PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Bionomics of Certain Air-Breathing Fishes of India, together with an Account of the Development of Their Air-Breathing Organs

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Phil. Trans. R. Soc. Lond. B 1928 **216**, 183-219
doi: 10.1098/rstb.1928.0003

III. *The Bionomics of Certain Air-Breathing Fishes of India, together with an Account of the Development of their Air-Breathing Organs.**

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(*Communicated by Prof.* E. W. MACBRIDE, F.R.S.)

(Received June 3,—Read June 30, 1927.)

[PLATES 3–11.]

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Introduction.

It has long been known that certain species of fresh-water fish, inhabiting the rivers, lakes and ponds of India, are in the habit of leaving the water and making considerable excursions over the adjacent marshes and meadows, and some have been credited with the power of climbing trees. The older authors (CUVIER, OWEN and GÜNTHER) explained

* A thesis, approved for the degree of Doctor of Science in the University of London, of which the paper as printed is a revised and abridged version.

the power which these fishes possessed of sustaining life outside the water by supposing that they carried with them, in reservoirs at the sides of the head, supplies of water by which the gills were kept moist. On the other hand, TAYLOR (1831) and specially DAY (1868) and HYRTL (1863) showed, as the result of close observation, that the reservoirs in question contained little or no water, and that the fish, when kept in tanks or globes, could be seen to come to the top at intervals and emit air-bubbles. It was, therefore, clear that the reservoirs in question contained not water but air, and that the fish must be regarded as true air-breathers.

The fact that certain fish, such as *Protopterus* in Africa, *Lepidosiren* in S. America and *Ceratodus* in Australia, possess organs for breathing air as well as gills for respiring in water is well known; the structure and habits of these "double-breathers" (Dipnoi) form an integral part of the instruction given in every elementary course of Zoology. But the air-breathing organs of the Dipnoi are homologous with the lungs of the higher vertebrates, and the Dipnoi must be regarded as comparatively unchanged survivors from the time when the Devonian fish were making their first attempt to invade the land, at a period when no land-inhabiting air-breathing vertebrates existed.

The fresh-water fish of India are widely remote in systematic position from the Dipnoi; most of them retain the air-bladder (*cf.* text-fig. 1 B, p. 189) which corresponds to the organ with which the Dipnoi breathe air, but they do not use the air-bladder for this purpose. The organs which these fish employ for air-breathing are new developments, which differ from genus to genus, and represent so many independent successful solutions of the problem how to pass from an aquatic to an aerial mode of existence.

As the conditions under which this problem arises and is solved are of fundamental importance for our understanding of the evolutionary history of the Vertebrata, it seemed to me that the close study of the habits and life-histories of certain of these fish might throw valuable light on this question. A search through the literature revealed the fact that although isolated observations existed, no systematic description of the habits of any of these fish had been made; indeed, in some cases no accurate description of the adult air-breathing organs was to be found, and in no case was anything known as to their development.

My residence and early training in Allahabad (India) afforded me the opportunity of studying several genera of these fish in their native environment. I selected for this purpose six genera, viz., *Anabas*, *Macropodus*, *Ophiocephalus*, *Clarias*, *Saccobranchus* and *Amphipnous*. Of these the first two belong to the same family (Anabantidæ); they have air-breathing organs of the same structural type. *Ophiocephalus* is the so-called "Snake-headed" fish, and has developed organs for breathing air which are utterly different from those of the Anabantidæ. *Clarias* and *Saccobranchus* belong to the family Clariidæ, of the sub-order Siluroidea, but their air-breathing organs are in each case peculiar. *Amphipnous* is one of the Symbranchoid "Eels"; its air-breathing organs, although in some respects resembling those of *Ophiocephalus*, have obviously been independently developed.

During the years 1918 to 1923 I made observations and experiments on these fish in India, the results of which are recorded in this paper. I collected the young post-larval stages, and these, together with adult specimens, were preserved. In the autumn of 1923 I came to England, bringing this material with me, as well as living specimens of all the genera, and entered the Zoological Department of the Imperial College of Science and Technology, where the research was completed under the supervision of Prof. E. W. MacBride, F.R.S. Some of the fish lived in the Zoological Department for over two years.

The young post-larval stages were collected from tanks and ponds all over Bengal, and also from the rice-fields. They were preserved in Mann's, Bouin's, Zenker's and Müller's fluids, as well as in a mixture of formalin and glycerine, containing 10 per cent. of glycerine. For the first three fluids an immersion of two days was allowed; for Müller's fluid four days, and for the formol-glycerine mixture a week. After Müller's fluid and formol-glycerine they were washed for 24 hours in tap-water, but after the other fixing fluids they were transferred at once to 50 per cent. alcohol. Where, owing to the presence of bone, decalcification was necessary, Schridde's fluid (a mixture of nitric acid and formalin) was used.

The specimens were examined by micro-dissection and by transverse sections, which were stained on the slide. The stains employed included Unna's Safranin and Wasserblau; Hæmatoxylin and Picrosäurefuchsin; Safranin and Nigrosin; Safranin, Gentian violet and Orange G.; Erhlich's triacid mixture of Orange G., Säurefuchsin and Methyl green; Borax carmine differentiated by Picro-indigo-carmine, and Mallory's triple stain (Säurefuchsin followed by a mixture of Aniline blue, Orange G. and Oxalic acid). The last two methods gave the best results. I modified Mallory's stain by increasing the strength of the Säurefuchsin solution from 0·1 to 1 per cent., mordanting the slide after immersion in it with Phosphomolybdic acid, and adding 0·5 per cent. methyl green to the second solution. I got by this method most excellent differentiation of tissues. The epithelia were stained pinkish-grey, the nervous system greenish-grey, the notochord greenish, muscles pink, cartilage deep green, bone pinkish-grey, blood corpuscles yellowish-brown and their nuclei red. Adult specimens were fixed in the formol-gylcerine mixture, which not only preserved the tissues, but kept them soft and in suitable condition for dissection.

In the pages which follow I shall describe in turn the habits of each genus, and then the development and adult structure of the air-breathing organs. As, however, two of the genera (*Clarias* and *Saccobranchus*) belong to the same family, their habits will be considered together, and a similar course will be followed with *Anabas* and *Macropodus*, both of which are members of the family Anabantidæ.

Here I wish to express my great indebtedness to my teacher, Prof. E. W. MacBride, F.R.S., under whose supervision the whole work has been carried out. My best thanks are also due to him for his constant encouragement, keen interest and kind criticisms, as well as for his assistance in writing up, correcting the MS. and proofs of this paper.

I am extremely grateful to Dr. C. Tate Regan, F.R.S., Director of the Natural History Museum, London, for his very kindly placing at my disposal some most valuable supplementary material, as well as much advice, kind criticism and the suggestion of a scheme of arrangement of the paper. My thanks are also due to Prof. Graham Kerr of Glasgow University for kindly favouring me with the latest information regarding the habits of the Lung-fish and the Crossopterygians, and also to my friend Mr. J. R. Norman of the Natural History Museum, London, for his kind advice and help.

Bionomics of Clarias magur *and* Saccobranchus fossilis.

These fishes are common inhabitants of the ponds and tanks of Northern India. They always keep to the shallow part of the water. In the dry season, when the tanks and ponds dry up, they bury themselves in the moist mud 5 or 6 inches below the surface, but when, with the advent of the monsoon, the rains begin, they emerge in great numbers from their hiding-places, and their sudden appearance gives rise to the superstition current amongst the peasantry that they have been rained from the clouds. They then invade the rice-fields, and in these fields they generally deposit their ova. As the temperature of the water in which they live rises to 85° F., they can be seen coming to the surface and emitting air-bubbles as often as every half-minute.

They emerge from tanks and ponds especially at night. On occasion they devour their young. Their principal prey consists of earthworms. They are much relished as food by most of the natives, but, like other Siluroids, they are scaleless, and are rejected as unclean by the orthodox Brahmins. Like other Siluroids, too, their mouths are provided with tactile organs in the shape of barbels, with which they probe the mud in search of their prey, and the barbels are richly supplied with taste-buds innervated by the branches of the 5th nerve.

Both genera have strong serrated pectoral spines with which they can inflict dangerous wounds; these wounds, irritated by the secretions of the mucous cells of the skin, are apt to fester; these fish are therefore reputed poisonous by the natives, although no special poison glands exist. *Saccobranchus* is regarded as the more poisonous of the two, and is termed the scorpion-fish in India. The spines are used in conflicts with other members of the same species; if too many specimens are placed in the same receptacle they will fight till the weakest are killed. *Saccobranchus* makes a whistling noise by grinding its pectoral spine against the coracoid when irritated or frightened.

The natives use various methods of capturing them. Sometimes a large cone-shaped basket of bamboo (known as " Poluwee " in Bengal) open at both ends is dragged through the shallow water. The native, with his hand well protected by wrappings against the pectoral spines, scoops out the fish from the narrow end, and immediately breaks off the spines. Sometimes the liquid mud is sifted through a net, or a piece of sheeting, or even palm-leaves are spread over a portion of the marsh. This prevents the fish from obtaining access to the air, and they can be picked up in an asphyxiated condition a few hours later by the fishermen. They can be kept alive for several days in pots, with an inch or so of water at the bottom, and can thus be marketed in a fresh condition.

When moving over land the fish progresses, as in water, by lateral strokes of the tail, aided by undulating movements of the long anal fin and rowing movements of the pectoral fins; these latter are extended horizontally from the body, pressed against the ground, and rotated backwards.

There are several species of *Clarias* in India; *C. magur*, which I have observed, is the only one commonly distributed over Northern India There are only two species of *Saccobranchus*: *S. fossilis* is characteristic of N. India and *S. singio* is obtained from the South.

Structure and Development of Air-Breathing Organs of Clarias magur.

In *Clarias* the air-breathing organs consist of two tree-like structures (Plate 3, fig. 4, *Ant. t.* and *Post t.*) growing from the upper ends of the gill arches and contained in an air-chamber situated above the gills. Of these the posterior and larger one is developed earlier than the anterior one. The earliest stage which I have observed was in a fish 2·2 cm. long. In this stage the respiratory chamber, which is a diverticulum of the opercular cavity, measures about 2·5 mm. by 1·2 mm., the posterior tree (Plate 3, fig. 1, *Post. t.*) has the form of a minute knob 0·4 mm. long growing from the epibranchial region of the fourth arch, and there is no trace as yet of the anterior tree. The knob contains cartilage (Plate 5, figs. 17, *a*, *b*, Plate 6, figs. 19 and 20, *Chond. ax.*) developed from the mesoderm of the arch, but having no connection with the epibranchial cartilage (fig. 17 (*b*), *Ep. br.*). It is covered by slightly pigmented epithelium (*Ep. l.*), which is several layers thick at the growing end (fig. 17 (*b*)), but elsewhere may be reduced to a single flattened layer; it contains numerous mucous cells (*Muc.*). The subjacent connective tissue (Plate 6, fig. 20, *Conn.*) is richly supplied with capillaries (*Bv.*), and these capillaries form loops which invade the epithelium and project as tags (*Vasc. pap.*) covered with a thin layer of ectoderm (*Ep. sq.*) into the air-chamber. Often these tags take the form of cups surrounding a mucous cell (fig. 20, *Muc.*). The central cartilage is composed of large parenchyma-like cells (figs. 19 and 20, *Chond. ax.*).

When the fish attains a length of 2·6 cm. the first trace of the anterior tree (Plate 3, fig. 2, *Ant. t.*) appears above the 2nd arch, and the posterior rudiment which has increased in length divides into two lobes, and one of these lobes immediately forks again so that the rudiment becomes trilobed (Plate 3, fig. 2, *Post. t.*), each lobe containing a branch of the cartilaginous axis (Plate 5, fig. 18, *Chond. ax.*). Where this division takes place the young cartilage cells are surrounded by capillary loops. When the fish is 3 cm. long the posterior tree becomes 4-lobed, and the anterior tree is represented by a small conical structure growing from the 2nd arch.

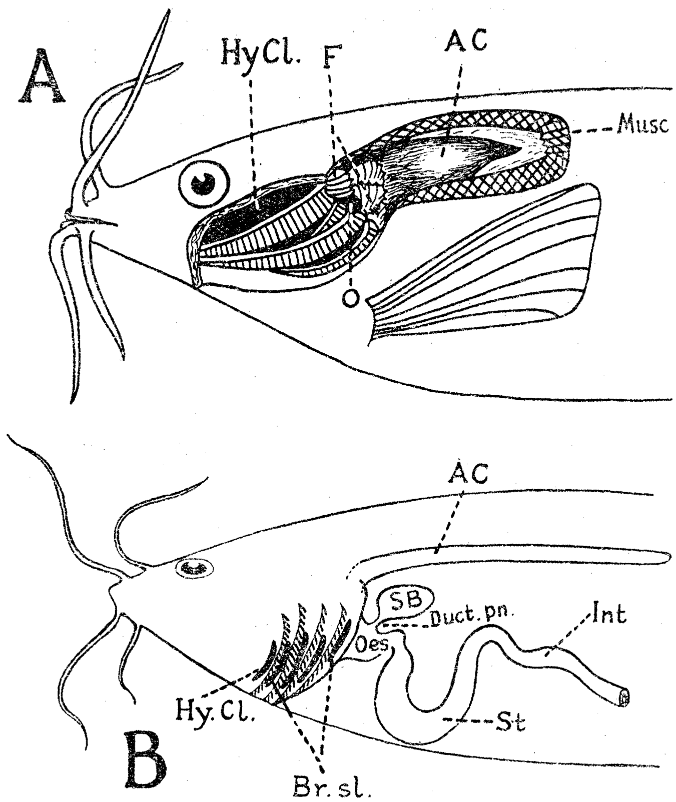
As growth proceeds the tips of the lobes of the posterior tree become first club-shaped and then flattened, and the general pigmentation of the ectoderm becomes reduced. These lobes (Plate 3, fig. 3, *Post. t.*) become arranged in two groups, which simulate the petals of a flower: six pigmented lobes form an upper petal, four non-pigmented an outer and lower petal. The primary petals divide and subdivide, whilst the chamber increases in volume and the tree grows in size. The vascular tongues (Plate 5, fig. 17 (*a*), *Vasc. pap.*) are more numerous near the bases of the branches, where the epithelium is relatively thinner, than at the growing point, where it is very thick. The development of the anterior tree is quite similar to that of the posterior tree; its base is embraced by a cushion of tissue developed from the 3rd arch.

We may now consider the air-chamber (Plate 3, fig. 5, *A.C.*) in which the trees are contained. It arises as a slight dorsal outgrowth of the opercular cavity (Plate 3, fig. 5, *Op. cav.*) between the hyoid (*Hm.*) and the 1st branchial arch. It is at first semicircular (Plate 3, fig. 6, *A.C.*) in section, owing to its being bounded by the 1st branchial arch, but this form is lost as it expands. The chamber as it grows impinges on the skull and expands into a large space adjacent to the otic capsule. It nearly meets its fellow in the mid-dorsal line. When the anterior tree is formed the chamber develops from its surface, chiefly from its roof and posterior walls, vascular tongues (Plate 5, fig. 16, *Vasc. pap.*) like those described as projecting from the air-trees; on its sides, however, are a series of vascular folds or pleats (fig. 16, *d. pul.*).

The chamber when fully developed leads by a somewhat narrow tubular neck into the opercular chamber, of which it is an outgrowth. The uppermost gill filaments growing from each branchial arch cohere to form a "fan" or "valve" (Plate 3, fig. 4, F_{1-4}) which projects into the air-chamber. In a fully grown fish, 21 cm. long, the chamber is nearly 18·5 mm. long, 11 mm. wide and 8 mm. deep. Approximately one-third of its volume is filled by the anterior air-tree, and two-thirds by the posterior air-tree. Its wall is separated by loose connective tissue from the auditory capsule and contains a very few muscle fibres towards its outer layer.

Development of the Air-Chamber in Saccobranchus.

