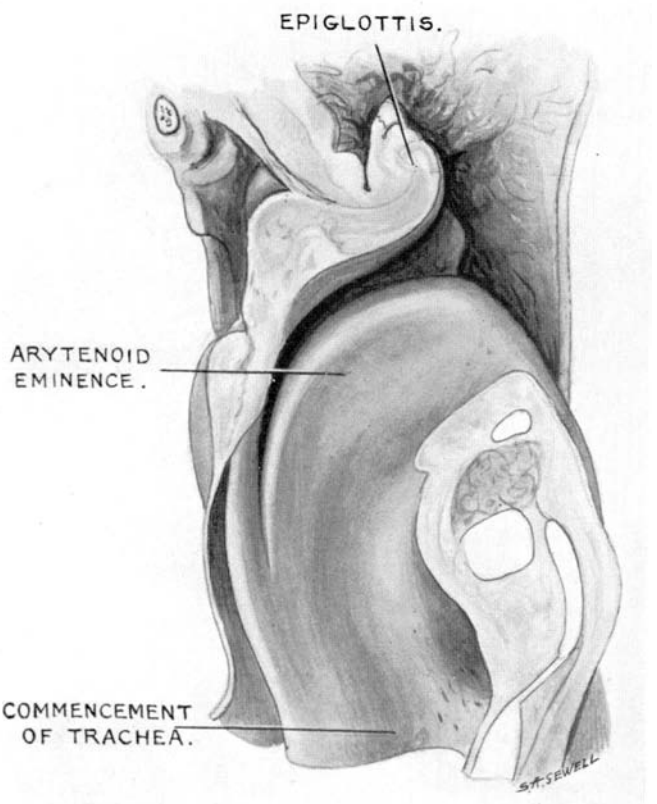


FIG. 12.—Right half of larynx of a Sea Lion. (Previously produced in *Journal of Anatomy*, October 1927.) To show the degenerate character of the epiglottis and the absence of a lateral food channel.



FIG. 13.—Elephant Seal (*Macrorhinus leoninus*). To show closure of the nostrils.
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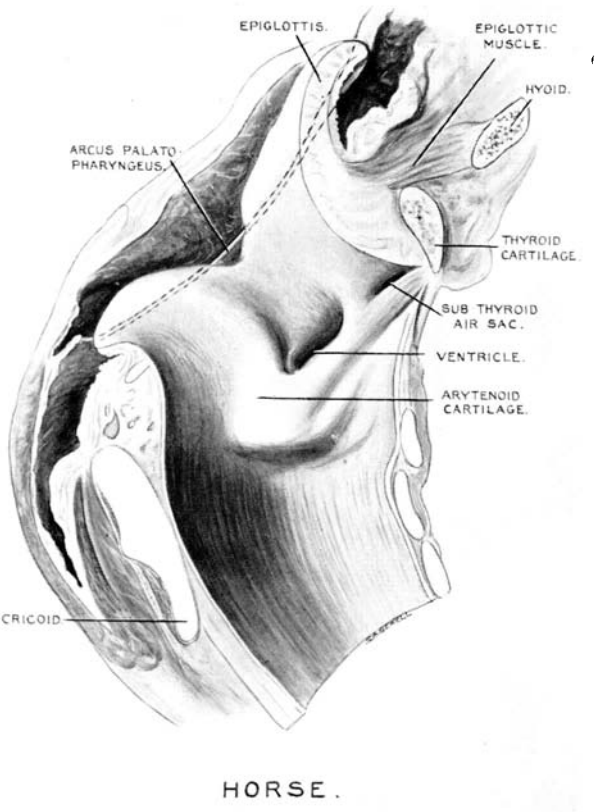


FIG. 14.—Left half of larynx of a Horse (*Equus caballus*) to illustrate the position of the lateral food channel below the arcus and external to the high ary-epiglottic fold. (Reproduced from *The Mechanism of the Larynx*, by permission of Messrs Heinemann.)

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being no lateral food channels (Fig. 11). A similar mechanism occurs in other carnivores even though the actual structure of the larynx does not necessarily resemble that of the cat tribe. Owing to this fact the sphincteric group is important primarily for prevention of entrance of food, owing to the absence of aquatic habits. As the food is only partially masticated there is less danger of its entrance into the trachea than in Man for example.

Turning to aquatic carnivores, it is obvious that in Sea Lions the larynx must be tightly shut during deglutition because the glottis is of considerable size, and even when the food consists of fish swallowed whole yet there would be danger of entrance of food and water, particularly if the swallowing took place under the surface of the sea. The Sea Lion (*Otaria*) has an extremely degenerate epiglottis and no lateral food channels, so that all food must pass over the aperture of the larynx (Fig. 12). In this animal therefore the sphincteric band of muscle is of particular importance, because of the habit of capturing prey under water.

Protective Closure of Nostrils.—In some other mammals which stay under water the mouth is shut off from the air-tract by a large epiglottis; closure of the larynx can be replaced by firm shutting of the nostrils, as may be seen in the Elephant Seal (*Macrorhinus leoninus*) (Fig. 13). In this animal the nostrils open during a very short period; expiration and inspiration are rapidly performed and the nose then shuts tightly for a long expiratory pause. In Seals the epiglottis lies usually above the soft palate. It is probable that water would not enter the larynx even if the mouth were open, so that if the nostrils are kept shut the animal may dispense with firm closure of its larynx except, of course, during deglutition.

Cetaceans show an extreme degree of specialisation of the larynx; they have the organ entirely shut off from the food tract; food and water cannot possibly enter from the mouth and pharnyx, and water is prevented from passing in through the nasal passage by closure of the muscular valve at the blow-hole, constituted by the fused anterior nares.

In terrestrial animals movements of the alæ nasi are obvious; they are not necessary to protect the lungs from entrance of water, but in many species they are retained for another purpose. The nostrils may be seen to dilate during inspiration and to shut partially during expiration, as, for instance, in a Horse (*Equus caballus*); these movements are, in

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my opinion, designed to expel dead space air from the air-tract in conjunction with expiratory contraction of the bronchial and tracheal musculature.

In Man the nostrils do not close, although they execute similar respiratory movements of small amplitude.

Changes Produced by Adoption of Certain Types of Diet.—Herbivorous animals all show modification of the larynx similar to that seen in cetaceans because they live on herbage which is chewed up and mixed with saliva, subsequently entering the œsophagus in a semi-solid form. A very large quantity has to be taken, and if the animal stopped breathing each time it swallowed there would be a great deal of delay. Consequently the glottis is protected by upraising of its margins above the level of the floor of the pharynx, in association with extension of the posterior palatine pillars in the form of an arcus palato-pharyngeus (Fig. 14). The semi-solid food passes along each side of the larynx through this lateral food channel, without danger to the lungs even when the glottis is open. In all animals provided with efficient lateral food channels, the sphincteric muscle is seldom required to protect the lungs, and its original vital function, as seen in Lung Fish, is much diminished in importance.

In most monkeys and the higher apes the diet consists of berries and leaves and other material containing less liquid than the food of herbivorous animals, and the lateral food channel is found to be inefficient; consequently the sphincteric muscles are required to close the larynx during swallowing.

Man has adopted an omnivorous diet and has an extremely inefficient lateral food channel, although it has been observed that during deglutition food passes not necessarily over the aperture of the larynx but rather on either side of it. Nevertheless any large mass would be in great danger of entering the larynx if the aperture were not closed by the sphincteric group of muscles, particularly for the reason that the food is masticated. When the sphincteric muscles have become paralysed on one or both sides, the individual is very liable to contract septic pneumonia because of the entrance of food into the larynx.

Alterations in Anatomy of Sphincteric Muscles in Man.—In Man a simple sphincteric muscle girdle is replaced by paired muscles on either side—the thyro-arytenoids and lateral crico-arytenoids—and a single muscle behind, namely, the inter-

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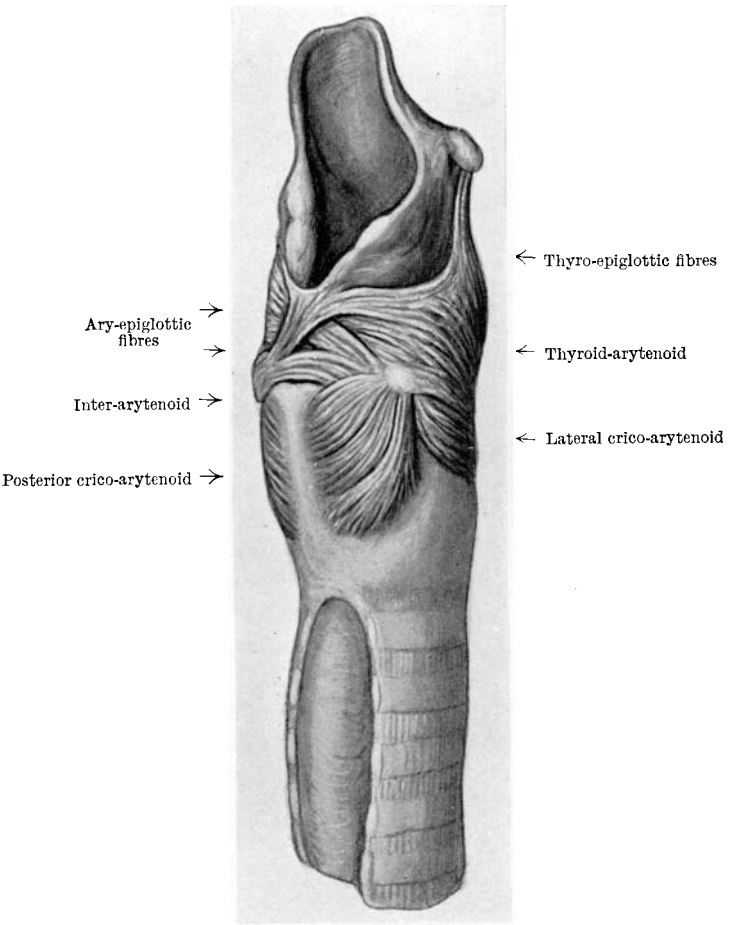


Fig. 15.—Dissection of larynx of a Man (Museum of R.C.S. England, 193). The dilator muscle and the components of the sphincteric group are illustrated.

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arytenoid; the girdle is incomplete anteriorly (Fig. 15). Closure during deglutition takes place at the level of the ary-epiglottic fold by virtue of contraction of the higher fibres of the muscular sphincter, together with other movements which need not be dealt with here.

Nerve Supply of Sphincteric Muscles.—Semon mentioned the possibility of partial supply of the thyro-epiglottic and ary-epiglottic muscles by the superior laryngeal nerve. The observation does not appear to affect the main question except that it draws attention to the necessity of remembering that it is not only the vocal cord but also the ary-epiglottic fold which is affected in cases of recurrent nerve paralysis, whether the disordered action concerns the dilator muscles alone or the sphincteric group as well; the vocal cord is moved by certain fibres of the sphincteric muscles, which are not, however, specialised for vocal purposes.

When there is complete paralysis of the recurrent laryngeal nerve, the ary-epiglottic fold on the affected side does not show signs of movement during deglutition; it is probable therefore that the main nerve supply of the ary-epiglottic muscle fibres is from the recurrent, although the superior laryngeal nerve may send some fibres to them, as it does to the interarytenoid muscle. In animals with an ary-epiglottic fold but without a ventricle there is a single sheet of muscle running from the arytenoid cartilage to the thyroid cartilage and epiglottis, so that there is less confusion in studying this type of larynx than that of Man; in many other animals closure of the larynx during both phonation and deglutition is carried out at one and the same level, and is executed by one and the same bundle of muscle fibres, components of the thyro-arytenoid constituent of the sphincteric group.

Whatever be the nerve supply of certain fibres, yet there is still the same factor of major vital function and older origin to explain the longer survival of the sphincteric muscle.

The possibility of contraction of parts of the sphincteric girdle after interference with the recurrent nerve—by stimulation through the superior laryngeal nerve—and also the action of the extrinsic laryngeal muscles in pulling the larynx bodily upwards against the base of the tongue, gives a greater degree of safety to Man, and to certain other species similarly constructed, than is enjoyed by animals with a more simple mechanism; there is however considerable danger of overflow of saliva,

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water or food into the trachea if the larynx cannot be closed efficiently.

The conclusions to be drawn are that in Man the function of preventing entrance of food into the larynx is of the very greatest importance, although the necessity for protection of the air-tract under water has almost disappeared.

Enough has now been said about the original protective function of the sphincteric musculature and about the modifications which have affected it to accentuate the vital importance of this muscular band in most animals and in Man, and to explain the reason for its vitality. The dilator muscles will now be examined.

Primary Function of Dilator Muscles.

Opening of Glottis during Inspiration.—A Lung Fish may be observed to come to the surface and to push its head above the water, opening the mouth widely and filling it with air. It then closes its mouth and leaves the surface. Some air escapes through the opercular aperture and it is probable that this is caused by contraction of the pharynx together with some elevation of the buccal and pharyngeal floor. The air in the mouth and pharynx is compressed, and if the sphincteric muscle surrounding the glottis be relaxed, some air will pass into the lung, there being an easier passage for it by that route than down the gut. There are no raised margins to the larynx, no valvular folds, and no rigid cartilages to prevent inward passage of air, and therefore no active dilatation is essential. The air can enter, just as air will pass through the crico-pharyngeal sphincter into the œsophagus by swallowing movements, but only when the sphincteric muscle is relaxed. It is seen therefore that not only is the sphincteric muscle of vital importance to the existence of the Lung Fish but that it is the only essential muscle. In the Amazon Mud Fish (*Lepidosiren*) I have found no true dilator fibres; such as appear to be present do not belong to the larynx. But on studying serial sections of the African Mud Fish (*Protopterus*) (Fig. 16) an extremely interesting structural arrangement is found; it must be mentioned that this fish lives a more active existence than the former species when respiring by means of its lungs only. Below the epithelium of the œsophagus, just in front of the entrance of the larynx, there is, as has

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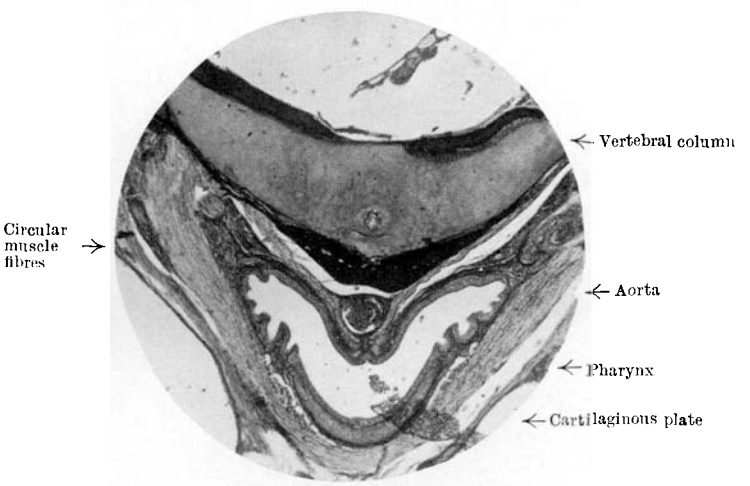


Fig. 16.—Transverse section of African Mud Fish (*Protopterus*). The transversely placed pharynx is seen with a plate of cartilage in its floor; circular muscle fibres pass below this.

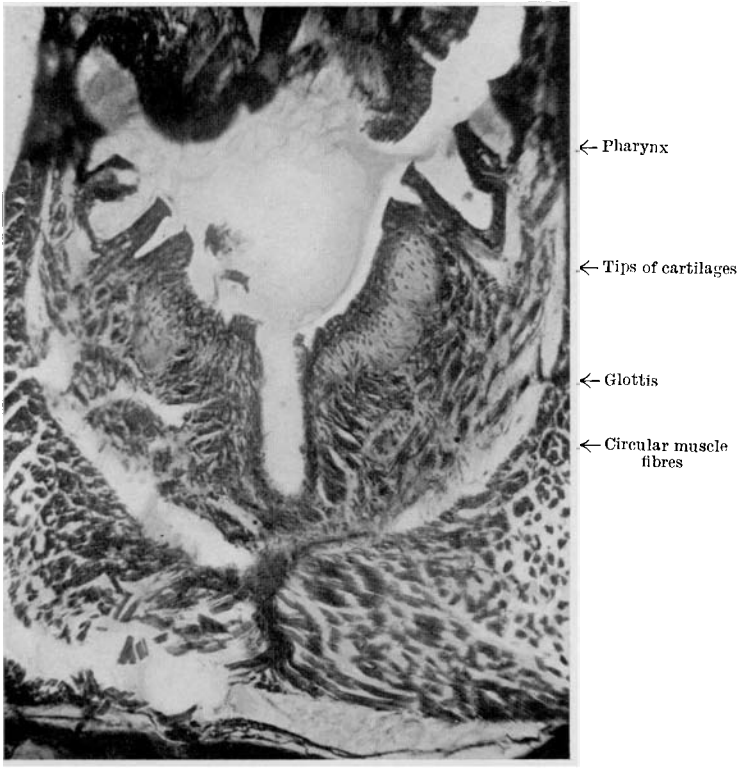


Fig. 17.—Transverse section of African Mud Fish (*Protopterus*). The sagittal fissure of the glottis is seen opening from the floor of the pharynx. The tips of the plate of cartilage are shown on either side of the glottic margins. Circular muscle fibres terminate near these cartilages, and also near the margins of the glottis.

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already been mentioned, a flat plate of cartilage, and passing beneath this cartilage are long circular muscle fibres which arise from connective tissue septa close to the base of the skull and vertebral column. Without doubt these fibres contract to raise the floor of the pharynx—supported by the plate of cartilage—and thus to propel the swallowed bolus of air. They are fibres corresponding to the constrictor muscles of Man. By examining serial sections further removed from the mouth, it is found that some of these long circular fibres terminate near the margins of the glottis (Fig. 17). Not only will they in their contraction compress the air but they will also draw apart the margins of the glottic aperture and flatten it out. As the margins of the glottis meet behind at the commencement of the trachea they cannot in this region be separated, and the lumen will remain open. It is easy to see therefore that the compressed air finds an easy passage down the trachea; it will not pass down the œsophagus beyond the opening of the larynx if mutual pressure or contraction of circular muscle fibres tend to close the gut in the manner in which the crico-pharyngeus closes the lower end of the pharynx in Man.