The air-chamber in *Saccobranchus* originates in the same place and manner as that of *Clarias* (*cf.* Plate 4, fig. 8, *A.C.*). As in *Clarias* it begins as a small eversion of the opercular chamber between the hyoid and the 1st branchial arch, and enlarges as in *Clarias*, so as to form a large space in contact with the skull (Plate 4, fig. 9, *A.C.*) in the auditory region (*Ot.*). It has a thin epithelial wall (Plate 5, fig. 15, *Ep. l.*) underlain by loose connective tissue (*Conn.*); it becomes richly vascular, deriving its blood-supply from the afferent and efferent vessels of the 4th branchial arch, which give rise to the vascular "tongues" (*Vasc. pap.*), each containing a capillary loop which projects into its cavity (as is also the case in *Clarias*). These loops are more abundant on the ventral than on the dorsal wall of the sac, and are more prominent in the young than in the adult fish. As in *Clarias*, the uppermost filaments on each of the four branchial arches become coherent, so as to form fan-like structures (text-fig. 1 A, *F*). These "fans" are stiffened by specially developed cartilages. Unlike the "fans" of *Clarias*, however, the 1st and 4th "fans" of *Saccobranchus* remain small and lie closely opposed to the 2nd and 3rd "fans" (*i.e.*, the 1st lies over the 2nd, and the 4th fan lies over the 3rd fan), whilst the 2nd and 3rd enlarge (Plate 4, fig. 11, F_2 and F_3). These enlarged "fans" are very vascular, and have vascular tongues projecting from them. They are convex outwards, and between them is a narrow slit (text-fig. 1 A and Plate 4, fig. 11, *O.*) leading into the chamber.



TEXT-FIG. 1.—A : Lateral dissection of an adult *Saccobranchus fossilis* showing the gills, the air-chamber and the "fans" guarding the entrance to the air-chamber. B : Diagrammatic side-view of the organs of an adult *Saccobranchus fossilis* showing the relative positions of gills, air-chamber, air-bladder and œsophagus.

A.C., air-chamber ; *Br. sl.*, branchial slits ; *Duct. pu.*, pneumatic duct connecting swim-bladder (air-bladder) with the œsophagus ; *F.*, fans guarding the entrance to the air-chamber ; *Hy. Cl.*, hyoid-cleft between hyoid and first branchial arches ; *Int.*, intestine ; *Musc.*, muscular body-wall ; *O.*, opening of the air-chamber which permits air to pass both inwards and outwards ; *S.B.*, swim-bladder (= air-bladder) ; *St.*, stomach.

Saccobranchus differs from *Clarias* in that (1) no air-trees are developed, and (2) the opercular sac, after attaining the dimensions described, extends gradually backwards in the form of a long tubular sac (Plate 4, fig. 10, *A.C.* and text-fig. 1 A, *A.C.*) till it reaches the middle of the tail region. Vascular tongues are abundantly developed, except over the mid-ventral ridge enclosing the afferent and efferent blood-vessels ; they disappear towards the posterior end of the sac. They do not, as in *Clarias*, form crescents or discs enclosing a mucous cell. In the posterior end of the developing air-sac there is a curious thickening in the ventral wall, which for want of a better name I have termed the " blood-gland " (Plate 4, fig. 10, *Gl.*). This is a conical thickening attached by its broad end to the posterior wall of the sac (*A.C.*). It is composed of mucous cells (Plate 5, fig. 13, *Muc.*) and a mass of rounded corpuscles (*Lym. c.*) interwoven with a network of capillaries (*Vasc. cap.*). It disappears when the fish becomes adult. As the sac grows backwards the connective tissue surrounding it becomes almost entirely displaced by capillaries. Its posterior half becomes clothed by a sheet of special muscles, and, in addition, it becomes embedded in the ordinary myotomes of the fish (fig. 12, *A.C.* and *Musc.*).

In the fish 2·6 cm. long the sac is only $\frac{1}{5}$ of the length of the fish, but when the fish reaches 4·5 cm. in length it is about half the length, and it retains these proportions in the adult fish 21 cm. long. In the adult fish, as already mentioned, the " blood-gland " disappears and vascular tongues are developed all over the surface of the sac, and mucous cells now make their appearance in the bases of these tongues ; these tongues now even arise from the ridge containing the afferent and efferent vessels as well as the rest of the surface of the sac ; they are shorter and become almost scale-like posteriorly. In the hindermost part of the sac the epithelium is folded (Plate 5, fig. 14, *Lam. pul.*) into a number of ridges (fig. 14, *Trab.*), which unite with one another and enclose " alveoli " (*Alv.*) which resemble the alveoli of a frog's lung. The muscular coats (figs. 14 and 15, *Musc. str.*) become greatly developed. They consist of spirally arranged as well as longitudinal fibres (some of them smooth and some striped).

It is interesting to note that in both *Clarias* and *Saccobranchus* the original air-bladder (text-fig. 1 B, *S.B.*) is as prominent in the young as in other Teleostei, but as growth proceeds it becomes relatively smaller, and is finally almost entirely enclosed in a bony capsule projecting from the skull, except its posterior lateral parts, which lie under the skin in the region of the pectoral girdle.

Bionomics of Anabas scandens (Dald.) *and of* Macropodus cupanus (Regan).

Anabas scandens is a small perch-like fish, common in the rivers, tanks and ponds of India. It possesses bright protruding orange-coloured eyes, is of a dark greenish colour on the back and paler below ; sometimes there are darker vertical bands ; the coloration changes with the environment. Like *Clarias* and *Saccobranchus* it migrates from pond to pond at night, and after a shower of rain it emerges from the water and invades damp gardens in search of earthworms. Here the males may be seen fighting with each other and chasing the females. The mode of progression on land, however, differs somewhat in *Anabas* from that of *Clarias* and *Saccobranchus*. *Anabas* uses its opercula as well as it pectoral fins. The opercula are armed with sharp spines which give them a purchase on the ground. They are spread out alternately and fixed to the ground, whilst a push is given by the pectoral fins and the tail. Sometimes, however, it lies on one side whilst moving.

When in water it comes to the surface at intervals, varying from one to four minutes according to the temperature, in order to inhale air. Just before fresh air is taken in by the mouth the opercular margins are slightly raised, and one or two large bubbles of air are exhaled. The fresh air is taken into two large chambers situated above the gills in the postero-lateral region of the head into which delicate shelly plates (Plate 8, figs. 28 and 29) with crenulated edges project. The plates are termed the "labyrinthic" organs. *Anabas scandens* derives its popular name (the Climbing Perch) from the legend current in the East that it climbs palm-trees and sucks their juice. This it is quite incapable of doing; these trees, however, grow on the borders of streams, and first project horizontally before the vertical portion of the stem is reached. Along this horizontal portion, covered as it is with rough scale-like leaf-bases, *Anabas* can make its way; and here, as during its other peregrinations out of water, it is exposed to the attacks of crows and kites, which very frequently seize the fish and deposit it high up in the forks of branches of the tree to be devoured at leisure. Hence the story that it can climb trees.

Anabas scandens is a food-fish which is highly esteemed in India, and reared in ponds and tanks. The fry are captured by means of a trap-net made of bamboo set across a running stream. The eggs are laid in shallow streams and sometimes in rice-fields; they are about 1 mm. in diameter. The adult fish are about 8 inches long, and are caught by rod and line baited with worms or the grubs of bees or wasps, or by a cast net. They can be kept alive for days out of water in moistened clay pots, and thus the fishermen are enabled to bring them by barge and cart from marshes about 150 miles distant from Calcutta and expose them for sale in the market there in a fresh condition. Though *Anabas* is found throughout Bengal, Madras, Burmah, Ceylon, the Malay Archipelago and the Philippines, it is everywhere rather local in its distribution, being confined to certain estuaries and fresh waters.

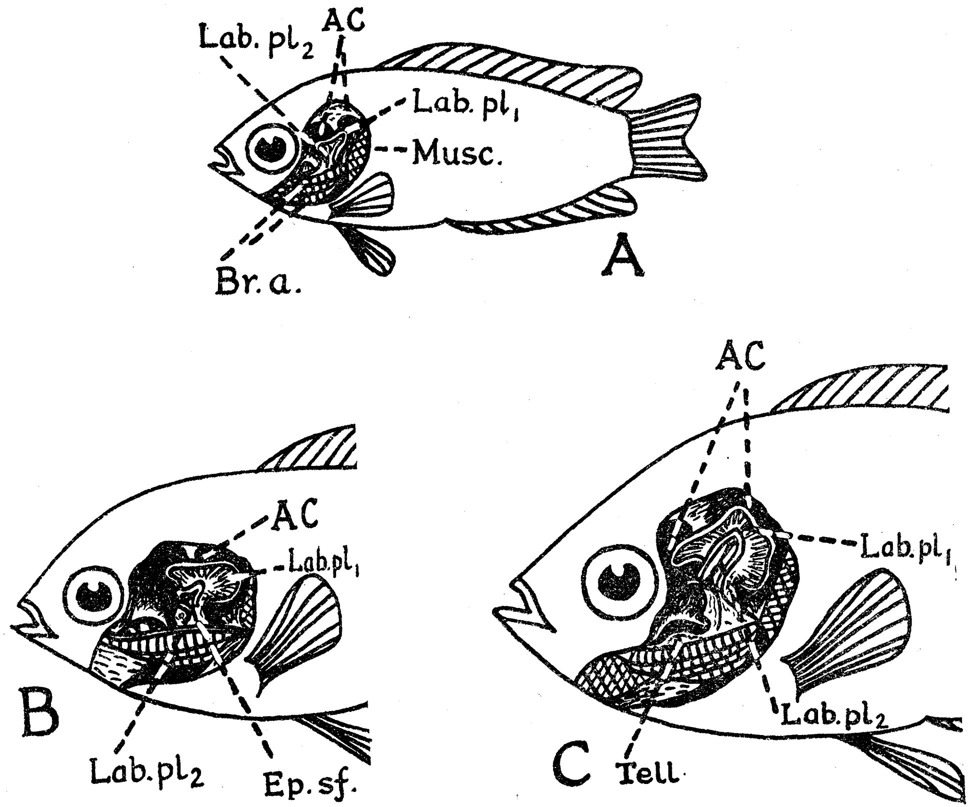
Macropodus cupanus is a smaller fish than *Anabas*, as it attains only a length of 3 inches when adult. It is coloured like *Anabas*, but it has a dark spot at the base of the caudal fin, some smaller spots on the head, and some fine dark bars on the caudal and dorsal fins; as in *Anabas*, the colour varies with the environment. It lives in ditches and small streams, lurking under stones, and is occasionally found in the rice-fields. There are two species of *Macropodus* distributed over Southern India, Ceylon, the Malay Peninsula, Cochin China, China and Formosa. *M. cupanus* is the Southern Indian species which I have studied. It is not nearly so well known as *Anabas*, as it is not regarded as good eating, and is consumed only by the poorer natives. It practically never migrates over land, but is found in holes at the base of brushwood in marshy streams, from which it darts out at intervals to inhale and exhale air, and then at once returns to its burrow.

Development and Structure of Air-Breathing Organs in Anabas *and* Macropodus.

As we have already seen, these organs consist of two chambers situated above the gills at the sides of the head into which delicate laminæ project. Each chamber (Plate 7, fig. 24, *A.C.*) begins (as in *Clarias* and *Saccobranchus*) as a small dorsal outgrowth of the opercular chamber (*Op. cav.*). This enlarges so as to press on the hind wall of the skull (*Ot. cap.*), and comes into contact by its ventral inner walls with a mass of lymphoid tissue which corresponds to the so-called "Pronephros" described in *Fierasfer* and certain other Teleostei; these bodies immediately underlie the hinder part of the cranium. The chamber has an epithelial wall (Plate 6, fig. 23, *Ep. vasc.*) two or three cells thick, which is richly supplied by blood-vessels (*Vasc. cap.*), but it has no mucous cells nor vascular papillæ like those of *Clarias* and *Saccobranchus*; it is, indeed, quite similar to the epithelium lining the inner side of the opercular fold. There are, however, abundant mucous cells (Plate 7, fig. 25, *Muc.*) developed in the wall of the pharynx (*Ph.*), which is thus widely different from the wall of the chamber. In *Macropodus* the chamber is relatively larger and more vascular than it is in *Anabas*, and it is provided with a thin muscular coat which is practically absent in *Anabas*, there being very few fibres in the latter.

Behind the "lymphoid" organs the right and left air-chambers come into contact and are separated only by a vertical partition of tendinous connective tissues (figs. 24, 25 and 26, *Part.*) which later becomes converted into cartilage. As the chamber swells above, its ventral portion assumes the form of a tubular passage (*cf.* arrow *Aex.* in fig. 24) leading into the opercular cavity (*Op. cav.*) just between the hyoid and the 1st branchial arch. Thus it communicates not only with the opercular cavity, but also with the pharynx through the first gill-slit (*cf.* arrow *Aen.*). Air passes into it from the gill-slit and out of it into the opercular cavity. The communication with the pharynx is controlled by a "valve" (fig. 24, *Tell. n.*) consisting of a thick pad-like outgrowth from the inner dorsal surface of the first Ceratobranchial (fig. 24, *Cbr.*). This outgrowth gives off three processes (*cf.*, Plate 6, fig. 22) which, when the ceratobranchial is raised, close the opening from the air-chamber into the gill-slit at the same time as the exit from the air-chamber to the opercular cavity is opened by a slight lifting of the operculum. This "valve" was termed the "Tellerförmiges Nebenorgan" by WILH. PETERS (1853) (*Tell.*, text-figure 2 C). The epithelium lining the anterior part of the air-chamber is thrown into pits and folds, but is quite smooth in the hinder part of the chamber. The whole chamber assumes the form of a right-angled triangle (*cf.*, fig. 24, *A.C.*) with a vertical hypotenuse stretching from the region of the Epiotic bone (*Ot. cap.*) to just above the first ceratobranchial (fig. 24, *Cbr.*).

When the fish has attained the length of 1·2 cm., the first trace of the so-called "labyrinthine" organ (fig. 25, *Lab. pl.*) appears. This is a shelf-like outgrowth (*Ep. ap.*) from the epibranchial segment of the 1st branchial arch, which projects into the chamber and soon afterwards fuses with the inner and anterior wall of the region of the auditory capsule, so as to divide the whole chamber incompletely into an antero-ventral (fig. 26, *A.C.V.*) and a postero-dorsal section (*A.C.D.*). The anterior part of the edge of the shelf grows as a thin lamina, which then projects upwards and backwards into the posterior chamber and forms the first "shelly plate" (fig. 26, *Lab. pl.*) of the "labyrinthine" organ. The shelf and plate are both supported by a thin layer of cartilage, which is a direct outgrowth of the 1st epibranchial cartilage. They are covered over with thin epithelium (fig. 27, *Ep. l.*, and *vasc. cap.*) part of which is supplied by capillaries. HENNINGER (1908), GÜNTHER (1880) and ZOGRAFF (1888) have each given descriptions of the development of the "labyrinthine" organs, but their descriptions are quite erroneous; the first two of these authors started with fishes nearly 3·5 cm. in length, whilst ZOGRAFF considered it to have developed from the 4th epibranchial.



TEXT-FIG. 2.—Lateral dissections of young specimens of *Anabas scandens,* in order to show the development of the labyrinthine organs. A: a specimen 1·5 cm. long; B: a specimen 2·2 cm. long; C: a specimen 3·4 cm. long.

A.C., air-chamber; *Br. a.*, branchial arches; *Ep. sf.*, Epibranchial shelf; *Lab.* pl_1, *Lab.* pl_2, first and second labyrinthine plates; *Musc.*, cut edge of the muscular body-wall; *Tell.*, "Tellerförmiges Nebenorgan."

The first-formed plate (text-fig. 2 A, *Lab.* pl_1) grows in length, and when the fish has attained a length of 1·5 cm. a second plate (*Lab.* pl_2) originates from its outer side at the base. This plate rapidly grows in length, and then becomes folded, so to speak, along its mid-rib (text-fig. 2 C, *Lab.* pl_2). The inner half forms the second plate of the "labyrinthine" apparatus, and the outer half forms the third plate of this apparatus. So that the three plates (Plate 8, fig. 29, *Lab.* $pl._{1-3}$) are really derived from *two* successive outgrowths of the epibranchial shelf (*Ep. sf.*). After giving off these outgrowths the edge of the shelf bends at right angles and forms a thick pad-like thickening, which fits into a groove on the inner side of the operculum, and which almost completely closes the antero-ventral region of the chamber off from the postero-dorsal one into which the major part (Plate 8, fig. 31, *Lab.*) of the plates project. From the upper inner edge of the first plate two so-called "stylets" (Plate 7, figs. 25 and 26, and Plate 8, fig. 29, *Styl. pr.*) arise which connect with the otic region of the skull.