These observations show that not only is the dilator muscle non-essential to the filling of the lungs, but that its place is taken by these constrictor fibres, which correspond to extrinsic muscles in the pharynx of Man; and it is interesting to observe that in cases of bulbar palsy the extrinsic muscles are very noticeably degenerated in association with degeneration of the dilator muscles, although the sphincteric group retains its efficiency for a longer time. Although Man is not derived from Lung Fish, and although he has not the same aquatic habits, yet, in studying the comparative anatomy of the larynx, so striking are the gradual evolutionary changes that it is impossible to avoid the conclusion that the larynx of higher species has been evolved from a correspondingly simple type, and that factors similar to those described have been in operation, on which depend the truth of Semon's Law, namely, the greater vulnerability of the dilator fibres. So as to examine the various factors affecting the importance and function of the dilator muscles, it is necessary to trace the stages of evolution upwards.

Changes due to Presence of Lateral Cartilages.—The next animals to be examined are amphibians. In Axolotls

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lateral cartilages are present, and to them dilator fibres are said to be attached; but unless there are other rigid cartilages from which the fibres may take origin there will not be any efficiency in their pull. In Newts (*Molge*) each lateral bar is divided into two, the posterior halves fusing to form a ring. This ring in reptiles like the Alligator is seen to encircle the top of the trachea and to be associated with other rings, each representing a tracheal cartilage; the topmost ring is called the cricoid. The dilator fibres have undergone a change; they are, as before, attached to the tips of the rod-like lateral cartilages—which now represent the arytenoids—but they have obtained attachments also to the cricoid cartilage; they represent the posterior crico-arytenoid muscles of higher species. When they contract the rigid cricoid remains stationary and a pull is exerted on the movable arytenoids, the anterior extremities of which separate. The advantage of this modification is, of course, that the glottis is opened rapidly and affords a free passage for air, instead of being passively relaxed as in the Amazon Mud Fish. This is the primitive function of the muscles under consideration, to which the term "dilator" will be applied, as it appears preferable to the word "abductor." Birds have a similar mechanism (Fig. 18). Their larynx resembles that of many of the reptilians very closely, there being long rod-like arytenoid cartilages which separate in front, forming a triangle with its base forwards, unlike the shape of the glottis in mammals, in which the triangle has its base posteriorly; the arytenoids rotate on the joints formed with the crico-thyroid plate, and do not move away from one another posteriorly as in mammals. In many of the lower animals, and noticeably in Frogs, the arytenoid cartilages are dome-shaped and tend to be forced together, not only by water, but also by air blown in by the bellows formed by muscles in the floor of the mouth. When this valvular modification is present, the function of the dilator muscles is, of course, enhanced in importance, because they must by their contraction hold the glottis open to enable air to enter. In amphibians air is forced down the trachea either by swallowing movements or by a bellows action in the floor of the mouth; but in birds and mammals, and in some reptiles, breathing by suction, by means of movements of the ribs and sternum, is employed. In suction-breathing animals the glottic margins—if dome-shaped—would tend to be sucked together,

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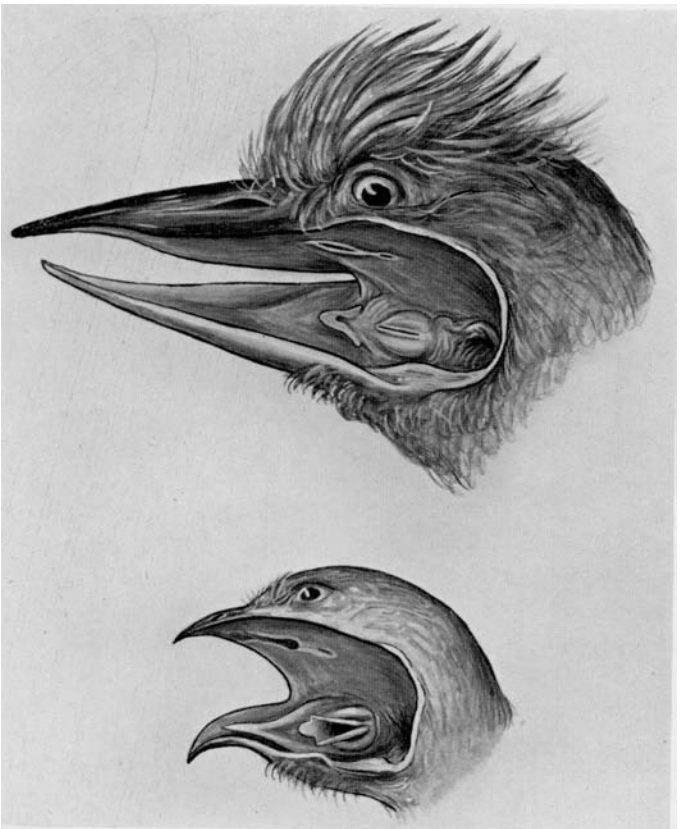


FIG. 18.—Laughing Jackass (above) (*Dacelo gigantea*) with pharynx opened to show the larynx closed, and
Bell Bird (below) (*Chasmorynchus*) with the larynx open.



FIG. 19.—Head of a Muntjac (*Cervulus muntjac*) illustrating straightness of the air tract.

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and would close unless held apart by the dilator muscles, while the trachea would collapse if not kept open by rigid cartilages. Not only does the negative pressure created by the ribs and sternum—and by the diaphragm in those animals so provided—tend to draw air down the trachea into the lungs, but it also tends to suck air into the œsophagus; the passage of air into the latter is easier than into the former, unlike the case of Lung Fish. Consequently, not only must the glottis be held open to provide a free air-way, but furthermore the œsophagus must be kept closed by the crico-pharyngeal sphincter in order to ensure that the air current shall enter the lungs and not the gullet.

We have now arrived at the stage of animals with a crico-thyroid plate or separate cricoid and thyroid cartilages, making the larynx a separate organ provided with a sphincteric muscle group and a pair of dilator muscles. It is impossible for the extrinsic muscles, such as the constrictors, to have any effect on the glottic margins, and the dilator muscle is separated and becomes a true intrinsic muscle of the larynx, without any connection with the pharyngeal musculature. There is, however, some connection between certain of the sphincteric laryngeal muscles and the rest of the pharyngeal musculature, some ary-epiglottic fibres passing up to the tongue and some fibres of the thyro-arytenoid muscle being in certain animals—such as the Dog—continuous with longitudinal fibres of the œsophagus.

Another modification to be noticed is a shortening of the arytenoid cartilage, designed to secure more efficient opening of the glottis. The optimum length of rigid cartilage both mathematically and in practice is seven-tenths of the diameter of the larynx. This length is found in Gazelles (*e.g.*, Persian Gazelle), which are highly efficient as regards speed.

Effects due to Tilting of Larynx.—One reason why the constrictor fibres cannot have any direct effect on the opening of the glottis, as they have in the African Mud Fish, is that the aperture of the larynx is tilted in most higher species so as to bring the entrance of the air-way into line with the trachea, thus eliminating friction as much as possible (Fig. 19). In certain animals the straightening of the air-tract is carried to a very marked degree, there being an almost straight passage from the anterior nares to the bifurcation of the trachea, as may be seen in a fast-running animal, such as the Indian Barking

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Deer or Muntjac. The larynx in such an animal is encased in a scaffold of cartilages and is tilted in such a way that its posterior end rises above the floor of the pharynx. It can be moved as a whole by extrinsic muscles, although these can have no direct effect on the actual margins of the glottis. The constrictor in Man may be seen when it contracts actually to assist in closing the laryngeal aperture, instead of opening it, as it does in the Lung Fish.

Further Alterations in Anatomy of Dilator Muscles.—Connected with alterations in length of the arytenoids are changes in attachment of the posterior crico-arytenoid muscle. In reptiles and birds the dilator muscle, because of its attachment to the tip of the long arytenoid cartilage, works at a mechanical disadvantage, and in certain reptiles, such as Tortoises and Turtles (*Chelonia*), and in all mammals the attachment is found to shift gradually backwards so as to give a greater degree of movement as a result of contraction (Fig. 20). The area of attachment becomes the muscular process and the tip of the arytenoid cartilage—where the muscle of lower forms is fixed—is left as a glottic process; it is generally known in man as a vocal process, although the former seems to be the better term, as it does not lay undue stress on the vocal function of the larynx. As a result of migration the dilator muscle suffers no change in importance, although there is a distinct difference in its action.

The arytenoid does not merely rotate, but the whole body of the cartilage slides outwards on the lax crico-arytenoid joint, being pulled away from its fellow by lateral fibres of the posterior crico-arytenoid muscle. These fibres are ignored in most descriptions although they have an important and independent function; they are, in fact, antagonists of the inter-arytenoid muscle, and cause the glottis to assume a triangular shape, with the base placed posteriorly, and the apex at the point where the inferior thyro-arytenoid folds meet to find attachment to the thyroid cartilage or crico-thyroid plate.

In Man the arytenoids are very short and a considerable part of the margin of the glottis is made up of the membranous inferior thyro-arytenoid folds, which have a valvular character, for reasons to be considered later.

Because of these alterations in length of cartilage and upturning of the folds, the dilator muscles in Man have an extremely important function. Even though they have thus

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attained a prominent position in the mechanism of the larynx, yet the nature of their origin still makes them more vulnerable than the sphincteric group, if there be any interference with their nerve supply. The nerve supply itself does not change basically from simple to complicated types of larynx, as appears if the various alterations of structure are unravelled; from this point of view the evidence derived from simple species concerning the truth of Semon's Law is not invalidated.

Effects of Paralysis of Dilator Muscles on Respiration.—If the abductor or posterior crico-arytenoid muscle of one side is paralysed, while the adductor or sphincteric group is still in action, according to Semon's Law, the ary-epiglottic fold falls partially inwards and the vocal cord is drawn towards the mid-line. Undue narrowing of the glottis is, however, avoided by an extra degree of contraction of the dilator muscle on the opposite side, so that there is a sufficiently large aperture for the passage of air. Horses with partial or complete paralysis of one side of the larynx can still gallop, owing to compensatory wide opening of the opposite side, although the vibration of the impeding thyro-arytenoid fold causes roaring.

Although a man is but slightly upset by inability to open one side of his larynx, he is, on the other hand, in a very dangerous position if both sides are affected by what is generally called "double abductor paralysis," because of the excessive narrowing of the glottis. A Cow or a Deer would not be in the same danger if both dilator muscles were out of action, because the margins of the glottis are smooth, and have not a valvular nature as in Man. It is the influence of an arboreal ancestry which has given to Man the upturned valvular inferior thyro-arytenoid folds, usually known as vocal cords; this function of the larynx will be referred to later. Because they form the narrowest part of the larynx, and because of their shape, these folds tend to be sucked together during inspiration if the muscles which pull them apart are paralysed and particularly if those which bring them together have still the power of contraction. Noisy stridor is produced at each inspiration, and powerful efforts are required to get air into the lungs, although expiration is almost unaffected.

Man has abandoned an arboreal existence, and has, in consequence, fixation valves of a degenerate type, unlike those of such active tree-living animals as Spider Monkeys (*Ateles*)

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or Chimpanzees (*Anthropopithecus troglodytes*); these animals, if affected by double abductor paralysis, would quickly die, because the sharp-edged, upturned inferior thyro-arytenoid folds would effectively prevent air from entering the lungs (Fig. 27).

Not only must the valvular vocal cords be held apart during respiration, but the ary-epiglottic folds also must be braced back and held taut; if they are allowed to fall towards one another there is danger that they will be sucked together during inspiration, as happens in laryngismus stridulus, due to weakness of the dilator muscles.

Interesting observations have been made by Dr R. D. Lawrence and myself on subjects of laryngeal obstruction, on lines of research suggested to me by Professor R. J. S. McDowall; the research was inspired by Sir St Clair Thomson, who inquired why the subjects of laryngeal obstruction sometimes died soon after apparently successful tracheotomy.

We found that in defective lung aeration, such as can be caused by paralysis of the dilator muscles, there may be a gradual accumulation of CO_2 in the lungs, although the supply of oxygen still remains sufficient to satisfy the blood, because of the large store already referred to.

The alveolar CO_2 may rise from its normal 5·6 per cent. up to as high a percentage as 8; if this change occurs there will be a rise of equal degree in the CO_2 contained in the blood leaving the lungs.

Respiration would be very violently affected by this rise, as the respiratory centre responds immediately to changes in the CO_2 content of the blood reaching it, a rise of 0·2 per cent. producing an increase in lung ventilation of 100 per cent. Some means must be found to compensate for the rise and to fix the increase of CO_2; this is carried out by the buffer substances of the blood, and is noticeable by an increase in excretion of ammonia as ammonium carbonate, there being at the same time a corresponding decrease in the amount of nitrogen leaving the body as urea.

A man may continue to breathe without excessive visible changes except stridor, even when the alveolar CO_2 has risen considerably, and a valuable guide to the degree of danger is provided by an estimation of the alveolar CO_2 or—if this is difficult to obtain—of the alkali reserve of the blood.

Treatment of Paralysis of Abductor Muscles. — Any marked rise is an indication for the necessity of immediate

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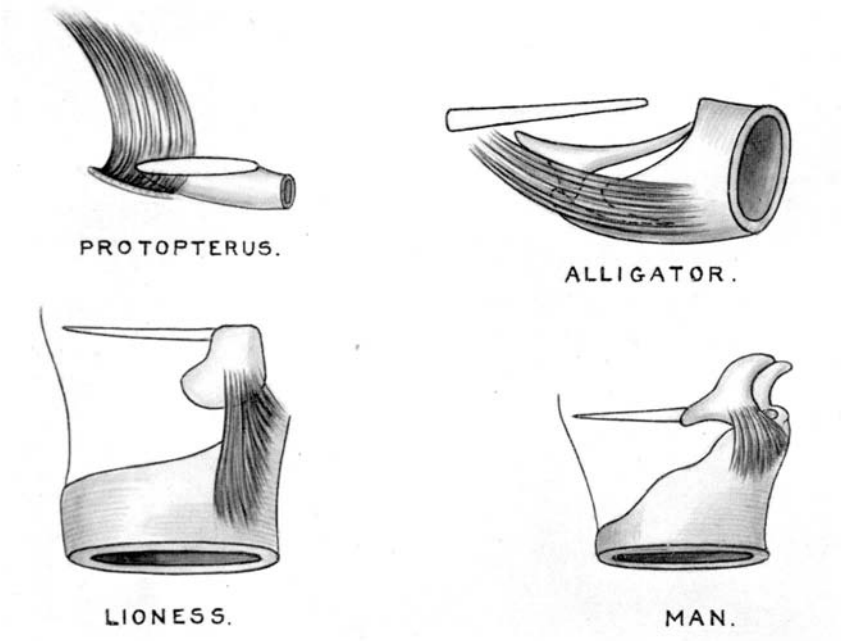


FIG. 20.—MIGRATION OF DILATOR MUSCLES.

In the African Lung Fish (*Protopterus*) circular muscle fibres of the pharynx run below and partly into the margins of the glottis at its anterior end. The Alligator has dilator fibres arising from the crico-thyroid ring and inserted partly into the tip of the long arytenoid cartilage and partly into the margin of the glottis anteriorly. The Lioness (*Felis leo*) has a fan-shaped dilator muscle capable of rotating the short arytenoid cartilage and of pulling it outwards. In Man the arrangement is similar to that of the Lioness.

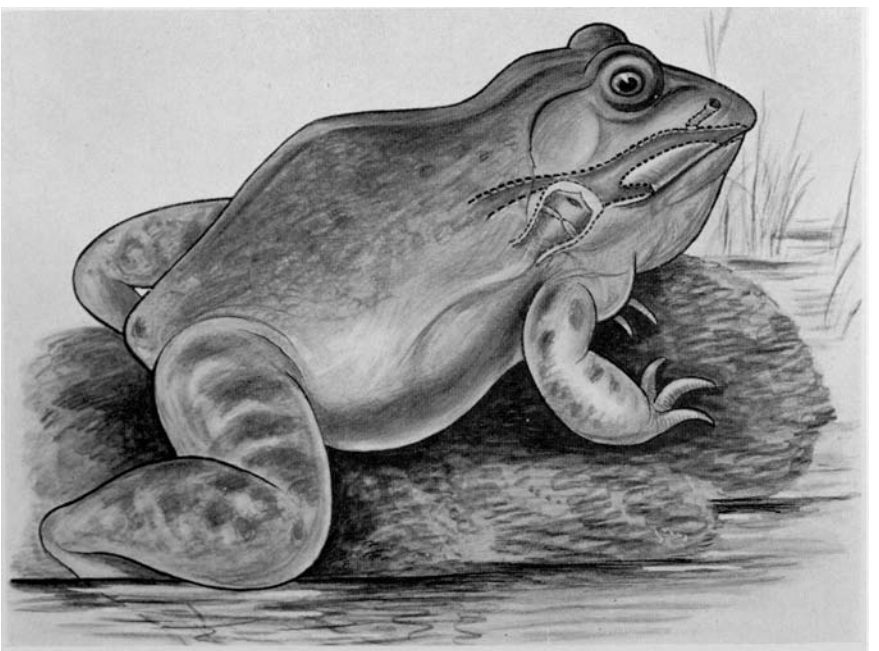


FIG. 21.—Bull-Frog (*Rana catesbyana*), with the outline of the larynx and non-return valve. The wide interval between posterior nares and laryngeal aperture is well shown.

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tracheotomy, an operation required early in cases of double abductor paralysis.