As the plates grow in size so does the air-chamber which contains them. The plates become covered over with a rich network of capillaries (fig. 27, *Vasc. cap.*), and their edges become crenulated. The air-chamber extends as far forward as the hinder end of the orbit, and penetrates dorsally into the cartilage of the auditory region, but it does not extend farther back than this region of the skull.

Macropodus differs from *Anabas* in a few details: The valve guarding the first gill-slit is a simple conical process; the first "labyrinthine" plate is T-shaped in section when it first appears, and lies across the air-chamber. The chamber itself extends farther back than it does in *Anabas*, and its wall also becomes more muscular. In its wall also are isolated "goblet" mucous cells and certain glandular pits (Plate 11, fig. 43) totally absent in *Anabas*. The "labyrinthine" plates themselves remain relatively simple. In *Anabas* as growth proceeds the edges become crenulated and curled in such a way as to hide their primitive simplicity of arrangement and to suggest a vastly more complicated mechanism than really exits. This has misled HENNINGER (1908), who speaks of 4 "*Grundplatten*" and 9 (secondary) "*Blättchen*"—a totally erroneous conception of the structure of the organ.

Bionomics of Various Species of "Snake-Headed" Fish (Ophiocephalidæ).

These fish are found in rivers, ponds and tanks, but also in foul stagnant pools in marshes amongst shrubby vegetation. They "walk" over ground from one pool to another, especially at night; indeed, this habit is so well known that they are frequently exhibited walking on the ground by jugglers. Unlike *Saccobranchus*, *Clarias*, *Anabas* and *Macropodus* they seem to prefer muddy water to clean water. In very hot and dry weather they bury themselves in the mud.

They are extremely voracious and dangerous to small fish of all kinds, and hence great care is taken to exclude them from tanks where fish like carp are reared. They lie hidden amongst marshy vegetation, with the head and eyes projecting from the water, and they snap at any worm, fish or frog that passes by. They are edible, and the largest species are usually fished for by rod and line. The angler goes out at dusk and sticks his rod into the mud near some river, in which he lets his line dangle, often baited with a small live frog. He returns in the morning, usually to find a "snake-headed" fish securely hooked. This is called "Shatka" in Bengal. Sometimes the angler moves about and casts his line in various likely places; this method the Bengalis term "Nerkey."

The four commonest species found in Bengal are *Ophiocephalus marulius*, which grows to a length of 4 feet; *O. striatus*, which reaches a length of 3 ft.; *O. punctatus*, which does not exceed a foot in length; and finally *O. gachua*, which averages 10 inches in length. They are long cylindrical fish with slightly flattened heads. *O. marulius* is dark green above and pinkish below; it has beautiful, dark, lozenge-shaped markings on its sides, and white spots on the hinder part of the head, and on the dorsal, anal and the caudal fins; the pelvic fins are orange. *O. striatus* derives its name from the dark obliquely transverse bars with which the body is covered; the two small species are soberly coloured.

The larger species usually inhabit the rivers, the smaller are denizens of the tanks, pools and marshes, and the smallest, *O. gachua*, invades rice-fields, in which its larvæ may frequently be found. These fry already exhibit the air-breathing habit, although no special air-chambers are at this period developed. They can be seen coming to the surface at frequent intervals and emitting air-bubbles from the mouth so as to make the pools frothy. Later, as they grow to the adult stage, the air-chambers develop, and then the bubbles of air are given off from behind the operculum. Children in India are fond of picking up tadpoles, and they frequently bring home Ophiocephalid fry in mistake for the tadpoles, which these fry strongly resemble.

The fry perform a valuable service in devouring the larvæ of mosquitoes and other noxious insects. They are fished for and caught by the same methods as those employed for capturing the young of *Clarias* and *Saccobranchus*. The fry of the different species differ in coloration. Those of *O. striatus* are brick-red in colour, with a couple of dark oblique bands meeting at an angle at the base of the caudal fin; those of *O. punctatus* are grey, with five longitudinal golden stripes, one in the mid-dorsal line and two on each side; those of *O. gachua* are dark grey.

The Ophiocephalids are edible, but not as much favoured as *Anabas*, although *O. gachua* and *O. punctatus* are regarded as strengthening diet. The various species differ as to their development of the air-breathing habit and their power of living out of water. *O. marulius*, the largest species, is found chiefly in rivers; it does not inhale air so often as the smaller species, since it generally lives in purer water; and it dies if kept for more than half an hour out of water, even though the skin remains moist. On the other hand, *O. gachua*, which lives in foul and muddy pools, inhales air much oftener, and can live for a far longer time out of water. *O. striatus* and *O. punctatus* construct nests of floating weed in which the ova are deposited. The ova are yellowish in colour, are from 1·00 to 1·5 mm. in diameter, and float in water.

The "walking" of the "snake-headed" fish is accomplished by strong "rowing" movements of the pectoral fins whilst the head is raised. As these fish have the habit of lurking in holes and darting out to seize their prey they have a bad reputation with some of the peasantry, who regard them as the embodiments of evil spirits, and the Karens of Burmah abstain from eating them, fearing that if they did so they would be changed into lions. The Ophiocephalidæ are found not only in India, Ceylon, Burmah and adjacent countries, but also in Africa.

Structure and Development of Air-Breathing Organs in " Snake-Headed " Fish.

The air-breathing organs of the " snake-headed " fish are not, as in the preceding types, developments of the opercular cavity, but *pouches of the pharynx*. The first indication of their development is a thickening of the pharyngeal epithelium on each side of the mid-dorsal line above the first gill-arch. This thickening a little later becomes hollowed out so as to form a pocket (Plate 9, fig. 33), which is the first rudiment of the air-chamber. The connective tissue surrounding the pocket is very vascular, and the capillaries soon invade the epithelial layer itself and give off loops which project as vascular papillæ (fig. 33, *Ep. vasc.* and fig. 36, *vasc. pap.*) covered with thin epithelium (fig. 36, *Ep. sq.*) into the lumen of the pocket. The pit lies just beneath the lymphoid organ (fig. 33, *Pronph.*) or the so-called " Pronephros," and is separated from it by a layer of striped muscle stretching from the basis cranii to the front border of the hyomandibular cartilage. Later, the posterior part turns upwards and becomes wedged between the hyomandibular (fig. 34, *Hm.*) and the otic capsule (*Ot. cap.*). Since the pocket lies over the region of the first gill-slit, the air which it contains can escape through this gill-slit. When the air is being taken in through the mouth, the gill-slit is closed by the contraction of the whole branchial apparatus.

Not only the pit but the pharynx, of which it is an outgrowth, is richly vascular, and probably assists in respiration; it certainly does so in the young fish before the pit is developed. Two large blood-vessels above the pits (branches (fig. 34, *B.V.*) of the jugular veins) return the oxygenated blood to the general circulation.

All the gill-arches of Ophiocephalids carry above the proper gills a few stiff detached filamentous processes. These are apparently modified gill filaments, and out of similar rudiments the characteristic " fans " of *Clarias* and *Saccobranchus* (see pp. 190 and 191) seem to have been developed. As the development of the pocket proceeds, its opening comes to be delimited by an inwardly projecting circular lip. Later, a conical process consisting of thickened epithelium underlain by a cartilaginous rod projects into the pocket from the inner wall of the hyomandibular cartilage. Still later, a similar process is developed from the epibranchial segment of the first gill arch extending upwards into the pocket. This process has on its surface glandular protuberances, each consisting of four or five vacuolated cells. The chamber (fig. 35, *A.C.*) grows backward behind the auditory region and extends as far as the 2nd branchial arch. The epibranchial segment (*Ep. br.*) of this arch gives rise to a shelf which grows inwards, and forms a support to the air-chamber on its ventral side. The wall of the anterior part of the chamber is thickened and vascular, and the posterior part is thin and slightly folded. As the adult condition is approached the hinder part becomes vascular also. In all the species except *O. gachua* a few glandular papillæ are found on the floor of the chamber. When the fish is fully grown, the air-chamber extends as far back as the third gill arch, and is pear-shaped, and its wall contains traces of a few muscle fibres lying towards the outer region of the connective tissue layer. Its mesial surface is very vascular, but its outer wall is practically non-vascular.

In *O. punctatus*, underlying the epithelium (Plate 9, fig. 37, *Ep. l.*), there are to be found a large number of lacunæ (*Lac.*) separated by thin septa of connective tissue. The capillaries extend up to the surface in these septa and form terminal tufts (fig. 37, *Vasc. cl.*). In the young stages these tufts project into the lumen of the air-chamber as vascular papillæ, and this condition persists to the adult stage in *O. gachua* and *O. striatus* (*cf.* fig. 36, *Vasc. pap.*), but in the adult of *O. punctatus* no such papillæ are to be found. Lacunar spaces are also found under the pharyngeal wall of *O. punctatus*, but no such spaces have been observed either in the pharynx or the chamber of the other species.

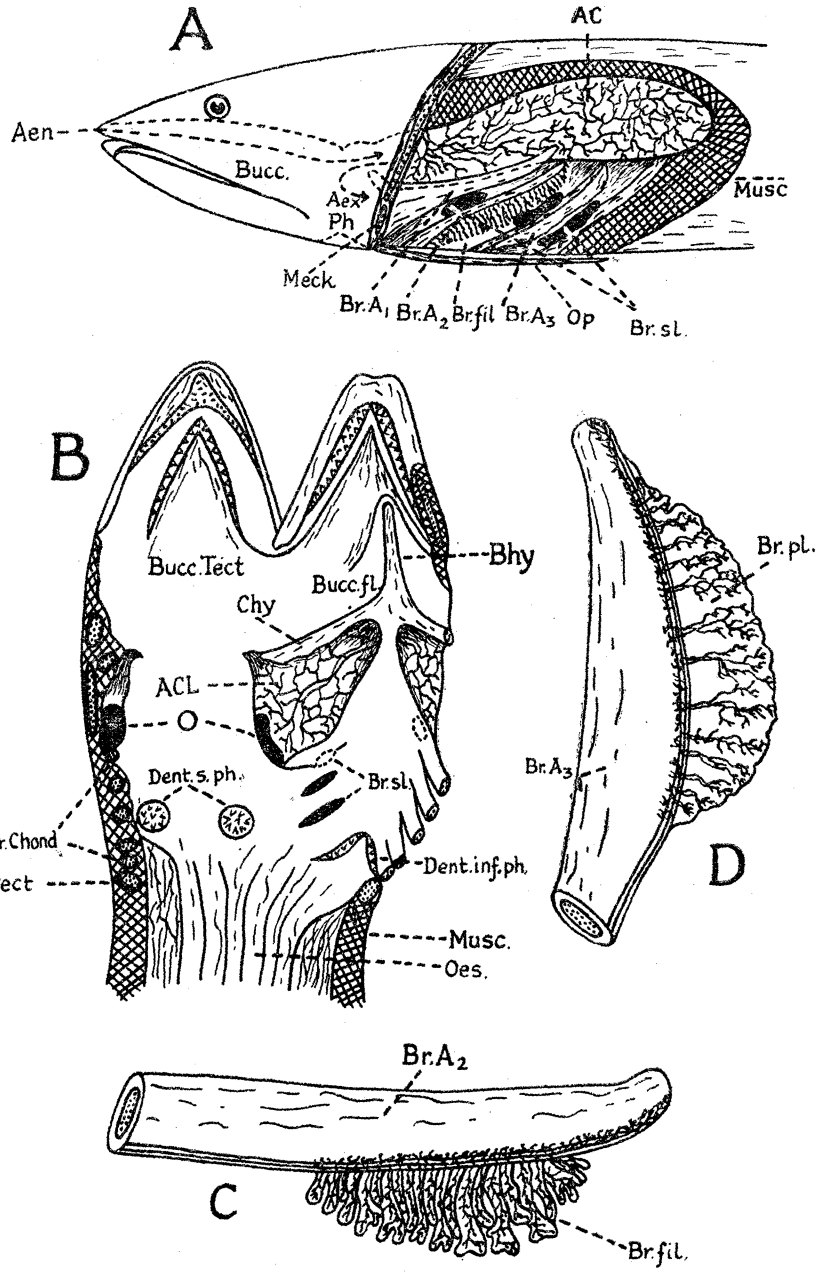
In *O. punctatus* a number of intercrossing epithelial ridges are developed in the hinder part of the wall of the air-chamber which enclose between them alveoli (*cf.* Plate 5, fig. 15), and the whole structure reminds one of an Amphibian lung. *O. punctatus* represents in this respect an intermediate condition between *O. gachua*, the smallest species, where the inner surface of the air-chamber, apart from its vascular papillæ, is smooth, and the large species *O. striatus*, where the air-chamber has still more ridges and its wall is extremely vascular. This seems to be a result of the law that volume increases as the cube of the linear dimensions, whereas surface increases only as the square; so that the surface of the air-chamber, which is the medium of respiratory exchange, must be increased by means of folds in order to keep pace with the still more rapidly increasing volume of the fish.

The Bionomics of Amphipnous cuchia (Ham. Buch).

Amphipnous cuchia is the so-called Cuchia "eel" of India. It is a member of the order Symbranchii, and is devoid of an air-bladder and of pectoral fins, and both opercular openings are united so as to form a single crescentic mid-ventral aperture.

Its skin is kept moist by the secretion of abundant unicellular glands; it appears to be naked, but close inspection reveals the fact that there are in it a multitude of minute cycloid scales. It spends the greater part of its life out of water, wriggling along the muddy banks of rivers and ponds; it is also found in grassy meadows and in muddy places among the roots of bushes. When the dry season approaches it burrows in the banks of streams, and here male and female pass the summer together in the same burrow. It visits the water in pursuit of food, which consists of worms, crustacea and small mollusca.

Amphipnous cuchia has developed a pair of air-chambers (*cf.* text-fig. 3 A, *A.C.*) as outgrowths of the pharynx, similar to the air-chambers of the Ophiocephalidæ; its gills have undergone great reduction, being represented by a few filaments (text-fig. 3 C) borne on the second gill arch only, so that it has almost lost the power of aquatic respiration. The young fry have five branchial arches, but these bear no gill filaments; the air-chamber is, however, developed, and this will be understood when it is realised that the fry are hatched from eggs laid in the burrows at the commencement of the rainy season, and pass the first part of their lives with their parents in these burrows, which are



TEXT-FIG. 3.—Dissections illustrating the anatomy of *Amphipnous cuchia*, the fresh-water "eel." A: Lateral dissection showing the relations of the air-chamber. B: Dissection showing both roof and floor of the buccal cavity and pharynx showing the entrance to the air-chamber and its relation to the gill-slits. C: Second gill arch with gill attached. D: Third gill arch with gill attached.

A.C., air-chamber; *A. en.*, entrance to same; *A. ex.*, exit from same; *A.C.L.*, ventro-lateral extension of same; *B. hy.*, basihyoid; *Br.* A_1, 1st branchial arch; *Br.* A_2, 2nd branchial arch; *Br.* A_3, 3rd branchial arch; *Br. chond.*, branchial cartilages cut across; *Br. fil.*, branchial filaments attached to 2nd arch; *Br. pl.*, branchial gill-plate attached to 3rd arch; *Br. sl.*, branchial slits; *Bucc.*, buccal cavity; *C. hy.*, ceratohyal; *Dent. inf. ph.*, inferior pharyngeal teeth; *Dent. sup. ph.*, superior pharyngeal teeth; *Meck.*, lower jaw-bone cut across; *Musc.*, muscular body-wall cut across; *O.*, opening of the air-chamber; *Oes.*, œsophagus; *Op.*, operculum cut across; *Pect.*, pectoral girdle cut across.

situated on the banks of rivers or ponds high above water level. Later, when they begin to accompany their parents in their excursions into the water in search of food, they develop rudimentary gills on three branchial arches, but of these only the gills on the second arch persist into the adult condition.

When in water the Cuchia "eel" rises at frequent intervals to take in air, and the air-chambers can be seen to swell out and distend the skin of the cheeks like two bladders. Sometimes only one air-chamber is filled at a time. By muscular contraction air is expelled from the air-chamber and escapes by the mid-ventral opercular slit already alluded to. Sometimes the intake of air causes an audible hissing noise. The Cuchia "eel" has a pointed snout with which it bores in the mud for its prey; it is of a dark grey or greenish colour above, and is yellowish beneath; when on land it moves like a worm by serpentine wrigglings. It is poor eating, and is despised by most Indians, but certain aboriginal tribes, like the Bhils and the Santals, consume it. They consider Cuchia blood mixed with potato curry a strengthening diet for an invalid.

The Cuchia "eel" has a much more limited distribution than the other air-breathing fish dealt with in this memoir. It is confined to the northern provinces of India, viz., the Punjab, Bengal, Orissa, Assam and Burmah.

Structure and Development of Air-Breathing Apparatus of Amphipnous cuchia.

As we have already seen, the air-breathing organs of the Cuchia consist of a pair of sacs (text-fig. 3 A, *A.C.*) developed from the dorsal wall of the pharynx. The adult fish attains a length of 48 cm., and these sacs begin to develop in a specimen about 3 cm. in length. They first appear as shallow pits (Plate 10, fig. 38, *A.C.*) of the dorsal wall of the front part of the pharynx in the region of the hyoid arch, each being separated by a considerable space from its fellow. The wall of the pharynx consists of a thickened epithelium (figs. 38–40, *Ep. vasc.*) underlain by an exceedingly rich vascular network, and the pouches, which are the first rudiments of the air-chambers, share this character.

The pits arise at an angle of about 80° with the horizontal plane of the pharynx, and extend up into the angle between the hyomandibular (fig. 39, *Hm.*) and the auditory capsule (*Ot. cap.*). The anterior part is lined by smooth non-vascular epithelium; the middle portion has an epithelial wall about 4-cells thick, with a rich capillary network underlying it; the hinder portion has a similar wall in which numerous mucous cells (fig. 40, *Muc.*) are developed. Folds (*cf.* fig. 42) also appear in this section of the wall, and capillary loops push slight protrusions (fig. 42, *Vasc. cap.*) into its lumen.

The epithelium is based at first on a bed of loose connective tissue, but soon this tissue gives rise to a network of elastic fibres (fig. 42, *conn. elas.*), in the meshes of which the capillaries lie.

As development proceeds the folds increase in size and numbers and become flattened at their free ends, so as to suggest in some cases rosettes of flowers (*cf.* fig. 42), these being richly supplied with blood-vessels. The lower end of the sac retains a relatively smooth epithelium; it lies directly over the ceratobranchial (fig. 40, *C. br.*) segment of the 2nd gill arch, and here communicates with the pharynx (*Ph.*). The edges of the opening, *i.e.*, dorsal and dorso-lateral walls of the pharynx, meet in this region and diminish the size of the opening, which now becomes restricted to a more anterior region of the pharynx.

In its full development the air-sac extends as far back as the 3rd branchial arch, and reaches upwards beside the notochord and the neural canal so as very nearly to reach the dorsal integument. Muscles, both striped and smooth, now appear in small patches on its wall, and eventually the whole sac is clothed with a muscular coat (Plate 10, fig. 42, *Musc. uns.* and *Musc. str.*). In addition to these intrinsic muscles, it must be remembered that the sac is flanked by the dorsal parts of the myotomes (text-fig. 3, *Musc.*) on its inner side, and on its outer side by a narrow band of muscle connecting the dorsal and ventral parts of the myotomes. The sac in its posterior and distal portion gives off numerous small pocket-like alveoli (Plate 10, fig. 41, *Alv.*) and comes to resemble an Amphibian lung. The opening into the pharynx is now restricted to an aperture (*cf.* text-fig. 3 B, *O.*) situated between the hyoid and first branchial arches.

The reduction of the gills is a most interesting feature in the development of Amphipnous. The larva after hatching has 5 gill arches, but only 3 gill-slits; no gills, however, are as yet developed. As the larva grows and leaves its muddy burrow to make excursions into the water, gill plates are developed on the 1st, 2nd and 3rd arches (Plate 11, figs. 44, 45 and 46); they might be described as fleshy plates hanging down into the ventrally situated opercular cavity. These plates have a rich vascular supply (*B.V.*). As the larva grows bigger the plate on the 2nd arch (fig. 45) increases in importance, and by a series of parallel furrows (figs. 44, 45 and 46, *Fr.*) on its surface a few gill filaments (*Br. fil.*) become marked out; these are finger-shaped and bud out from the ridges between the furrows; they first appear in a fish 6 cm. long. Later, a few smaller processes develop on the 3rd gill plate (fig. 46, *Br. fil.*), and still later one or two vestigial ones (fig. 44, *Br. fil.*) on the 1st gill plate. In the adult condition the filaments on the 1st and 3rd plates completely disappear, whilst those (text-fig. 3 C, *Br. fil.*) on the 2nd arch grow longer. This change occurs hand in hand with a modification in the habits of the larva, which from being semi-aquatic becomes nearly terrestrial.

Physiology of Air-Breathing Organs.

Before giving an account of the results of the physiological experiments on the air-breathing fish which I carried out in India, it is desirable to give a very brief account of the adult anatomy of these organs, in order to enable the experiments to be more easily understood. The anatomy has, of course, been previously described, chiefly by HYRTL, SENNA, HENNINGER, MEYER and RAUTHER (*cf.* Bibliography), but the papers containing the descriptions are scattered and not always easy of access.

In both *Clarias* and *Saccobranchus*, as already described, there are "fans" (Plate 3, fig. 4, and Plate 4, fig. 7, F_{1-4}) developed from the upper parts of the ceratobranchial segments of all 4 gill arches. These "fans" are formed by the coalescence of gill filaments, the 1st and the 4th (*cf.* fig. 7, F_1 and F_4) remaining small. In *Clarias* there are two notches guarded by these "fans," one (fig. 7, *Aen.*) between the 2nd and 3rd "fans," which allows the air to escape from the pharynx into the air-chamber, and a second (*Aex.*) between the 3rd and 4th "fans," which allows the air to leave this chamber when the operculum is raised. In *Saccobranchus* (*cf.* text-fig. 1 A, *F.* and *O.*) the 1st "fan" is small and lies in close contact with the 2nd, and the 4th is also small and is in close contact with the 3rd. The 3rd (Plate 4, fig. 11, F_3), which is the biggest, overlaps the 2nd (F_2) in such a way as to leave a slit (*O.*) which serves both for the entrance of air from the pharynx into the air-chamber and for its exit from that cavity to the exterior behind the operculum.

In *Anabas* the inner portions of the hyobranchial (Plate 8, fig. 30, *Hybr. cl.*) and 1st branchial clefts (*Br.* sl_1) unite to form an oval notch (*Ntch.*), which is the passage leading from the pharynx into the air-chamber. From the middle of the inner aspect of the first ceratobranchial there arises a plug (*Tell. n.*) which fits over this notch, and when the mouth is shut covers it almost completely. The covering is made total by a similar but smaller plug, which arises from the 2nd arch. From the 1st arch above and behind this plug arises the modified epibranchial, which gives rise to a shelf (fig. 29, *Ep. sf.*) running upwards and forwards obliquely across the air-chamber. From this epibranchial, as we have already learnt, the "labyrinthine" plates (fig. 31, *Lab.*) arise. The tip of the shelf is bent forwards and downwards at right angles to the rest, and fits into a groove on the inner side of the operculum. Thus the air-chamber, as we have seen, is divided into a small antero-ventral (fig. 31, *A.C.V.*) and a large postero-dorsal portion (fig. 31, *A.C.D.*), and in the latter the major part of the shelly "labyrinthine" plates (*Lab.* and also *cf.* fig. 29) is lodged. From the inner side of the posterior and largest of these plates there arises a bony process, the so-called "styliform process" (fig. 29, *Styl. pr.*), which is joined at its tip to a second process which is tied by connective tissues to the auditory capsule (Plate 7, fig. 26, *Styl. pr.*).

Behind and above the epibranchial shelf which we have just described there is another notch (fig. 28, *Aex.*) which allows the air to escape from the air-chamber into the outer part of the opercular cavity and so to the exterior. When *Anabas* opens its mouth to take in air the whole branchial apparatus is lowered ; this pulls the ceratobranchial plug out of the first notch described, and so allows the air to escape from the pharynx to the air-chamber. When the mouth is shut the branchial apparatus is raised, the plug covers the notch, and no more air can enter ; the air already taken passes up over the front surface of the "labyrinthine" plates (fig. 31, *Lab.*) into the posterior section (*A.C.D.*) of the air-chamber. When the operculum is raised the air escapes to the exterior from the second notch described above.

Ophiocephalidæ.—When the mouth of a "snake-headed" fish is opened we at once perceive the openings of the air-chambers at each side of the posterior part of the parasphenoid bone. Each opening is more or less round, and its front and inner edge is produced into a thickened rim. Projecting from the posterior edge of the hyomandibular into the air-chamber is a process ; this incompletely divides the air-chamber into an anterior and a posterior portion. A small process arises from the front edge of the 1st branchial arch; this second process is broad and rolled up into a half tube which fits against the first process, and thus gives rise to a tubular passage leading from the air-chamber to the opercular chamber.

When the mouth is opened and the branchial apparatus pulled down air rushes into the air-chamber and below the ventral edge of the hyomandibular process into its posterior division. When the mouth is shut and the gill arches raised this process cuts off communication between the anterior and posterior regions of the air-chamber, and the air now escapes (Plate VI, fig. 32, *Aex.*) through the tube formed by the opposition of the two processes into the opercular chamber and so to the exterior. This description applies most exactly to *O. punctatus* and *O. gachua*, the two smaller species. In *O. marulius* and *O. striatus* the two processes are curiously folded and studded with vascular papillæ, evidently for absorbing oxygen; *O. striatus* expels a considerable portion of the vitiated air by the mouth.

In *Amphipnous* the large openings (*cf.* text-fig. **3** B, *O.*) into the air-chambers are at once seen when the mouth is opened. These apertures are situated at either side of the middle line above the dorsal ends of the hyoid and the first branchial arches. The air-chamber (*cf.* text-fig. **3** A, *A.C.*) lies above and external to the branchial arches ($Br.\ A_{1\text{-}3}$) (which in this fish are small and ventrally placed). Externally the chambers are bounded by the thin opercular and subopercular bones and the branchiostegal rays. As we have already seen there are only **3** gill-slits (*A.*, *Br. sl.*) on each side, which are very much reduced in size. When the mouth is opened the aperture of the air-chamber is also opened, and the air rushes (*cf.* arrow *Aen.* in A) in and fills the air-chamber. When the mouth is shut this aperture is closed, partly by the intrinsic muscles in its rim and partly by the floor of the mouth being pressed against the palate. The intrinsic musculature of the wall of the air-chamber now contracts, and the air is forced through (*cf.* arrow *Aex.* in A) the minute gill-slits into the opercular chamber and then by the median ventral opening to the exterior. Occasionally, however, the fish shoots its muzzle above the water and drives the air out between half-closed lips with a hissing noise.*

The physiological experiments, the results of which I now proceed to describe, were carried out in the natural habitat of the fish. I camped out on the banks of the rivers

* Regarding the mechanism of respiration in these air-breathing fishes the following facts should be carefully noticed :—

In *Clarias* the fish lifts its head above the surface of water, opens its mouth and takes a gulp of air. All this is performed very rapidly, and during this process the ceratobranchials sink backwards and downwards and the gill-clefts lying between them are closed, whilst at the same time the epibranchials become almost vertical, and the large anterior slit between the 2nd and 3rd branchial "fans" opens, allowing the air to pass from the pharynx into the air-chamber. When the mouth is closed the slit between the "fans" is also closed, but when the operculum is lifted up then it releases the posterior slit, viz., between the 3rd and the 4th "fans," and hence allows the escape from its posterior extremity.

In *Saccobranchus*, however, the 1st and 4th "fans" are very small and they overlap the 2nd and the 3rd "fans," thus leaving no slit between the 1st and the 2nd "fans," nor between the 3rd and the 4th "fans," and ponds in which the fish lived, and used the very water in which they were caught for the purpose of experiments. As controls in these experiments I used specimens of *Cirrhina mrigala* (a common Indian carp) of the same size as the specimens of air-breathing fish under examination. Previous workers, DAY (1868) and DOBSON (1874), had made a few isolated experiments on these fish in India. Others, such as MEYER (1904) and HENNINGER (1908), had transported the fish to Europe and them experimented on them under conditions widely differing from those in their native environment.

I may remark in passing that the "snake-headed" fish exhibited in the aquarium of the Zoological Society of London are living in far cooler water than that to which the fish are accustomed, and their infrequent excursions to the top to obtain air give no conception of the extent to which this habit is developed in India, where the fish are found in small pools, the temperature of which may be as high as 98° F. In these pools the presence of "snake-headed" fish can often be detected by the froth or bubbles of air which they have exhaled.

whereas the 3rd "fan," as in *Clarias*, is the largest, and this comes to lie over the 2nd "fan," leaving a small slit between them—the common opening for the passage of air in and out of the air-chamber (*cf.* text-fig. 2).

In *Ophiocephalus* there are two large holes bounded by pad-like thickenings of the palate allowing the air to pass into the large air-chamber when the mouth is opened. The hyomandibular gives off a process which hangs downwards across the air-chamber at its anterior end, and when the mouth is opened it is pulled slightly upwards allowing the air to pass along its ventral edge and then into the air-chamber. There is also a second process lying behind the first process which is given off by the first branchial arch. We shall term it, following HYRTL (1853), the epibranchial process; it is slightly curved upwards. When the mouth is shut the floor of the buccal cavity comes into close contact with the roof and closes the holes, but there remains open on each side a gutter enclosed between the hyomandibular and the epibranchial processes, which opens in front in the air-chamber and behind into the hyobranchial cleft, and through this gutter the air escapes when the operculum is raised.

In *Amphipnous* as in *Ophiocephalus* there are two large holes bounded by muscles in the roof of the mouth-cavity. When the mouth is opened the holes also open, allowing the air to enter the air-chambers, which become bulged out like "bladders" along the posterior sides of the head. When the mouth is shut the holes get closed by the contact of the floor of the mouth-cavity with its roof as well as by the contractions of the muscles round the rim. By a sudden contraction of the muscular walls of the air-chambers, and also by the spring-like action and pressure caused by the opercle and the subopercle, the air is forced out of the narrow gill-slits, and thus out of the median ventral branchial opening.

It is interesting to note that, whereas in all other air-breathing fishes the air is allowed to escape by the gaping elevation of the opercula, in *Amphipnous* the reverse is the case, the air is pumped out by double action, viz., by simultaneous muscular contractions of the wall of the air-chamber, and the squeezing process brought about by the pressing together of the opercula against the sides of the head.

The air-breathing mechanisms of *Anabas* and *Macropodus* have been fully dealt with in the foregoing pages. REGAN, in his Monograph of the Fishes of the family *Loricariidæ* ('Trans. Zool. Soc. London,' vol. 17, p. 191, 1903–1906), describes an extremely interesting case of structural modifications, *i.e.*, the breathing mechanisms in certain Loricarids correlated with the influences of environment and habits:—"It appears that in nature these fishes fasten themselves to stones by means of the sucker-like mouth, whilst in captivity they have been observed to adhere to the bottom or sides of the vessel in which they are placed. Respiration seems then to be effected by taking in water through the gill-openings and expelling it again by the same passages in a reverse direction."

The experiments can be divided into four series:—

Series I. Asphyxiation and recovery. (α) Asphyxiation ("drowning") of the fish by preventing access to the air. (β) Their recovery by exposure to the aerated water.

Series II. Effects of injury to special air-breathing organs.

Series III. Survival out of water.—(*a*) In damp surroundings. (*b*) In dry surroundings.

Series IV. Effects of specially treated water.—(*a*) Muddy water. (*b*) Boiled water. (*c*) Water saturated with oxygen. (*d*) Water saturated with CO_2 gas.