Even when tracheotomy has been performed there is still danger, because the sudden increase in lung ventilation restores the percentage of alveolar CO_2 to normal limits after a few breaths; simultaneously the CO_2 contained in the blood leaving the heart is greatly reduced, so that the respiratory centre receives insufficient stimulation and respiration is reduced or suspended. The subsequent gradual accumulation of CO_2 would at normal times lead to efficient lung ventilation, but is prevented from doing so by the excess of buffer substances, which do not return to normal as rapidly as does the alveolar CO_2; the respiratory centre fails to respond in time to prevent the patient from suffering from lack of oxygen. Respiration becomes dangerously shallow or may cease altogether and cause death. The means of preventing danger, and the remedy in case of necessity, is suggested by the research; CO_2 must be inhaled by the patient, if necessary by means of artificial respiration, the remedy remaining by the bedside for a couple of hours after tracheotomy.

Research has been carried out by Ballance and Colledge on anastomosis of the laryngeal nerves, and remarkable results have been obtained. The method found most successful in restoring movement to a paralysed larynx has been by anastomosis of the divided recurrent laryngeal to part of the phrenic nerve.

Secondary Function of Sphincteric Muscles.

Having studied the primary object for which the sphincteric band of muscle comes into being, and having compared its function with that of the dilator muscles, it is now necessary to see what other duties have been taken on. Certain of these are carried out in conjunction with the dilator muscles, but one is a function of the muscles of closure alone and will be dealt with first.

Retention of Air in Lungs.—Air-breathing animals, particularly those of aquatic habits, gain considerably in efficiency if they have a big reserve of air in the lungs. To increase this reserve the air may, in fish and some amphibians, be forced into the lungs under pressure by swallowing movements, being retained there by tonic contraction of the

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sphincteric muscle surrounding the glottis. The Siluroid Fish (*Saccobranchus*) already referred to, has no valve by means of which to retain air in its respiratory diverticulum. The Bichir (*Polypterus*), however, has a larynx. The air-sac is not reticulated but is of a very simple type; it is covered by a double layer of striped muscle which can expel the contained air when necessary. A similar mechanism appears to exist in the Lung Fish in which the lungs are again of simple type, with, however, some degree of division into compartments.

The power of the small sphincter of the glottis is extremely feeble. An idea of its inefficiency may be gained from experiments with a Cat; in this animal it is found that the most powerful contraction of the sphincter can withstand a pressure equal to 4 mm. of mercury only, although the larynx by mechanical valvular action can withstand a negative pressure of 100 mm. of mercury. It is no doubt because of this fact that in some species, which require a considerable store of air, a change is found from the simple muscular sphincter to a mechanical means of air retention. Such a mechanism is seen in Frogs and Toads, many of which are able to blow themselves up to an enormous size (Fig. 21). In their larynx there are two folds below the level of the arytenoid cartilages, looking like vocal cords, with their free margins turned downwards. These folds lie in contact with one another and would prevent the escape of air until pulled apart. They are generally called vocal cords because the Frog makes a noise, but there is no doubt that they are non-return valves, called into use occasionally for purposes of phonation. A similar mechanism is seen in the Chamaeleon and in crocodilians, but not in the great majority of mammals. In some mammals air may be imprisoned by closure of the glottis, but part or the whole of the duty of retaining air in the lungs of aquatic species is taken on by the nostrils, which close at the end of inspiration. This may be well seen in Seals (e.g., *Macrorhinus leoninus*), the Hippopotamus, and also in cetaceans, which have a single orifice at the blow-hole.

It is interesting to note in this association that some aquatic animals not only store air in the lungs for use under water but further increase their power of staying under the surface by means of air-sacs on the nose, as in the case of the Gharial (*Garialis gangetica*) and the Bladder-Nosed Seal

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Fig. 22.—Chamaeleon: to show the diminutive size of the larynx in position in a wide pharynx. Below the larynx there is a small air sac.

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(*Cristophora cristata*); it is probable that air contained in the lungs is driven into these air-sacs for mixing purposes, returning afterwards to give up more oxygen and to take up more CO_2 from the pulmonary epithelium. In certain Seals and some of the cetaceans the retention of air in the lungs is associated with the presence of large vascular spaces in the liver and splanchnic area, in which venous blood is stored up as a result of obstruction to its return to the heart by increased pressure in the lungs while the animal is under water; the blood is dammed back ready to fill the dilated pulmonary capillaries as soon as the surface is reached, thus increasing the rapidity of oxygenation. In this mechanism the laryngeal muscles may take some part in retaining air under pressure, but they are probably superseded in importance by closure of the nostrils.

In mammals the area of respiratory epithelium is enormously increased by complexity of the lung; the fine divisions provide a big store of air which cannot escape even at the end of the deepest inspiration. The sphincteric muscle therefore has not in them an important function in imprisoning air.

In the higher apes and in Man there is a mechanical means of retaining air under pressure in the lungs; this takes the form of ventricular bands. By virtue of their downturned margins they act as valves preventing the escape of air; they are held in apposition by part of the sphincteric girdle. By their aid it is possible for the lungs to be distended, and it is likely that the mechanism is of assistance when it is necessary to increase intra-abdominal pressure. Ventricular bands are not evolved for storage of air for respiratory purposes, although they may be used for that purpose during diving.

From these observations it may be gathered that the function of the larynx for retaining air in the lungs is not an important one as far as Man is concerned.

Coughing.—In Man the sphincteric muscles have an important function in closing the glottis for the production of cough. Contraction of the muscle girdle brings the vocal cords together, but owing to the funnel shape of the opening these folds are easily blown apart. If however the valvular ventricular bands are brought into apposition by the adductor group of muscles, then a considerable rise of pressure can be raised before the glottis blows open with an explosive sound.

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Secondary Function of Dilator Muscles.

Contraction during Simultaneous Respiration and Deglutition.—An animal with a larynx which lies flat in the pharynx must close the glottis during deglutition to prevent entrance of food or water (Fig. 22).

If large quantities of food must be swallowed, the repeated closure of the air-way would impede respiration, as already referred to in dealing with deglutition in herbivorous animals. To avoid this necessity a high rampart is evolved, surrounding the glottis and preventing inflow of food or water; this rampart is provided by the ary-epiglottic folds. They fill up a gap between the epiglottis and the arytenoid cartilages; the latter are raised in height, usually by the addition of a high cartilage of Santorini. The folds are stretched between the two rigid structures and are in some cases strengthened by the addition of cartilages of Wrisberg. They are kept taut by the backward pull of the dilator or abductor muscles, and in some cases—when the epiglottis is big and mobile—by an opposing pull of a glosso- or hyo-epiglottic muscle.

This function of the dilator muscles is a secondary one, and is mainly acquired by herbivorous animals or by aquatic mammals which live on small fish taken in with large quantities of water, that is to say, by Toothed Whales, Dolphins, and Porpoises (Fig. 23).

Many of the cetaceans chase their prey at great speed and would be seriously impeded if they had to empty the mouth and pharynx of water before swallowing. To avoid this necessity the larynx extends in a spout-like manner into the nasopharynx and is surrounded by a band of sphincteric muscle —the arcus palato-pharyngeus.

An efficient lateral food channel leads from the mouth to the œsophagus on either side of the larynx, so that respiration can continue through the blow-hole, even when the mouth is full of water; as the blow-hole is placed on the top of the head it is the first part to reach the surface and therefore respiration can commence immediately the animal comes up to take air.

It is essential that the laryngeal aperture should be kept open in these animals by opposing pull of the epiglottic muscle on the one hand, and the dilator muscles on the other; other-

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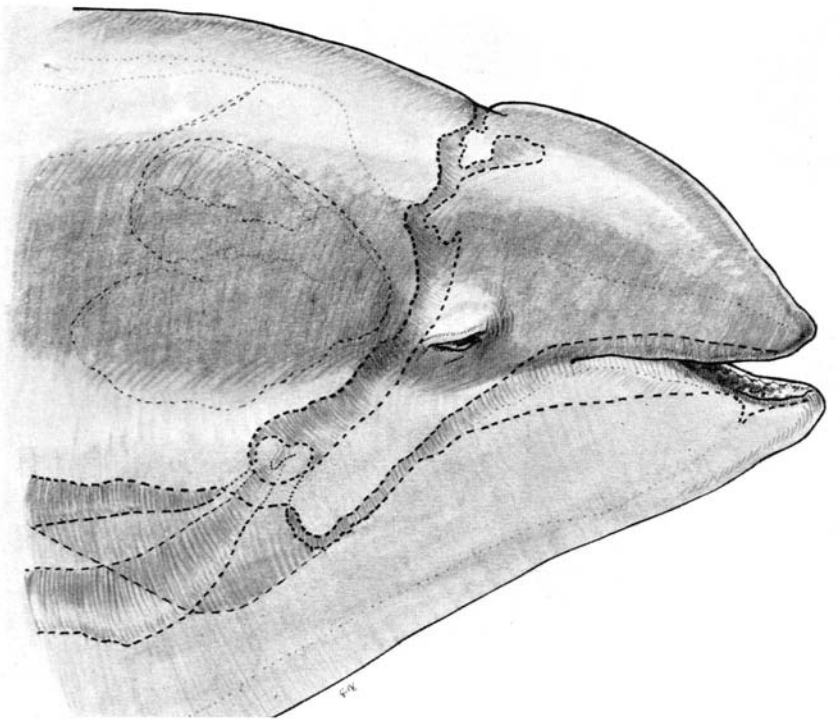


FIG. 23.—Head of a Porpoise (*Phocæna communis*) to show the position of the blow-hole, the direction of the nasal passage, and the intranarial situation of the larynx. The continuity between mouth and œsophagus, by means of a lateral food channel, can be seen.