For the purpose of these experiments I used small aquaria, 2 ft. high and 1 foot in diameter. A diaphragm of copper gauze was made to fit the mouth of one of these aquaria. It was provided with a square frame of stout copper wire to which it was tied. It was then suspended by four hooks of stout wire passed over the edges of the aquarium, so that it hung about an inch below the surface of the water, to prevent the fish reaching the surface and inhaling air.

These experiments were mostly carried out during the summer months of April, May and June, when the temperature of the air varied from 83° to 102·5° F., and the temperature of the water from 82·5° to 93·5° F. Out of the large numbers of experiments which I made I shall select for detailed description a typical one of each series for each type of fish.

Series I. (α) *Asphyxiation of the Fish by preventing Access to the Air.*

(*a*) Experiment on *Clarias magur*.—At 2.45 p.m. a specimen was placed in the aquarium. The branchial respiration as indicated by movements of the operculum was 94 per minute. At 3.8 p.m. they had decreased to 75 per minute, and at 3.25 p.m. they were 50 per minute, and had become even and regular. Excursions to the top to obtain air took place at intervals varying from 3 to 15 minutes. At 5.7 p.m. the diaphragm was placed in position. Immediately the fish began to get agitated and struck against the diaphragm every minute or so. The rapidity of the branchial movements at first increased, but they then slowed down and ceased at 5.36 p.m. After an interval of 15 minutes they recommenced and went on intermittently. After making a few more spasmodic efforts to reach the surface, and only attaining half the height of the aquarium, it turned over on its back, emitting a few minute bubbles of air as it did so. All movements ceased at 6.57 p.m. The fish was "drowned" in 1 hour and 50 minutes.

I took the "drowned" fish out and exposed the heart, which went on beating. At 7.5 p.m. it gave 23 beats per minute. At 8.10 p.m. 45 beats per minute, and at 11.15 p.m. 87 beats per minute. After 2 hours it began to fail and ceased by 1.23 a.m., *i.e.*, 6 hours 26 minutes after "drowning."

(*b*) Experiment on *Saccobranchus fossilis*.—The experiment began at 3.32 p.m., the branchial movements being then at the rate of 92 per minute. By 4.20 they had calmed down to 68 per minute. The fish came to the surface to inhale air at intervals varying from 1 to 4 minutes. At 4.32 p.m. the diaphragm was placed over the aquarium. The fish became excited, and its branchial movements increased to 79 a minute. The fish repeatedly dashed against the diaphragm in vain attempts to get air. It became exhausted, its branchial movements slackened and completely ceased by 6.15 p.m., *i.e.*, in 1 hour 43 minutes. The heart continued to beat till 9.2 p.m., *i.e.*, 2 hours and 47 minutes after all external movements had ceased.

(*c*) Experiment on *Anabas scandens*.—The experiment began at 8.42 a.m. When the fish was placed in the aquarium the gill movements were momentarily suspended, but soon recommenced, and at 9.46 a.m. were proceeding at the rate of 27 a minute. The fish rose to the surface to inhale air at intervals of from 3 to 11 minutes. The used-up air was exhaled from the operculum, apparently simultaneously with, but really a little before, the intake of fresh air. The diaphragm cover was placed over the aquarium at 10.17 a.m. The fish became greatly excited and dashed against the diaphragm every minute and subsequently every half minute. It soon exhausted itself, sank to the bottom and fell over on one side, then rolled from side to side, and after a few spasmodic branchial pulsations all movements ceased at 10.33 a.m., *i.e.*, 16 minutes after the fish had been excluded from access to the air. The heart ceased beating at the same time, but recommenced 3 minutes afterwards and executed 57 beats per minute at 10.38 a.m., but failed completely at 10.55 a.m., *i.e.*, 22 minutes after " drowning."

(*d*) Experiment on *Trichogaster chuna*.*—This is a small fish, belonging to the family Anabantidæ, which differs from Anabas in inhaling air at more frequent intervals ($\frac{1}{2}$ minute to 3 minutes) and expelling the exhaled air principally from the mouth. The diaphragm was placed over the aquarium at 4·2 p.m. The branchial movements became accelerated to 158 pulsations per minute at 4.7 p.m., the fish lost its balance and rolled on one side. It still made wild attempts to reach the surface at intervals of about 17 minutes, falling like a stone to the bottom after each attempt. Branchial movements ceased at 8.23 p.m.; a few gasps followed and the fish was completely " drowned " at 8.25 p.m., *i.e.*, 4 hours and 23 minutes after being excluded from air. The heart beat after branchial movements ceased was 148 per minute, and lasted for 48 minutes.

(*e*) Experiment on *Ophiocephalus punctatus*.—The fish was introduced into the aquarium at 2.25 p.m., and was then inhaling air at intervals of from 2 to 5 minutes. The rapidity of its inhalation increased till it came to the surface to inhale air every minute. Air was exhaled as the fish was descending from the surface. The diaphragm was placed over the aquarium at 3.10 p.m., when the branchial movements were 37–47 per minute. Wild agitation followed, but the fish was exhausted and ceased its branchial movements at 4.45 p.m., and at 4.50 p.m. the fish was completely " drowned " and was lying on its side.

(*f*) Experiment on *Ophiocephalus striatus*.—The fish was introduced into the aquarium at 7.30 a.m. Its branchial movements were slow, about 18 to 20 pulsations a minute.

* In the preceding pages I have given an account of the anatomy and the development of *Macropodus cupanus*, but owing to my inability to procure living specimens of this species I was unable to carry out physiological experiments on it, and for the sake of convenience of comparison I have chosen another member of the same family commonly found in Bengal, viz., *Trichogaster chuna*. The anatomy of this species is already known, and is practically the same as that of *Anabas*.

It rose to the surface to inhale air every few minutes, and though the air was usually given off from behind the opercula as the fish was descending, yet occasionally bubbles of air were given off from the mouth as the fish was rising.

The diaphragm was placed over the aquarium at 8.30 a.m. The fish became agitated and struck the diaphragm every half-minute in its efforts to reach the air, and its branchial movements increased to 22 per minute. It rolled on its side in 16 minutes, and at 8.59 a.m. all movements ceased, just about half an hour after it was prevented access to the air. The heart continued to beat, and at 9.25 a.m. its pulsations were 77 per minute, but it failed and stopped at 10.11 a.m.

(*g*) Experiment on *Amphipnous cuchia*.—The fish was introduced into the aquarium at 9 a.m. It rose to inhale air every 2 minutes. The mouth projected beyond the surface; the lips were opened and the air was drawn in with a hissing noise, the air-chambers becoming at once dilated. The fish then withdrew itself beneath the surface, and by active contraction of the intrinsic muscles of the air-chambers, aided by wriggling, expelled the air through the gill-clefts and the mid-ventral opercular opening in minute bubbles. When the air is being breathed no branchial movements are discernible, but when, after getting rid of its air, the fish drops to the bottom, then such movements begin.

At 10.50 a.m. the aquarium was covered by the diaphragm. The fish instantly became greatly disturbed, and dashed against the diaphragm every 40 seconds. It became exhausted, and after gasping repeatedly just under the diaphragm fell to the bottom, and movements ceased at 12.32 p.m., *i.e.*, in one hour and 42 minutes. The heart-beat at 12.38 p.m. was 33 per minute, but failed completely at 1.15 p.m.

Series I. (β) *Recovery after "Drowning" by Exposure to Aerated Water.*

(*a*) Experiment on *Anabas scandens*.—A specimen placed under the diaphragm at 8.45 a.m., and at 9.11 a.m. lying at the bottom on one side and gasping, was transferred to a shallow dish, half-filled with water of just sufficient depth to cover the fish. Gill breathing started at 9.25 a.m., and at the same time the fish inhaled air rapidly ten times, and at 9.26 a.m. recovered its balance and appeared perfectly normal. Another specimen, placed under the diaphragm at the same time, ceased all movements at 9.31 a.m., but on being transferred to the shallow dish completely recovered by 10.6 a.m.

(*b*) Experiment on *Ophiocephalus punctatus*.—A specimen was placed under the diaphragm at 8.5 a.m., and was lying on one side at 9.20 a.m. On being placed in the shallow dish branchial respiration started in 2 minutes and proceeded at the rate of 30 pulsations per minute. At 9.33 a.m. it began to inhale air once a minute, and by 10.5 a.m. had regained its balance and was normal.

After complete recovery I several times held the head of the fish under water and squeezed the branchial region, in order to get rid of all traces of air. Each time as soon as I released the fish it darted to the surface and inhaled air with widely open mouth.

Series II. Effects of Injury to Special Air-Breathing Organs.

(*a*) Experiment on *Clarias magur*.—In one specimen the dorsal wall of the right air-chamber was cut away and the air-trees removed by cutting through their bases. The fish when released rose at once to the surface to take air. This air, however, was at once given off through the large opening on the right side, instead of being given off before the fish inhales, as is the case in the normal fish. After a time, however, it became obvious that air was being taken into the left uninjured air-chamber also, for the fish when lying at the bottom gave off a few bubbles from under the left operculum. The same fish was eventually placed beneath the diaphragm at 9.25 a.m. It showed the usual symptoms, *i.e.*, acceleration of branchial movements, which by 9.50 were 53 per minute, dashing against the diaphragm. It lay on one side, and movement ceased at 10.32 a.m. The heart was still beating at 11.30 a.m., at the rate of 44 per minute, but it failed completely at 1.20 p.m.

In another specimen both air-chambers were opened and the air-trees removed from both sides. The shock of the operation stopped the branchial movements completely, which were not resumed until 9 minutes after the fish had been replaced in the aquarium. The fish made a series of mad rushes to the surface to obtain air, which it inhaled with widely opened mouth, but all this air was almost immediately lost through the widely open air-chambers. Gill movements ceased in 38 minutes, and at 12.48 p.m. (*i.e.*, in 40 minutes) the fish lay motionless on its side. The heart continued beating, and at 2 p.m. its rate was 57 beats per minute. It failed at 4.30 p.m.

(*b*) Experiment on *Saccobranchus fossilis*.—In one specimen the left air-chamber was exposed for the posterior half of its length. The operated fish was put into the aquarium at 4.15 p.m., when the sac, freed from its surroundings, floated upwards at right angles to the body. The gill breathing was 58 pulsations per minute at 4.20 p.m., but at 4.37 p.m. it had increased to 118 pulsations per minute. Air was inhaled at more frequent intervals than usual. Exhalation followed inhalation of air so quickly that the two processes were almost simultaneous. When the fish was placed beneath the diaphragm it was "drowned" in 2 hours and 7 minutes. It was seen that the exposed air-sac became flaccid and sank down, so that it is obvious that the fish uses up all its reserves of air in these air-sacs before succumbing.

(*c*) Experiment on *Anabas scandens*.—In one specimen the left air-chamber was opened and the left "labyrinthine" apparatus was removed. The fish when placed in the aquarium inhaled air every two or three minutes; nearly all the air at first escaped from the injured side, but afterwards air was given off from beneath the uninjured operculum also. It was noticeable that in this fish exhalation occurred after inhalation, whereas in the uninjured fish the reverse is the case. This fish when placed beneath a diaphragm succumbed in 15 minutes.

(*d*) Experiment on *Ophiocephalus punctatus*.—In one specimen the left operculum was removed and also the posterior wall of the left air-chamber, and the blood-vessels supplying the left gills severed. The fish rose to the surface to inhale air every three minutes, and nearly all this air at once escaped from the injured side. After the expiry of 52 minutes the fish regained its control of air-breathing. It rose to the surface about every minute, and gave off air bubbles from the right and left sides alternately. Placed beneath the diaphragm this fish succumbed in half an hour.

In another specimen not only were the left operculum and the left outer wall of the left air-chamber removed and the blood-supply to the left gills severed, but the internal wall of the left air-sac was removed as well. In this fish all branchial movements ceased from the start, though slight movements of the pectoral fins continued; 45 minutes after the operation it made a struggle to rise, but succumbed completely 4 minutes afterwards.

In another specimen the posterior portions of both air-chambers were punctured. This fish rose at $\frac{1}{2}$-minute intervals to inhale air, which was given off from the right and left sides alternately. Placed beneath the diaphragm this fish succumbed in 16 minutes.

Still another specimen, similarly treated, rose to inhale air every 20 seconds. Every time that the air bubbles were given off from a particular side the fish bent its head to the opposite side, apparently to facilitate the lifting of the operculum. In another specimen the blood-supply to the gills was severed on both sides. Branchial movements ceased from the very beginning. The fish made one struggle to get out of the water, but succumbed immediately afterwards, 4 minutes after the operation.

These three series of experiments, described above, include all the detailed work carried out exclusively on these air-breathing fish; but in addition to these experiments I performed another series, in which I subjected both air-breathing and exclusively water-breathing fish to the influence of water vitiated in various ways and to exposure to air. I proceed now to give some details of a few selected experiments of this kind.

Series III. Survival out of Water.

(*a*) *In Damp Surroundings.*—Three specimens of *Clarias* put in wet grass in an earthenware pot at noon, temperature at 86° F. Found dead next morning, having survived 18 hours. Several specimens of *Anabas*, *Trichogaster*, *Ophiocephalus gachua*, *Ophiocephalus punctatus*, *Ophiocephalus striatus* and *Amphipnous cuchia* put together in a pot in wet grass. *Anabas* died in 12 hours, *Trichogaster* in 5 hours, *O. gachua* in 14 hours, *O. punctatus* in about 20 hours, *O. striatus* in 9 hours, and the different specimens of *Amphipnous* in periods varying from 36 to 60 hours.

(*b*) *In Dry Surroundings.*—(i) Experiment on *Trichogaster chuna*. Two specimens placed on a dry marble floor, temperature of the air 91° F. Time, 1.45 p.m. Both specimens inhaled air; the first at intervals varying from 3 seconds to 1 minute 17 seconds (*i.e.*, 77 seconds), the second at intervals from 3 seconds to 35 seconds. At

2.50 p.m. the scales were dry, and shortly afterwards, with some convulsive movements, both fish died, about 1 hour and 10 minutes after being removed from water.

(ii) Experiment on *Ophiocephalus punctatus*.—Two specimens placed on a dry marble floor, the temperature of the air being 100° F. These fish inhaled air; one every 2 minutes and the other about every 4 minutes. Both died in 5 hours and 40 minutes. Two other specimens died in about 3 hours. It was interesting to note that the rate of inhalation increased as the time went on. Death came after a final convulsive struggle.

Series IV. Effects of specially treated Water.

(*a*) *Muddy Water.*—(i) Experiment on *Ophiocephalus punctatus*. A specimen exposed to the influence of an artificial mixture of mud and water. The branchial movements, which had been 37 per minute, slackened to 25 per minute; but inhalation of air, which had been once every 12 minutes, increased to one every 3 minutes. Placed under a diaphragm the fish was asphyxiated in 15 minutes.

(ii) Experiments on *Anabas*, *Trichogaster*, *Clarias*, *Saccobranchus* and *Amphipnous* gave similar results.

(iii) In order to control the foregoing results I experimented with a number of ordinary water-breathing fresh-water fish. I used the common carp species (*Cirrhina mrigala*, and *C. reba*, *Labeo cœruleus*) and small species of Barbus, Catla, Chela, Aspidoparia, Rohtee; Siluroids such as Macrones, Eutropiichthys, Wallago, Ailia, Gagata and Pseudotropius; Cyprinodonts (*Haplochilus panchax*); Mugilidæ (*Mugil cascasia*); Percidæ (*Ambassis*); Sciænidae (*Sciena coiter*) and Gobidæ (*Gobius*).

These fish were placed in small jars with clean water; afterwards the clean water was replaced by muddy water. After 18 hours in clean water all the fish came to the top and gulped down air; all died in 24 hours owing to the loss of the air from the limited quantity of water in which they were placed. If prevented from having access to the air by the diaphragm, they died 2 to 4 hours earlier. In muddy water all these phenomena took place in a much shorter time; branchial respiration became very slow, all came to the surface to seek air inside an hour, and all died within 5 or 6 hours.