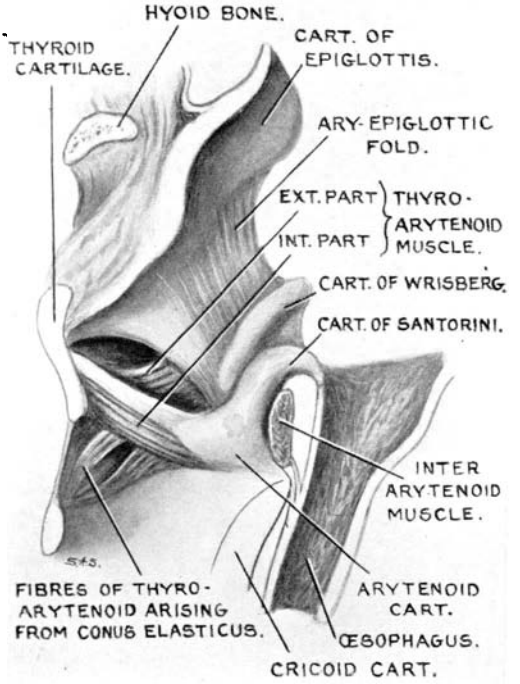


FIG. 24.—Dissection of right half of larynx of a Man aged fifty. To show the position of the cartilage of Wrisberg in the ary-epiglottic fold. (Reproduced from the *Lancet*, 17th May 1924.)

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wise it would be closed by contraction of the arcus palato-pharyngeus.

In herbivorous animals the same dual rôle of support of the ary-epiglottic folds, and maintenance of the air-way is undertaken by the muscles which open the larynx.

In the species under consideration the upraising of the margins of the glottis and the flatness of the ary-epiglottic folds destroys the valvular nature of the larynx possessed by other animals The passage of air in and out is not impeded by sharp-edged folds and therefore the importance of the dilator muscles, as concerns respiration, is diminished.

It is seen from these observations that the dilator muscles hold open the larynx at the level of the ary-epiglottic folds, and are not merely abductors of the vocal cords, which, in fact, do not exist in the animals under consideration.

In Man the ary-epiglottic folds are low and the posterior palatine folds do not form an arcus palato-pharyngeus; the lateral food channel is inefficient, but nevertheless it is present, and is of greater use in infants than in adults (Fig. 24). The dilator muscles — the posterior crico-arytenoids — at times brace back the arytenoid cartilages and thus keep taut the ary-epiglottic folds—in which are placed the cartilages of Wrisberg as rigid stays—to prevent inflow of small quantities of liquid food or saliva.

Combined Actions of Sphincteric and Dilator Muscles.

(*a*) **During Phonation.**—Emphasis has already been laid on the necessity of recognising that phonation is not a primary function of the larynx, and mention has been made of the confusion which results if this fact is ignored.

It is necessary, however—now that the vital purposes of the laryngeal muscles have been dealt with—to examine the other functions taken on by them, and of these the first to be considered is phonation.

Neither group of muscles acts independently of the other, and therefore the two will be considered together, by the same method as that adopted throughout this paper, namely, by commencing with the simple and working up to the complicated type of mechanism.

If the simple muscular sphincter of the Lung Fish be partially contracted while air is passing out of the lung the

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elasticity of the glottic margins throws the air current into puffs; the pressure of air alternately blows the margins apart and then allows them to recoil. Lung Fish are known to make breathing sounds thus, although they do so without purpose.

In the human being after laryngectomy circular muscle fibres at the mouth of the œsophagus may act in a similar way, causing vibration of air expelled from the stomach.

In birds and reptiles the rigid cartilages bounding the margins of the glottis make this partial opening and recoil more difficult, because they are not elastic. For this reason birds have evolved a specialised organ of sound at the bifurcation of the trachea, called the syrinx; most reptiles do not produce sounds, and have no specialised vocal apparatus.

In mammals the glottis is bounded at its posterior extremity by the arytenoid cartilages, which do not vibrate at ordinary times during phonation, and in front of them by membranous folds; alternate separation and approximation of the latter is the determining factor in sound production (Fig. 25). From the evidence of comparative anatomy, and from the result of experiments, it appears that contraction of the thyro-arytenoid element of the sphincteric muscles is the important factor during phonation; the degree of contraction determines the pitch, the latter rising as the muscles contract more forcibly; the rest of the sphincteric band contracts in order to approximate the arytenoid cartilages. The dilator or abductor muscles play a secondary rôle, as they contract in order to brace back the arytenoid cartilages against the pull of the sphincteric group.

In Man the internal parts of the thyro-arytenoid muscles are covered by a firm membranous coat known as the vocal cords. To this covering undue importance has been attached; in most animals it is soft, thin, and flaccid, and in many it is practically absent. The phonatory function, depending on associated action of the muscular sphincter and dilator muscles of the larynx, is an important one in the case of animals in whom much use is made of sound production and particularly in Man, but it is not a primitive function, and offers no direct evidence as to the truth of Semon's Law.

It is interesting to note that in unilateral abductor paralysis the vocal cord on the affected side is shortened owing to lack of bracing back of the arytenoid cartilages; the thyro-arytenoid muscle pulls the cartilage forward as far as its capsule will

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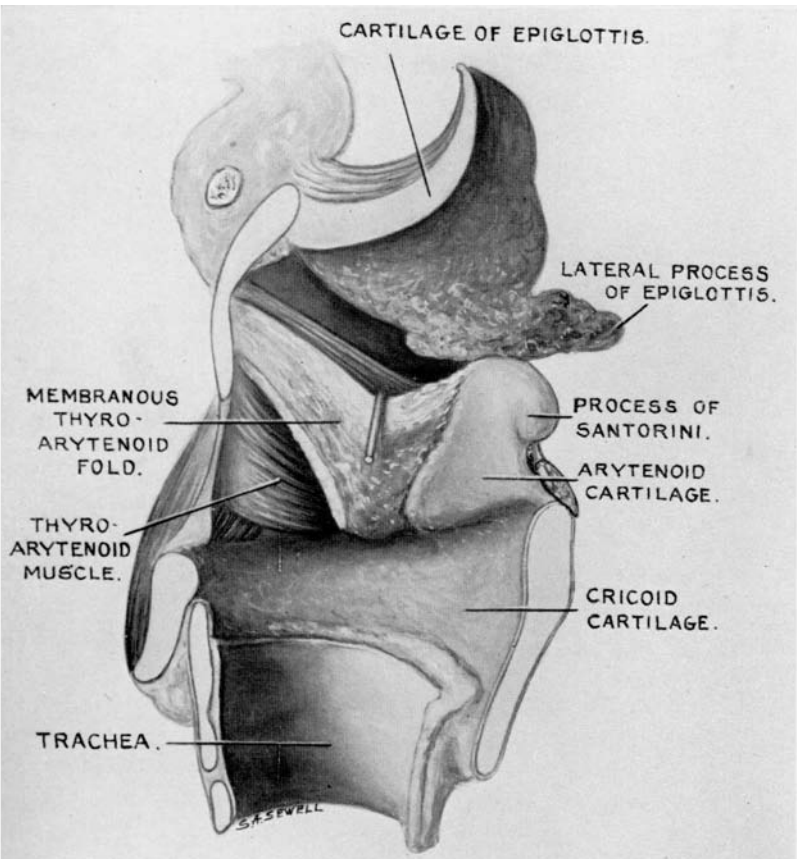


Fig. 25.—Dissection of right half of larynx of a Hyæna (*Hyæna crocuta*). The lax connective-tissue fold, lying over the thyro-arytenoid muscle, is illustrated. (Previously produced in the *Mechanism of the Larynx*, Heinemann.)

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permit, and when it has accommodated itself to the shortened length between its origin and attachment, it is able to make the vocal cord tense and to give it a sharp edge by means of which phonation is carried on with little change. If the mechanism of phonation depended on stretching of the membranous part of the vocal cord, as usually described, the cord would appear flabby and the voice would not recover.

Not only is the affected cord shortened, but it also lies at a lower level than its fellow, because of downward tilting of the unsupported arytenoid cartilage.

In bilateral abductor paralysis there is again no possibility of stretching of the vocal cords, but as the thyro-arytenoid muscles are capable of contraction, they can provide elastic margins to the glottis, which is closed by the other members of the sphincteric group. Phonation can be carried on, but the individual is so short of breath, owing to the difficulty of inspiration, that the production of sound is seriously upset.