(*b*) *Boiled Water*. (Water boiled for 6 hours in order to expel dissolved oxygen.) The water was tested with pyrogallic acid to be certain of the absence of oxygen. Specimens of *Clarias*, *Saccobranchus*, *Anabas*, *Ophiocephalus* and *Amphipnous* were immersed in jars filled with this water. At first these fish behaved normally, but soon became extremely agitated and snapped for air with increased frequency. *Clarias*, *Saccobranchus* and *Anabas* survived for 6 hours, then made convulsive movements and died; *Ophiocephalus* survived for 8 hours, but *Amphipnous* after three days appeared to be in quite a healthy condition. As controls water-breathing fish were subjected to the same condition. In all branchial movements were suspended in 2 to 5 minutes, and in every case death occurred in half an hour.

(*c*) *Water saturated with Oxygen from a Generator.*—The air-breathing fish (viz., *Anabas*, *Clarias*, *Saccobranchus*, *Ophiocephalus*), placed in water through which oxygen was bubbling, appeared completely at their ease, frequently snapping at the bubbles of gas. Even under these circumstances, however, they rose to the surface to inhale air every 20 minutes. When prevented from doing so by a diaphragm they became agitated and dashed against the diaphragm several times, and ultimately succumbed in periods varying from 3 to 8 hours. Control water-breathing fish placed under a diaphragm in similar water were quite unaffected and normal after 24 hours.

(*d*) *Water saturated with* CO_2 *Gas.*—The same species of air-breathing fish were placed in water through which a stream of CO_2 bubbles was kept passing. At first some fish snapped at these bubbles, but after inhaling them became excited and fled to the farthest corner of the aquarium, where they vigorously and rapidly inhaled air. All came to the surface in less than an hour, and all succumbed in less than 6 hours. When kept below a diaphragm they were " drowned " in 45 minutes. Control water-breathing fish under similar circumstances all came to the top in 5 minutes and died within half an hour.

General Discussion and Conclusions.

The observations and experiments recorded in the foregoing pages point to certain general conclusions. They show that the habit of seeking oxygen by swallowing bubbles of air, when the dissolved oxygen in the surrounding water fails, is widely distributed amongst Teleostean fish. I have observed it myself in not less than 100 species. The air-breathing fish differ from their normal congeners in the intensification of this habit, and the reasons for the intensification may be easily inferred : Fishes that live in shallow ponds and streams which periodically become dried up (*e.g.*, *Clarias*, *Saccobranchus*, *Anabas* and *Macropodus*) or in pools rendered foul by decaying vegetation (*Ophiocephalus*), or in muddy holes which periodically dry up (*Amphipnous*), must constantly snap air in order to survive at all. This habit, long continued and deeply engrained in the constitution, has eventually led to structural alterations in the form of reservoirs adapted to contain the inhaled air.

As we have seen, these reservoirs may be developed as outgrowths either of the pharynx (*Ophiocephalus* and *Amphipnous*) or the opercular cavity (*Anabas* and its allies, and *Clarias* and *Saccobranchus*). We may remark in passing that the resources of nature are not exhausted by these two alternatives. In Great Britain and in Europe generally it has long been known that eels can survive for a long time out of water, and wriggle over grassy meadows at night in their passage from one pond to another. It has been supposed that they were able to do this owing to the fact that they possessed narrow opercular openings, so that their gills did not dry up. But P. BERT* (1868) has shown that eels survive out of water just as well when their opercula are removed, and that they

* P. BERT, " Sur la raison pour laquelle certains poissons vivent plus longtemps à l'air que certains autres." ' Comp. Rend. Soc. Biol.,' vol. 5, p. 49 (1868).

received the necessary oxygen by respiration through the skin. Then certain loaches (*Misgurnus fossilis*, *Cobitis tænia* and *Lepidocephalichthys balgara*) and certain scute-covered South American Siluroids (*Callichthys*, *Doras*, *Loricaria*, *Hypostomus*, *Otocinclus*) swallow air into the intestine, and develop a reservoir for this air by a dilation of the intestine immediately behind the stomach. This is also the case with a Symbranchoid fish, *Monopterus javanensis*. The air from this reservoir in one species was analysed and found to contain 15·73 per cent. of oxygen and 3·04 per cent. of CO_2, so that the atmospheric air had given up 5 per cent. of its oxygen and taken up 3 per cent of CO_2 (CALUGAREAUNU,* 1907).

It is most interesting to speculate on the circumstances which have led to the air being stored in one position rather than in another. We can easily see that in *Amphipnous*, where the gill-slits are of small vertical extent and almost ventral in position, the swallowed air would naturally create bulgings in the roof of the mouth. In *Anabas*, *Macropodus*, *Clarias* and *Saccobranchus* it would appear that wide gill-clefts facilitated the escape of air into the opercular cavity, in the upper angle of which it became lodged.

Why the Ophiocephalidæ developed air-pouches by bulges of the pharynx, rather than of the opercular cavity, is not so clear. One may perhaps hazard the surmise that since in the case of *Anabas*, *Clarias* and *Saccobranchus*, the young fry living in clean water are pure water-breathers, and the air-breathing habit is only developed as the growing fish begins to make excursions out of the water in pursuit of prey, or in search for new ponds; whereas in Ophiocephalids, which are bred in foul water, the young snap air from the beginning, and absorb oxygen from the lining of the buccal cavity long before special pouches of this cavity in the form of air-chambers are developed, therefore this air would naturally become lodged in pouches of the pharyngeal wall.

Whatever may have been the exact circumstances which led to the intensification of the habit, it is important to notice that it has now become an absolute necessity for the life of these fish. As we have seen, even when they are kept in water saturated with oxygen they die if deprived of access to the air. Few sights are more impressive than to watch an *Anabas* under these conditions resting at the bottom of a vessel, working its branchial apparatus vigorously and opening its opercular cavities widely, and yet unable to avoid death by asphyxiation. On the other hand, they can survive in water deprived of the last traces of its dissolved oxygen for at least 6 hours if allowed access to the air; and, most wonderful of all, *Amphipnous* in its adult condition has become a pure air-breather, for in such water it exhibited no discomfort and was in perfect health 3 days after. If, as RIGNANO in his 'Biological Memory' states, "Habit is second nature,"—"nature" is only a name for first habit.

The gap which separates aquatic from land vertebrates is a two-fold one. The land vertebrates breathe air and have pentadactyl limbs, whereas aquatic vertebrates have branchial respiration and paired fins. We have now seen that many species in comparatively recent times have learned to breathe air, and we have followed in detail the

* *Cf.* WINTERSTEIN'S 'Handbuch der Vergleich. Physiol.,' vol. 1, hft. 2, Jena, 1921.

means by which this change is achieved. It is easy to see that in Devonian times similar circumstances, such as life in marshes and shallow rivers liable to desiccation must have led to similar results. The air-reservoirs developed by Devonian fish have survived to the present day in the air-bladders of modern fish. In the most archaic types of these which survive to the present day the air-bladder still retains its respiratory functions. This is the case not only in Dipnoi (studied in detail by GRAHAM KERR and SEMON), but also in *Lepidosteus* and *Polypterus*. The capacity of this last-named fish to live out of water and its dependence on access to the air have been described by BUDGETT. In nearly all other modern fish the air-bladder* has become a purely hydrostatic organ, and it is most instructive to notice that even in fishes such as the Siluroids, in which the bladder retains its connection with the pharynx, when a renewed demand for an air-reservoir arises, it is never possible to utilise the bladder, and an entirely new structure is developed.

According to Prof. MACBRIDE, the embryonic origin of the air-bladder in the Dipnoi, and of its homologue the lungs in Amphibia, shows that it was originally paired, and represented the last pair of gill-slits. As in these archaic fish the gills were formed on the walls of deep pharyngeal sacs, this is comprehensible. One can picture the Devonian fish rising to the surface to snap air and diving down again, and the swallowed bubble passing back till it was caught in this last pair of sacs, the outer openings of which were small. The gap between fish and land vertebrates which has not been bridged lies in the structure of the fin. It is instructive then to see how the structure of the air-bladder of the Dipnoan fish, *Ceratodus*, and of the primitive lung of the anurous Amphibian is mimicked by the *opercular* " lung " of *Saccobranchus* and the *pharyngeal* " lung " of *Ophiocephalus* and *Amphipnous*. The reaction to a similar environment has produced in all cases similar structural " variations." After all, as the late Dr. BATESON stated at the Linnean Society in 1923, there are ultimately only two possible causes for " variation," either (1) chance, or (2) reaction to environmental changes, and the study of the Indian air-breathing fish leads unequivocally to a decision in favour of environmental change.

* The primitive air-bladder in these Siluroid fishes, *Clarias* and *Saccobranchus*, is very much reduced and degenerate in character. The lateral portions of the air-bladder in these fishes come to lie almost immediately beneath the skin, quite adjacent to the base of the pectoral fin. The pectoral spine in the case of *Saccobranchus*, when the fish is disturbed or agitated, is rubbed against the rough surface presented by the coracoid of the pectoral girdle, and thus produces a sound which is apparently amplified into a sharp squeak (so clearly heard during the experiment) by the neighbouring air-bladder, which evidently acts more or less like a resonator rather than as a hydrostatic organ.

Furthermore, the close association of the air-bladder in all Siluroid fishes with the otic capsule and the skin might suggest that probably it also acts as a transmitter of sound vibrations, and thus functions as an accessory hearing organ rather than being hydrostatic in these types. It is quite unlikely that such a degenerate air-bladder in fishes having much migratory habits, and occasionally living on land for a considerable time, should have any hydrostatic function. (*Cf.* REGAN's views, 'Ann. Mag. Nat. His.,' Ser. 8, vol. 8, p. 555, 1911.)

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* With a view to avoid encumbering the present list with the names of works in which the secondary air-breathing is only incidentally mentioned, the reader is requested to refer to the complete list up to 1921 given in HANS WINTERSTEIN'S 'Handbuch der Vergleichenden Physiologie,' vol. 1, hft. 2, Jena, 1921.

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LIST OF ABBREVIATIONS USED.

AC. = Air-chamber. ACD. = Postero-dorsal compartment of the air-chamber. ACL. = Ventro-lateral extension of the vascular wall of air-chamber. ACV. = Antero-ventral compartment of air-chamber. AC. vas = Vascular epithelial lining of air-chamber. ACW. = Posterior thin vascular wall of air-chamber. Aen. = Air-entrance. Aex. = Air-exit. Alv. = Alveolus. Ant. end = Anterior end. Ant. t = Anterior air-tree. AT. = Ventral narrow part of the air-chamber which temporarily remains non-vascular.

Bbr. = Basibranchial. Bhy. = Basihyal. Blg. = So-called blood-gland. B. occ. = Basi-occipital. Br. a. = Normal gill. Br. A. = Branchial arch. Br A_{1-3} = Serial order of branchial arches. Br. af. = Afferent branchial vessel. Br. chond. = Branchial cartilage. Br. ef. = Efferent branchial vessel. Br. fil. = Branchial filaments. Br. pl. = Branchial plate. Br. sl. = Branchial slit. Br. sl_1 = First branchial slit. Br. V. = Main branchial vessel. Bucc. = Buccal cavity. Bucc. fl. = Floor of buccal cavity. Bucc. tect. = Roof of buccal cavity. BV. = Blood vessel.

Cbr. = Ceratobranchial. Cent. = Centrum. Chond. = Cartilage. Chond. ax. = Main cartilaginous axis. Chy. = Ceratohyal. Cœl. = Cœlom. Conn. = Connective tissue. Conn. elas. = Elastic tissue fibres. Conn. rad. = Radiating fibres of connective tissue. Conn. ret. = Connective tissue reticulum. Cop. = Cartilaginous junction. Cr. = Cranium. Cr. bas. = Basis cranii.

d. ao. = Dorsal aorta. Dent. = Teeth. Dent. inf. ph. = Inferior pharyngeal teeth. Dent. s. ph. = Superior pharyngeal teeth. D. lymph. = Lymph space. d. pul. = Disc-shaped highly vascular outgrowths. ds. = Dorsal side. duct. pn. = Ductus pneumaticus.

Ep. = Epithelial cells. Ep. ap. = Epibranchial outgrowth over the first gill-arch. Ep. br. = Epibranchial. Ep. l. = Epithelial layer. Ep. sf. = Epibranchial shelf. Ep. sq. = Squamous epithelium. Ep. vasc. = Vascular epithelium.

F. = "Fan." F_{1-4} = Serial order of "fans." Fr. = Furrow.

Gang. = Nerve ganglion. Gang. aud. = Auditory ganglion. Gl. = Gland cells.

Hep. = Liver. Hm. = Hyomandibular. Hm. ap. = Hyomandibular process. Ht. = Heart. Hybr. cl. = Hyobranchial cleft. Hyp. br. = Hypobranchial.

Int. = Intestine.

Lab. = Labyrinthine organ. Lab. pl. = Labyrinthiform plate. Lab. pl_{1-3} = Serial order of labyrinthiform plates. Lac. = Lacunar cavity. Lam. pul. = Highly vascular air-breathing laminæ. Lu. = Lumen. Lym. c. = Lymph corpuscles. Lym. cav. = Lymph cavity.

Meck. = Lower jaw elements. Mesonph. = Kidney. Met. enc. = Hind brain. Muc. = Mucous cell. Musc. = Muscle. Musc. str. = Striated muscle. Musc. uns. = Smooth muscle.

N. = Nerve. Nc. = Nerve cord. Nch. = Notochord. Ntch. = Notch for entrance of air into air-chamber. nu. = Nucleus.

O. = Aperture of the air-chamber. Occ. = Occipital bones. Œs. = Œsophagus. Op. = Operculum. Op. b. = Opercular bone. Op. cav. = Opercular cavity. Oss. = Ossification around the cartilages. Ot. = Ear. Ot. cap. = Otic capsule. Otl. = Otolith. Ov. = Ovary.

Part. = Vertical tendinous partition. PCV. = Posterior cardinal vein. Pect. = Pectoral arch. Peri. = Pericardium. Pgc. = Pigment cell. Ph. = Pharynx. Post. ax. = Post axial. Post. t. = Posterior air-tree. Pr. ax. = Preaxial. Pronph. = Head-kidney. Psph. = Parasphenoid.

Rect. = Rectum.

SB. = Swim-bladder. St. = Stomach. Sub. ling. f. = Sub-lingual fold of mouth cavity. Sub. op. b. = Sub-opercular bone. Styl. pr. = Styliform process.

Tell. N. = Tellerförmiges Nebenorgan. Trab. = Vascular trabeculæ.

V. ao. = Ventral aorta. Vasc. cap. = Vascular capillary. Vasc. cl. = Club-shaped vascular process. Vasc. ep. f. = Vascular epithelial folds. Vasc. pap. = Vascular papillæ. Vert. = Vertebra.

EXPLANATION OF PLATES 3–11.

All the outlines of figures represented in these plates, unless otherwise stated, have been drawn with the aid of the camera lucida.

Plate 3.

Fig. 1.—Lateral dissection of a young *Clarias magur*, 2·5 cm. in length, to show the beginning of the first (posterior) air-tree. Magnif. $5\frac{1}{2}$ diam.

Fig. 2.—Lateral dissection of a young *Clarias magur*, 2·6 cm. in length, to show trilobed condition of the posterior air-tree. Magnif. $5\frac{1}{2}$ diam.

Fig. 3.—Lateral dissection of a young *Clarias magur*, 3 cm. in length; early stages in the development of both anterior and posterior air-trees. Magnif. 4 diam.

Fig. 4.—Dorsal dissection of left air-chamber of adult *Clarias magur*, to show relative positions and branchings of two air-trees, the "fans" guarding the openings into air-chamber, and capillary network on wall of chamber. Magnif. 2 diam.

Fig. 5.—Transverse section through hinder region of head of young *Clarias magur*, 2 cm. in length, to show first rudiment of air-chamber. Magnif. 45 diam.

Fig. 6.—Transverse section through hinder region of head of young *Clarias magur*, 2·2 cm. in length, to show semicircular stage in the development of air-chamber. Magnif. 45 diam.

Plate 4.

Fig. 7.—Hand section through hinder region of head of adult *Clarias magur*, in order to show breathing mechanism. Section is viewed from posterior aspect. Magnif. 2 diam.

Fig. 8.—Transverse section through hinder region of head of young *Saccobranchus fossilis*, 2·1 cm. in length, to show rudiment of air-chamber. Magnif. 24 diam.

Fig. 9.—Transverse section through slightly older specimen of *Saccobranchus* to show tubular character of air-chamber. Magnif. 24 diam.

Fig. 10.—Parasagittal section through head of young *Saccobranchus fossilis*, 2·3 cm. in length, to show development of air-chamber. Magnif. 24 diam.

Fig. 11.—Hand section through hinder region of head of adult *Saccobranchus fossilis*, to show disposition of air-chamber, and position of single aperture (*o*) for both inspiration and expiration. The section is viewed from posterior aspect. Magnif. 4 diam.

Fig. 12.—Hand section through hinder region of trunk of adult *Saccobranchus fossilis*, to show disposition of air-chambers. Magnif. 4 diam.

Plate 5.

Fig. 13.—Transverse section of small portion of so-called blood-gland lying at posterior end of developing air-chamber of *Saccobranchus*. Series T, row 2, sec. 15. Magnif. 1400 diam.

Fig. 14.—Sagittal section of posterior end of air-chamber of adult *Saccobranchus*, showing alveoli, trabeculæ and air-breathing laminæ. Series N, row 1, sec. 3. Magnif. 60 diam.

Fig. 15.—Transverse section of small portion of wall of air-chamber of young *Saccobranchus*. Series R, row 2, sec. 15. Magnif. 1400 diam.

Fig. 16.—Same as fig. 15 above, of *Clarias magur*, showing disc-shaped vascular outgrowths and papillæ. Series B, row 3, sec. 5. Magnif. 780 diam.

Fig. 17.—*a*, Cross-section of basal part of developing posterior air-tree of *Clarias*. Magnif. 66 diam. *b*, Frontal section of advanced condition of posterior air-tree of *Clarias*. Magnif. 36 diam.

Fig. 18.—Transverse section through trilobed condition of posterior air-tree of young *Clarias*. Magnif. 81 diam.

PLATE 6.

FIG. 19.—Frontal section of distal end of the finger-like anterior air-tree of young *Clarias magur*, 2·8 cm. in length. Series N, row 4, sec. 17. Magnif. 360 diam.

FIG. 20.—Transverse section of small part of advanced stage of posterior air-tree of *Clarias magur*, 3·5 cm. in length. Series J, 5 post, row 4, sec. 4. Magnif. 780 diam.

FIG. 21.—Cross-section through small portion of air-tree of adult *Clarias magur*, showing cut ends of air-breathing lobes. Slide Series H. Magnif. 30 diam.

FIG. 22.—Sagittal section of the Tellerförmiges Nebenorgan of a young *Anabas scandens*, the third (or lowest) lobe not being represented. Series G, row 3, sec. 5. Magnif. 310 diam.

FIG. 23.—Transverse section of small portion of inner wall of air-chamber of young *Anabas*. Series M, row 3, sec. 5. Magnif. 1400 diam.

PLATE 7.

N.B.—The arrows in the following figures indicate mode of entrance and exit of air.

FIG. 24.—Transverse section through hinder region of head of post-larval stage of *Anabas scandens*, about 10 mm. in length, showing extent of development of air-chamber, *A.C.* Series G, row 3, sec. 5. Magnif. 30 diam.

FIG. 25.—Same as fig. 24 above of *Anabas*, 14 mm. in length, showing further development of air-chamber. Series H, row 1, sec. 5. Magnif. 23 diam.

FIG. 26.—Same as fig. 24 above of *Anabas*, 22 mm. in length, showing stage of development of air-chamber, as well as the labyrinthine organ, *Lab. pl.* Series J, row 2, sec. 7. Magnif. 23 diam.

FIG. 27.—Vertical section of small portion of first-formed labyrinthiform plate of a young *Anabas*. Series N. row 2, sec. 5. Magnif. 780 diam.

PLATE 8.

N.B.—The arrows indicate as in Plate 7.

FIG. 28.—Lateral aspect of head of adult *Anabas scandens*, with the operculum lifted outwards and the branchial apparatus as a whole pulled upwards showing the position of air-exit, *Aex.* Modified after HENNINGER. Magnif. 2½ diam.

FIG. 29.—End-on view of the left labyrinthine organ of an adult *Anabas*. Modified after HENNINGER. Magnif. 4 diam.

FIG. 30.—Mouth-cavity of *Anabas* opened up to show air-breathing mechanism. Magnif. 2½ diam.

FIG. 31.—Anterior aspect of a hand section passing through hinder region of head of adult *Anabas*, to show position of labyrinthine apparatus, *Lab.*, inside the air-chamber. Magnif. 2½ diam.

FIG. 32.—Under-surface view of head region of adult *Ophiocephalus punctatus*, with left operculum fully stretched out to show position of exit-hole, *Aex.* Magnif. 1½ diam.

PLATE 9.

FIG. 33.—Transverse section of the anterior region of the pharynx of a young *Ophiocephalus striatus*, 1·6 cm. in length, showing the development of the air-diverticulum. Series B, row 1, sec. 6. Magnif. 47 diam.

FIG. 34.—Same as fig. 33 above of *O. striatus*, 1·8 cm. in length, showing more advanced condition of air-chamber, *A.C.* The arrow shows the mode of entrance of air into the air-chamber. Series D, last row, sec. 16. Magnif. 35 diam.

FIG. 35.—Same as fig. 33 above of *O. striatus*, about 2 cm. in length, showing still more advanced condition of development of air-chamber, *A.C.* Series 3, row 3, sec. 12. Magnif. 45 diam.

FIG. 36.—Transverse section of small portion of inner wall of advanced condition of air-chamber of *O. striatus*. Magnif. 780 diam.

FIG. 37.—Same as fig. 36 above of *O. punctatus*, showing club-shaped vascular processes, *Vasc. cl.*, and lacunæ, *Lac.* Magnif. 780 diam.

PLATE 10.

FIG. 38.—Transverse section of the anterior region of the pharynx of a post-larval stage of *Amphipnous cuchia*, 3·3 cm. in length, showing the development of the air-chamber, *A.C.* Series A, row 3, sec. 15. Magnif. 60 diam.

FIG. 39.—The same as fig. 38 above of *A. cuchia*, showing a further stage of development of the air-chamber. Series B, row 1, sec. 15. Magnif. 60 diam.

N.B.—The arrows in the above two figures show the mode of entrance of air into the air-chamber.

FIG. 40.—The same as fig. 38 above of *A. cuchia*, showing more advanced condition of air-chamber. Arrows indicate direction of entrance and exit of air. Series C, row 1, sec. 9. Magnif. 60 diam.

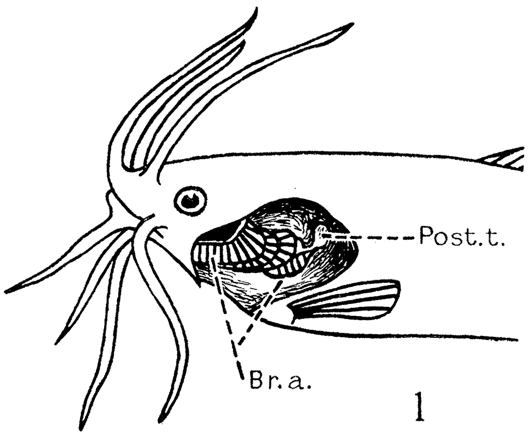
FIG. 41.—Frontal section of the air-chamber ("lung") of an advanced stage of *Amphipnous*, 4·5 cm. in length. Slide 8, sec. 7. Magnif. 38 diam.

FIG. 42.—Part of the wall of the air-chamber of the same as in fig. 41 above, highly magnified. Magnif. 360 diam.

PLATE 11.

FIG. 43.—Small portion of the transverse section of the wall of a young *Macropodus cupanus*, showing glandular pits highly magnified. Magnif. 1400 diam.

FIGS. 44, 45 and 46.—Transverse sections of the 1st, 2nd and 3rd gill-arches respectively of young stages of *Amphipnous cuchia* (6 cm. in length and upwards), showing mode of origin of rudimentary gill-filaments. Magnif. 140 diam.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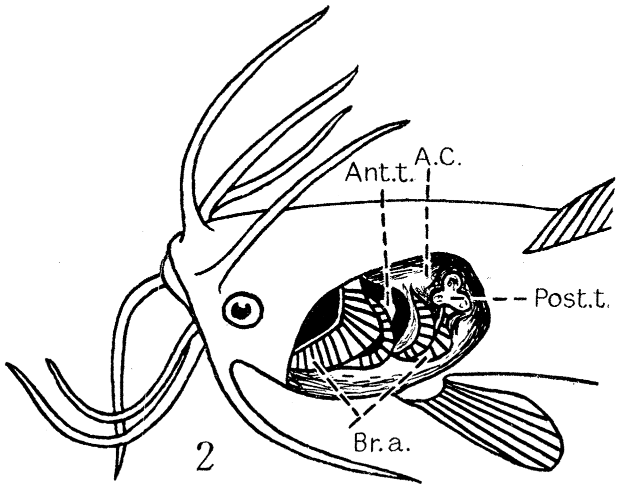
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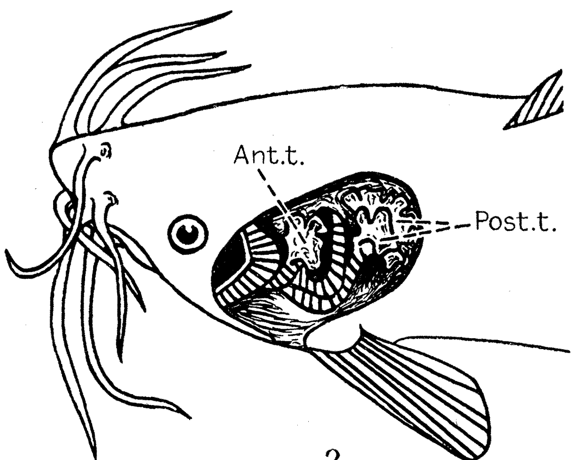
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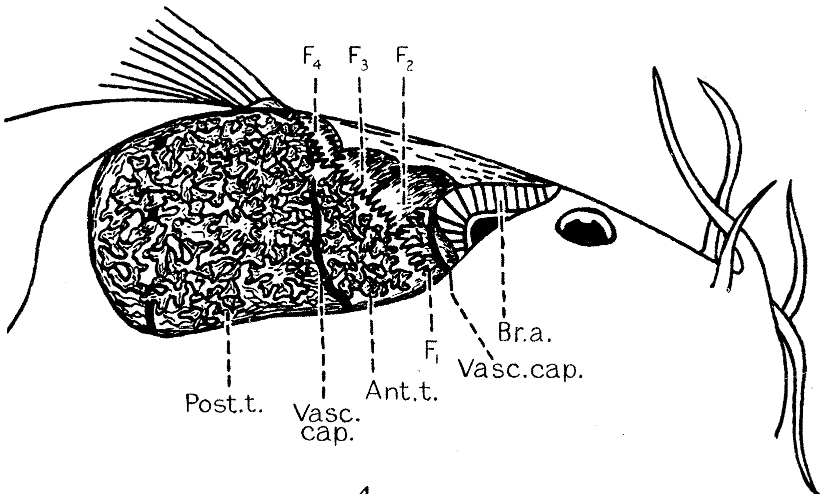
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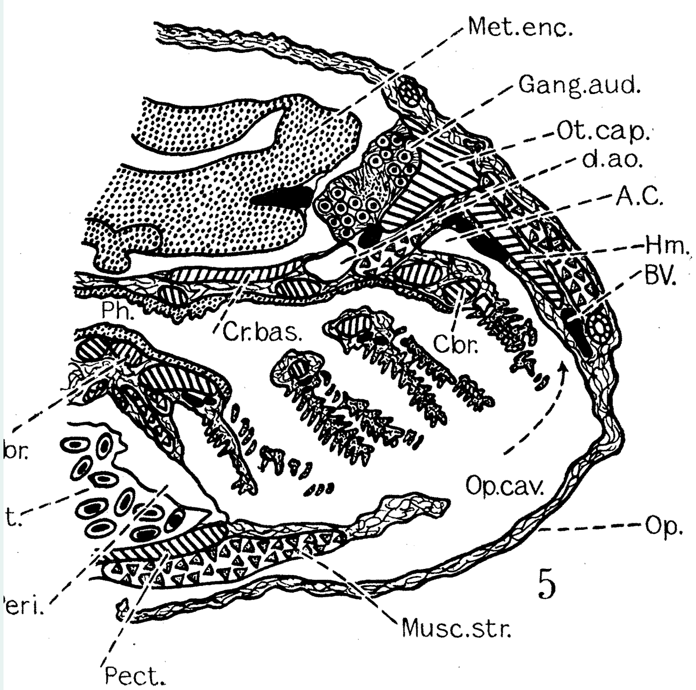
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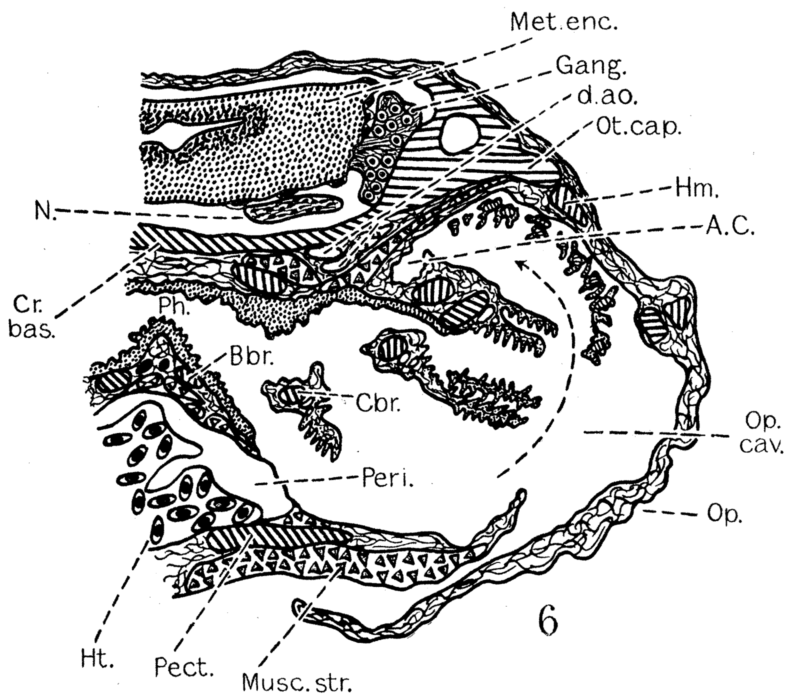
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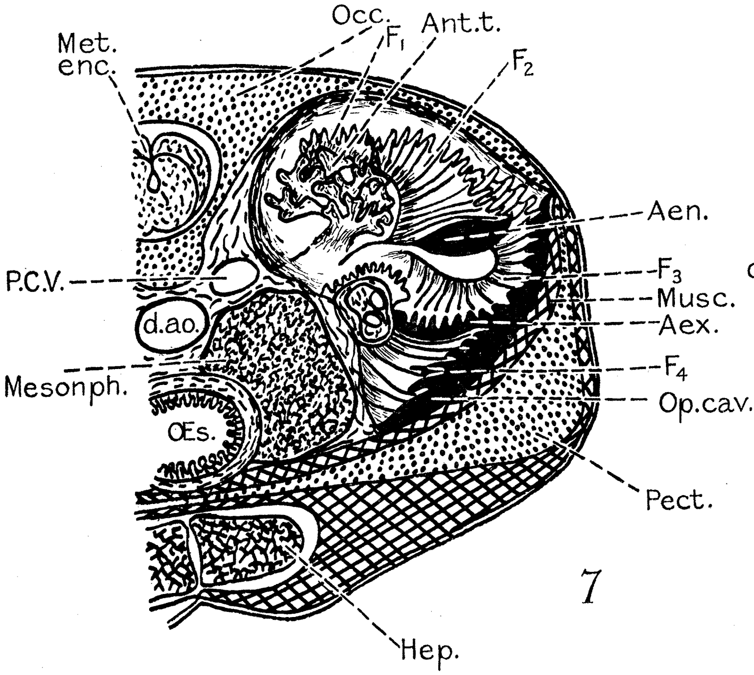
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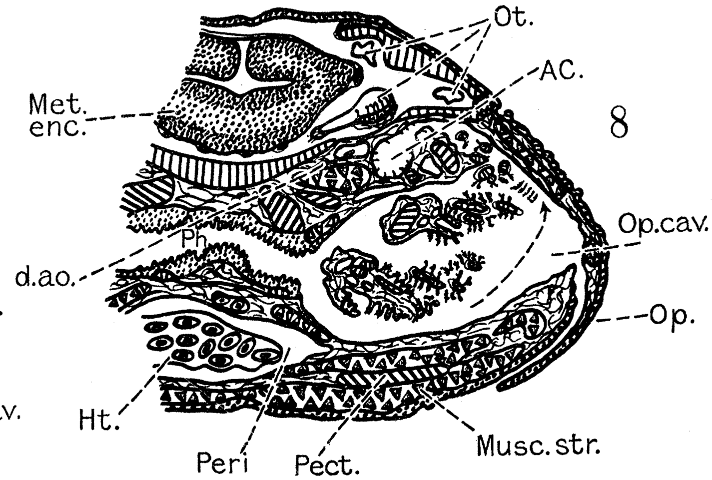
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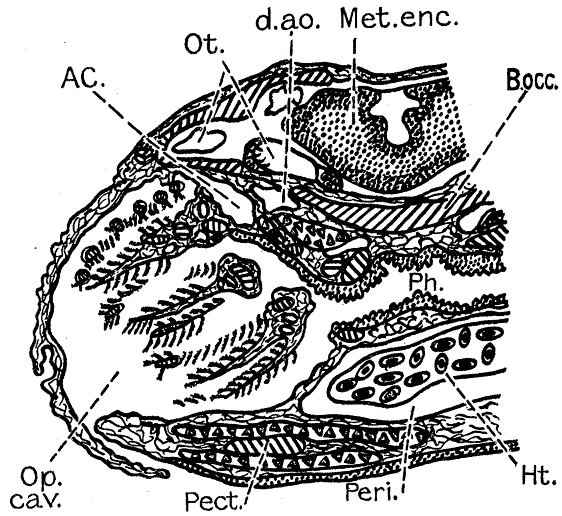
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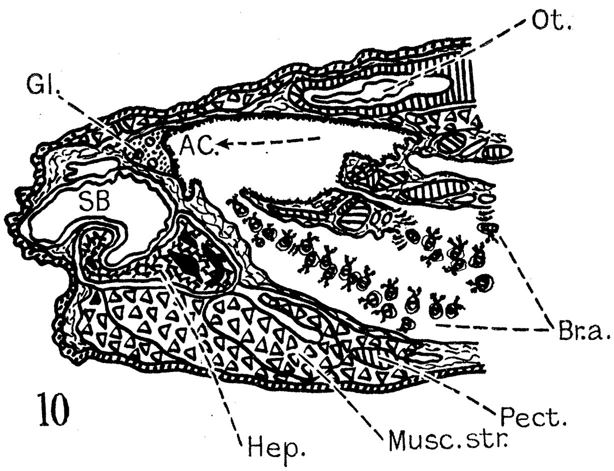
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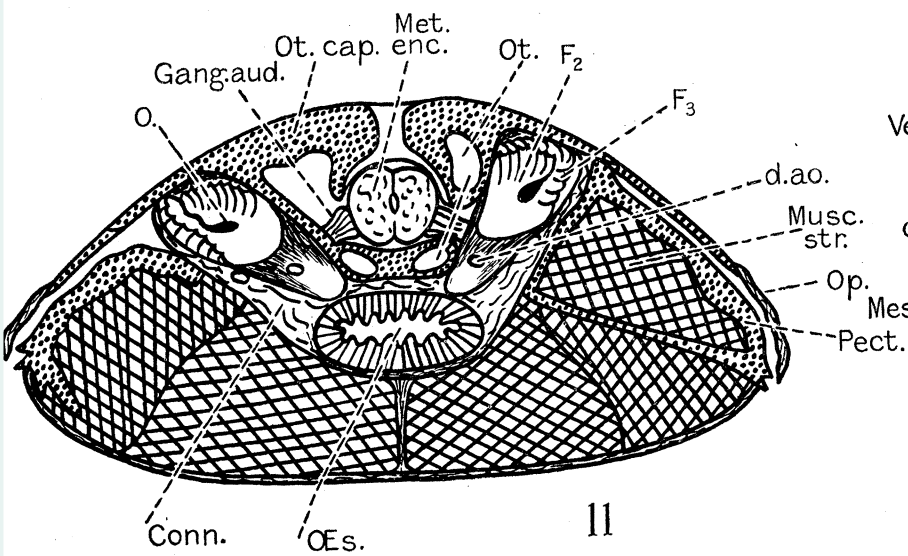
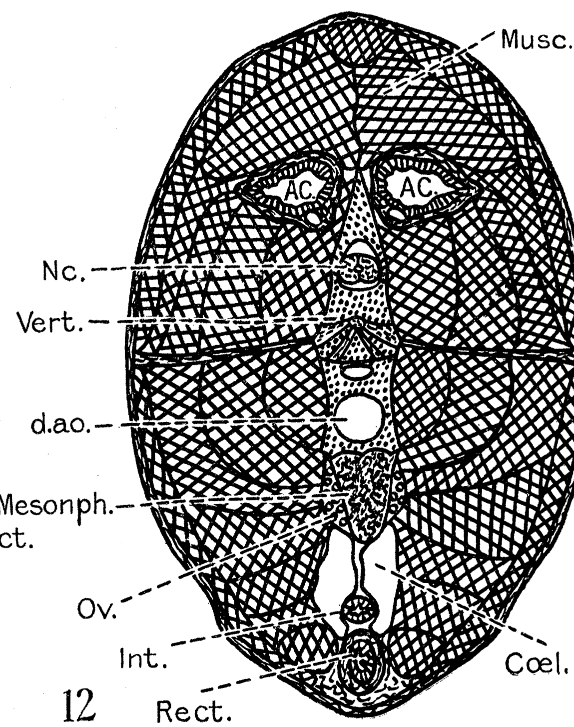
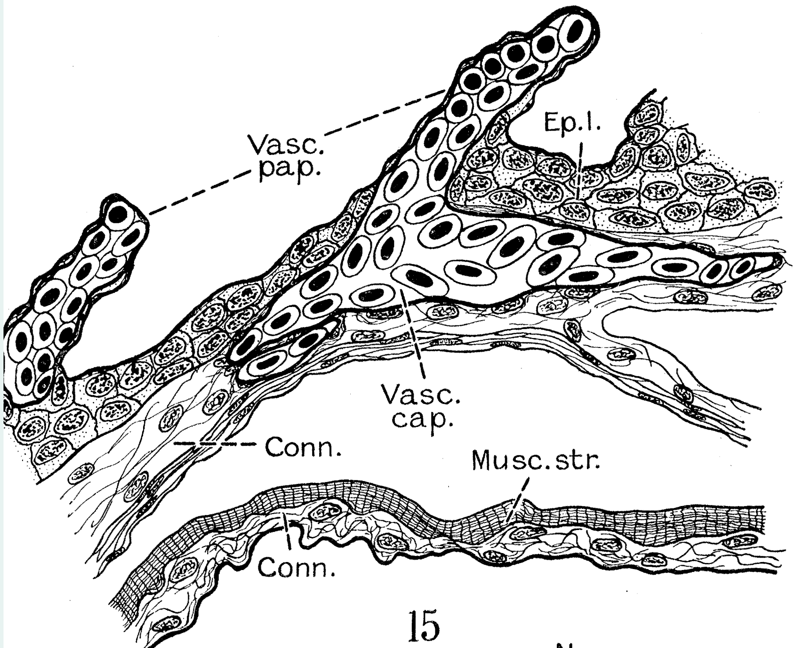