(*b*) **For Respiratory Movements at the Glottis.** — Most aquatic animals open the glottis widely at the beginning of inspiration and close it firmly towards the end of expiration, to prevent entrance of water. The movements of opening are performed by active contraction of the dilator muscles—when these are present—and those of shutting by firm closure of the sphincteric group.

In mammals and in Man, even when there is no necessity for protective closure of the glottis, movements of dilatation and contraction are seen, varying according to circumstances, and tending to increase in amplitude when respiration is forced. The object of the movements appears to be designed to correlate entry of air into the lungs with blood-flow through the pulmonary capillaries.

As to the part played by the two groups of muscles, it appears that both are in action, in opposition to one another; the dilators or abductors slide the arytenoid cartilages outwards and backwards, while rotating the glottic or vocal processes outwards, and the sphincters or adductors draw the cartilages inwards and forwards, together with inward rotation of the processes.

Semon thought that normally the small extra opening of the glottis during inspiration was due to slightly increased half-tension of the dilators and that the partial closure during expiration was a recoil due to elasticity of the elastic membrane.

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Although the latter no doubt has an influence in bringing the glottis into the cadaveric position, yet it is certain that in fish, amphibians, and some reptiles, and in aquatic birds and mammals, the closure is due to active muscular contraction, and it seems probable that the movements in terrestrial animals and in Man are of similar nature.

The movements in adult Man are of minor importance and are a refinement added to respiration, so that a study of them does not affect the question of Semon's Law, except in as far as they concern the automaticity of the laryngeal movements. Semon thought that under normal conditions of breathing the action of the glottis-opening muscles is quite as automatic as that of respiration in general, but at the same time he did not see why the more energetic contractions of the abductor muscles, during deep inspiration, should not occasionally be quite as much under the control of the will as the act of deep inspiration itself. He asked why the wider opening of the glottis in a voluntary deep inspiration should be regarded as an exclusively involuntary and reflex movement, following the voluntary act of deep inspiration, and not as a part of this act itself.

His supposition can be more than confirmed by experiments carried out on animals by McDowall and myself. We found that dilatation of the glottis precedes movements of the chest wall, diaphragm, and alæ nasi, and similarly that its partial closure takes the first place in expiration.

Not only, therefore, do the movements form part of the mechanism of respiration, but actually they precede all the other movements; they originate as a result of stimulation from the respiratory centre through the recurrent laryngeal nerves, and are automatic, although no doubt influenced as regards amplitude by the effect of the cerebrum.

The conclusions to be drawn are that dilatation and partial closure of the glottis in Man are the result of active muscular actions of automatic nature; but the observation does not appear to influence the general argument.

It is of interest to note that after anastomosis of the phrenic nerve to the divided recurrent laryngeal, the movements of the glottis on the affected side show a slight delay as compared with the unaffected cord; the glottic movements are no doubt in time with those of the diaphragm, and not in advance as in the normal subject.

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(*c*) **During Fixation of Thorax.**—In animals which use the fore-limbs for grasping or climbing, the ribs must at times be kept at rest in order to give the pectoral muscles a fixed origin from which to exert a pull on the limb; otherwise the ribs will be pulled upwards and the fore-limbs will not move.

Contraction of the abdominal muscles plays a part in this fixation, but in the majority of animals which perform the actions mentioned there is an additional mechanical aid, if the evidence of comparative anatomy is correct. The mechanism consists in closure of the glottis in order to prevent entrance of air into the lungs; if the lungs cannot expand, the thorax generally is prevented from increasing in capacity, and elevation of the ribs is resisted (Fig. 26).

Muscular sphincteric closure of the glottis alone offers less efficient obstruction to the entry of air than if the glottic margins are of a valvular nature, so designed that when brought into approximation they tend to be sucked together; a valvular larynx of this type will withstand an enormous pressure although a purely muscular sphincter will allow air to pass with comparative ease.

Such animals as members of the cat tribe possess a simple type of larynx, which is efficient for the purpose mentioned; the thyro-arytenoid folds act as a valve in conjunction with their cartilages, provided they be stretched between the arytenoid and thyroid cartilages by the dilator or posterior crico-arytenoid muscles, while being brought into approximation and made tense by the several members of the sphincteric group.

Both dilator and sphincteric muscles take part in the mechanism, but no fresh light is thrown on the subject under consideration, because, like phonation, this function of the muscles is a secondary one.

In herbivorous animals upraising of the ary-epiglottic folds causes the margins of the glottis to be flat, and to lose the valvular nature to be seen in the larynx of such an animal as the Leopard (*Felis pardus*). Independent use of the fore-limbs is not required by most herbivorous animals, and therefore no disability is experienced.

If however, an animal provided with ary-epiglottic folds—designed to facilitate the swallowing of a vegetable diet—adopts an arboreal existence, or otherwise requires to use its fore-limbs for grasping, it will be found to acquire a secondary valve in the larynx. This valve is produced by the formation of inferior

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thyro-arytenoid folds, usually called vocal cords, associated with ventricles.

Man has a larynx of this type and is found to use it when the arms are pulled downwards or inwards; the action of the two groups of muscles is similar to that already described for the simpler type of larynx of one of the cat tribe.

The presence of this secondary valve gives Man many advantages connected with use of the arms and it also provides him with a convenient organ for use in phonation; at the same time it causes him to suffer grave disability if both dilator muscles are paralysed, because the upturned folds tend to be sucked together and to prevent entrance of air into the lungs.

It has been explained that air will pass into the trachea of a Lung Fish if the sphincteric muscle be relaxed, and that the dilator mechanism is not essential; in Man, on the other hand, the effect of an arboreal ancestry makes the dilator muscles of vital importance, and helps to confuse the question of Semon's Law.

Luckily, the larynx of Man is in many respects a degenerate organ and, among other signs of change, it may be observed that the inferior thyro-arytenoid folds or vocal cords are far less efficient as inlet valves than the similar structures in species of active arboreal habits, as, for instance, the Chimpanzee (*Anthropopithecus troglodytes*) in which the folds have extremely sharp upturned edges (Fig. 27). In this animal, and in other arboreal apes and monkeys, paralysis of both dilator muscles would cause a speedy end to life.

Conclusion.

An attempt has been made to unravel the history of the laryngeal muscles, to describe their functions, and to distinguish between the primitive and the more recently acquired duties.

The outstanding factors in support of the truth of Semon's Law are the observations that the sphincteric muscle band serves a vital function, on which depends the very existence of the individual, and that it is of more ancient origin than its antagonists, the dilators.

At a discussion held by the Section of Laryngology of the Royal Society of Medicine on the 2nd May 1913, Sir David Ferrier pointed out as an explanation of Semon's Law, that the extensor and abductor muscles generally are more

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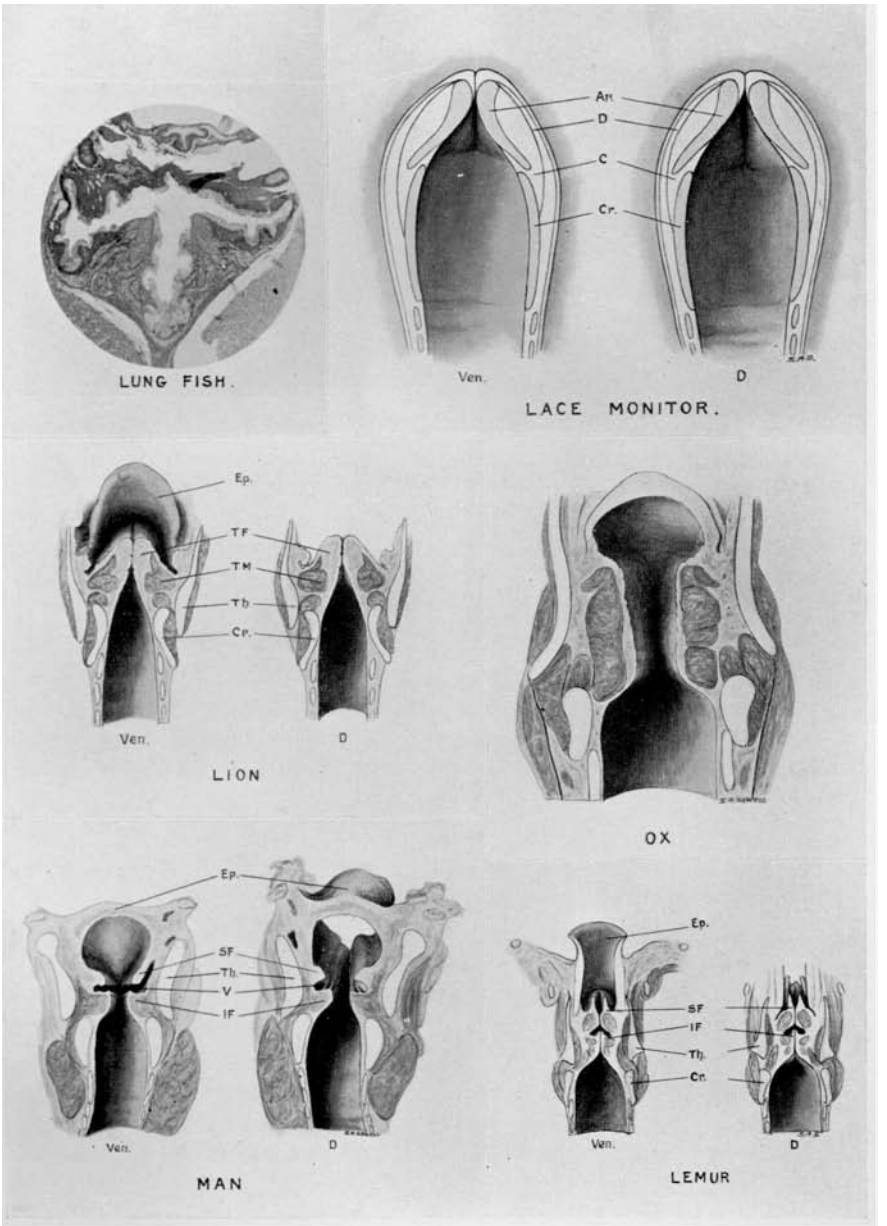


FIG. 26.—VALVULAR NATURE OF THE LARYNX (Coronal Sections of Larynx).

Lung Fish (*Lepidosiren*); feeble inlet valve (photographed from a microscopical section). The larynx is seen as a fissure in the floor of the transversely placed pharynx. Lace Monitor (*Varanus varius*); powerful inlet valve. Lion (*Felis leo*); powerful inlet valve. There is no division of thyro-arytenoid fold into vocal cord and ventricular band. Ox (*Bos taurus*); no valve; flat undivided thyro-arytenoid folds. Man; powerful inlet and exit valves, the former formed by the vocal cords and the latter by the ventricular bands. Lemur (*Lemur flavifrons*); very powerful double inlet valve, consisting of the vocal cords and ventricular bands. (Reproduced from *Journal of Laryngology and Otology*.)

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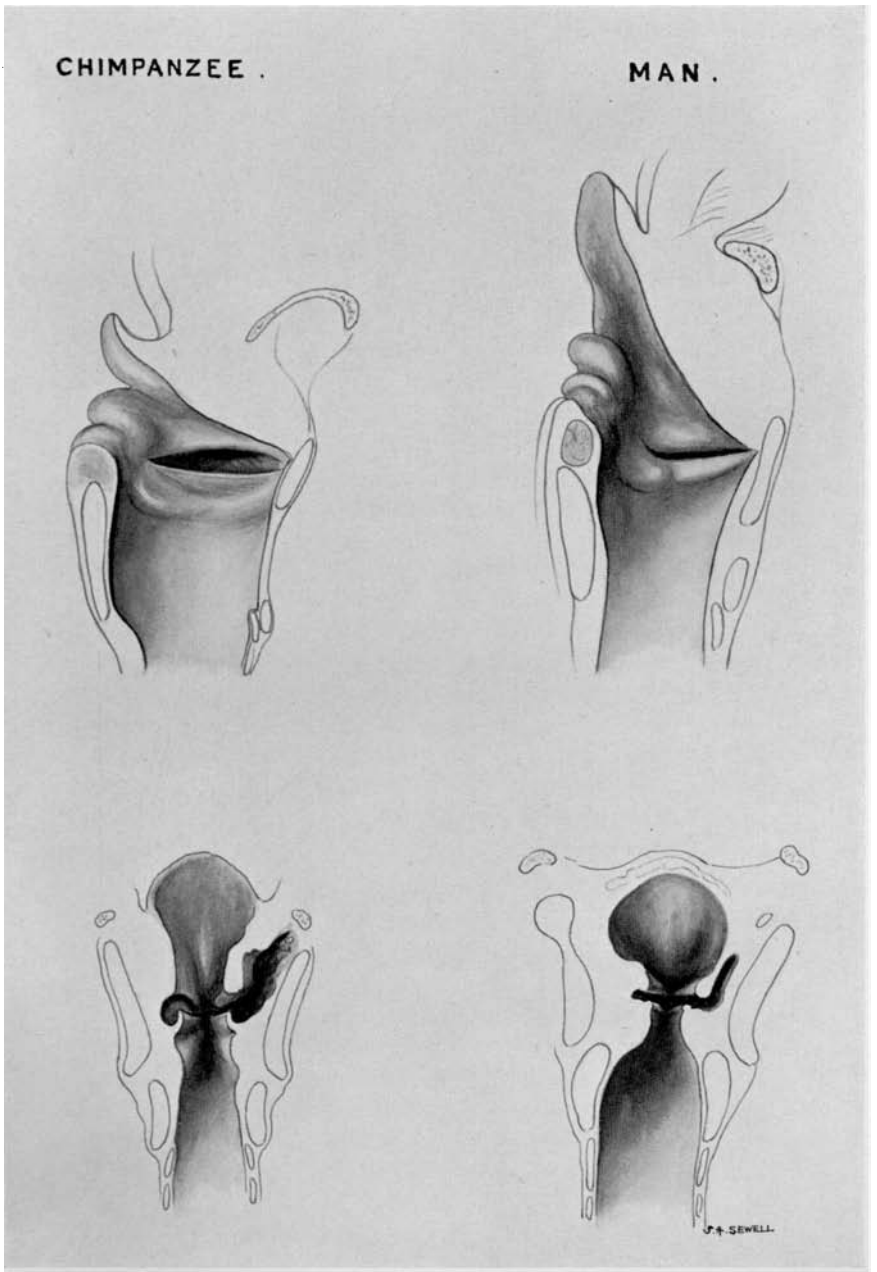


Fig. 27.—Sagittal and coronal sections illustrating the comparative efficiency of the inlet and exit valves. (Previously produced in *Acta Oto-Laryngologica*, Vol. xii., fasc. 1-2.)

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vulnerable and lose their vitality sooner than the flexors and adductors.

It is possible that this may have some connection with the vital necessity for arboreal animals to retain the power of the grasping muscles, so as to hang on to branches and not fall to the ground.

Sir Felix Semon's reply to Ferrier's explanation was that, whilst the antagonistic muscles of the limbs served physiologically equivalent factors, those of the larynx served two different functions (phonation and respiration), which were differently represented in the cortex and in the medulla.

In the light of the evidence of comparative anatomy it would appear that Semon was raising objections disguising the true explanation of his law, for it has been shown that the muscles of the larynx are primarily antagonists serving one and the same function—that of respiration—and that representation is in the medulla for each group.

Realisation of this observation allows attention to be diverted from the confusing secondary function of phonation; it is then possible to compare Semon's Law with Ferrier's Law and to add the further observation that the explanation of both may be found in the survival of the muscle group originally serving the most vital function.

The author wishes to express his renewed indebtedness to the Zoological Society of London, whence the specimens examined and dissected in the preparation of this paper were obtained. Three illustrations were kindly lent by Mr Bond.

He also renews his expression of gratitude to the Council of the Royal College of Surgeons of England for permission to work in their laboratories.

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HAUPTINHALT

Um die grössere Verwundbarkeit der Abziehmuskeln des Kehlkopfes (Semon's Gesetz) zu erklären, untersucht man den ursprünglichen Kehlkopf vom Dipnoi oder Lungenfisch.

In einigen befindet sich ein Schliessmuskelnband, welches, um die Lungen zu beschützen, die Lebensverrichtung den Luftrohr zu schliessen bedient.

Andere haben keine Muskeln um den Luftrohr aufzumachen. Wenn der Schliessmuskel erschlafft ist, so kann die Luft hineinfliessen.

Die Abziehmuskeln oder aufschiebende Muskeln sind von späterer Entwicklung, und in dem einfachen Kehlkopf Typus, welcher nicht vielklappig ist, von weniger Wichtigkeit.

Sollte es eine Unterbrechung der allgemeinen Nerven Ausgabe geben, so überleben die schliess oder Anziehmuskeln die dilator oder Abziehmuskeln, weil sie von früherem Ursprung und schützender Lebensverrichtung sind.

Die evolutions Bestimmungen, und das für Phonation, später erworbene Gebrauch des Kehlkopfes, machen die Faktoren, welche die Wahrheit des Gesetzes Semon's unterstützen, nicht ungültig.

RÉSUMÉ

Pour expliquer la vulnérabilité plus grande des muscles abducteurs du larynx (la loi de Semon), il faut examiner le larynx primitif des Dipnoi ou poissons à poumons. Quelques uns de ces poissons ont une bande sphinctérique de muscles qui sert à remplir la fonction essentielle de fermer le sphincter et protéger les poumons. D'autres n'ont pas de muscles pour ouvrir la glotte. Si le sphincter se relâche l'air entre dans les poumons. Les muscles abducteurs ou dilatoires sont d'un développment plus tard, et d'une importance moins grande dans le larynx simple, qui est non valvulaire. Grâce à leur origine précoce, et à leur fonction essentiellement protectrice, les muscles sphinctérique ou adducteurs survivent les muscles dilatoires ou abducteurs en cas d'intervention de la prévision nerveuse commune. Les modifications évolutionaires, et l'usage phonatoire acquis plus tard par le larynx, n'invalident point les facteurs qui soutiennent la vérité de la loi de Semon.

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