Met.
enc.
Ot. cap.
Ot.
F2
Gang.aud.
F3
O.
d.ao.
Musc.
str.
Op.
Pect.
Conn.
Œs.

11


Musc.
AC.
AC.
Nc.
Vert.
d.ao.
Mesonph.
Ov.
Int.
Cœl.
Rect.

12



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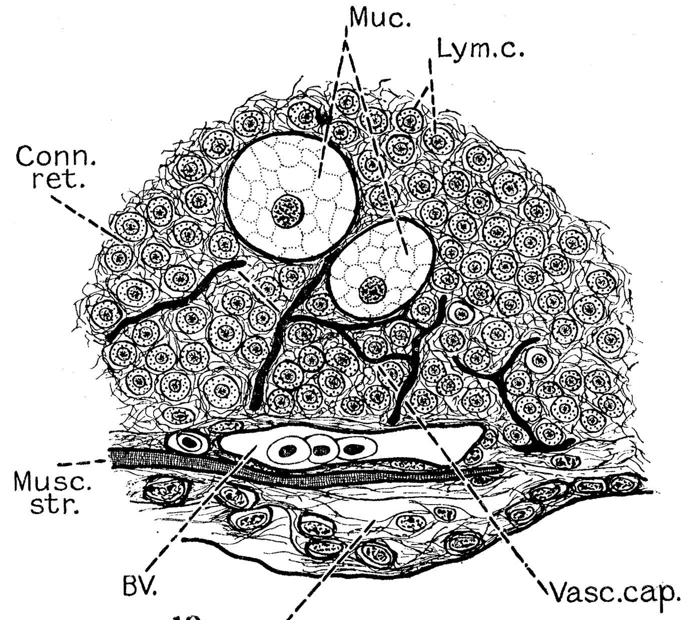

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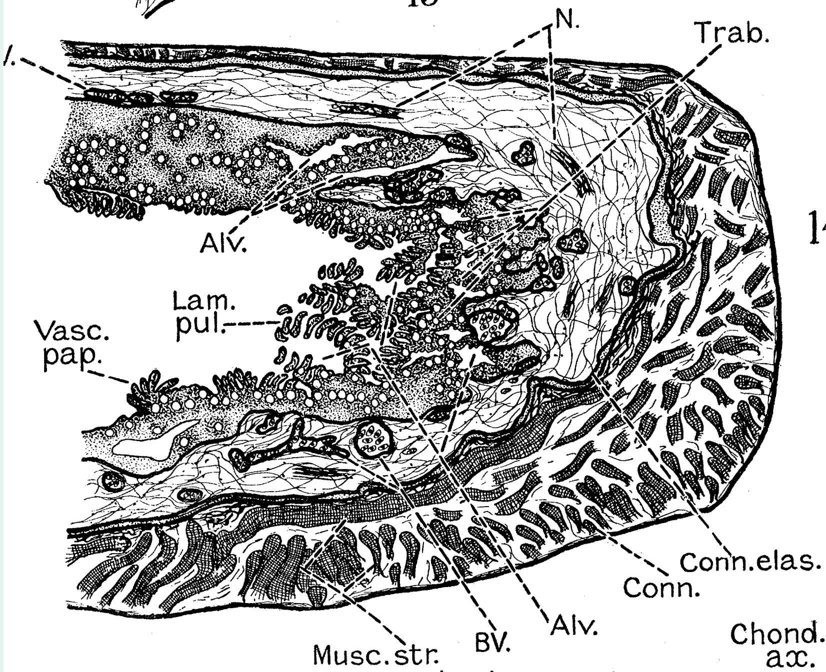
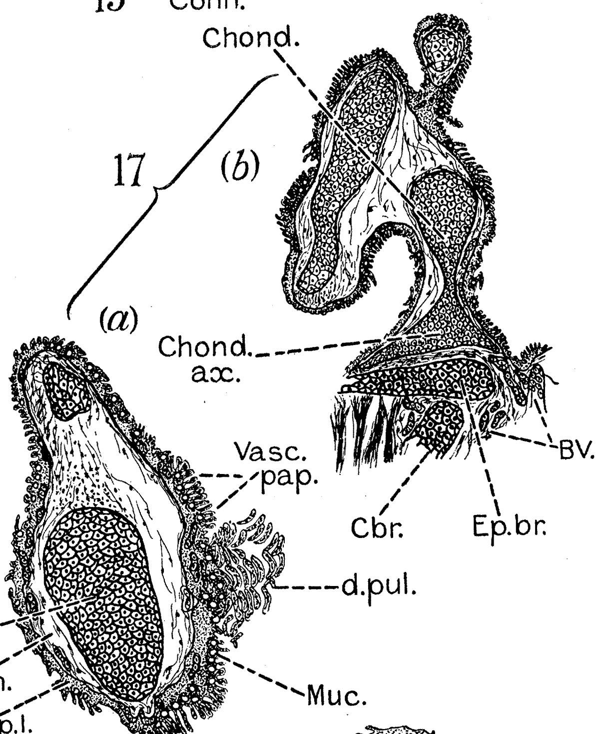
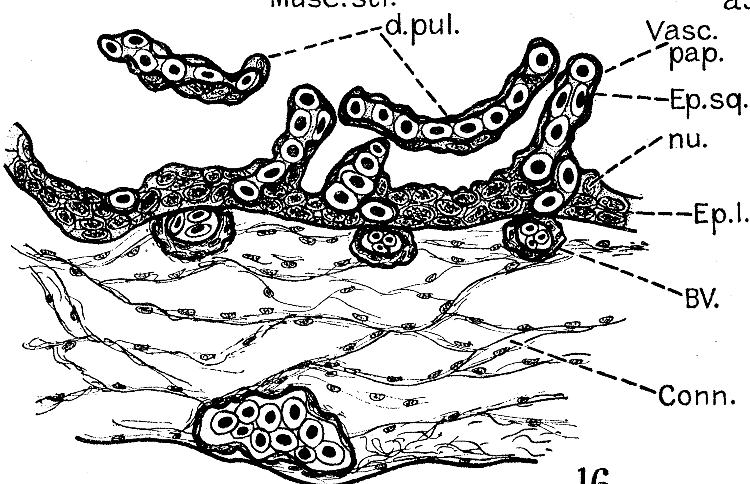


14

17





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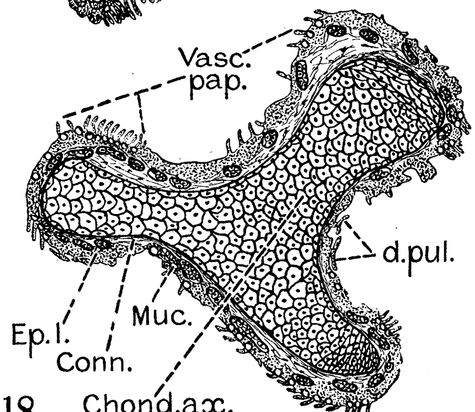

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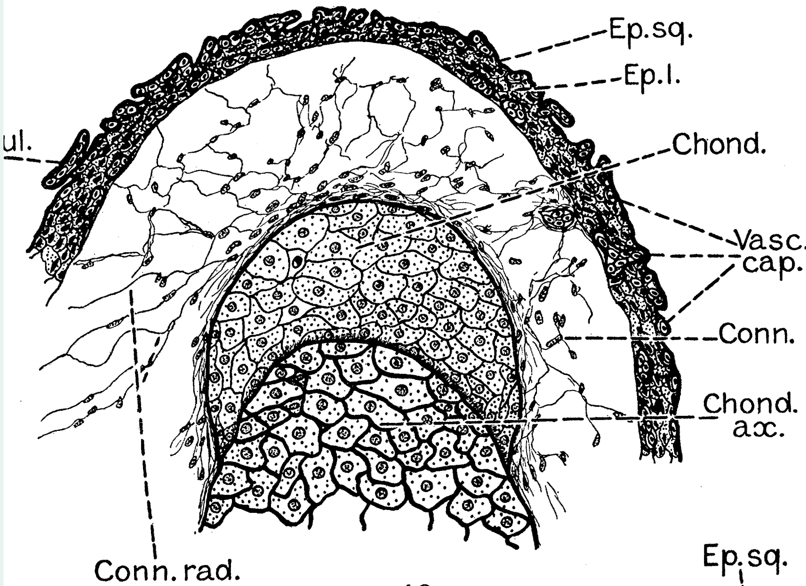
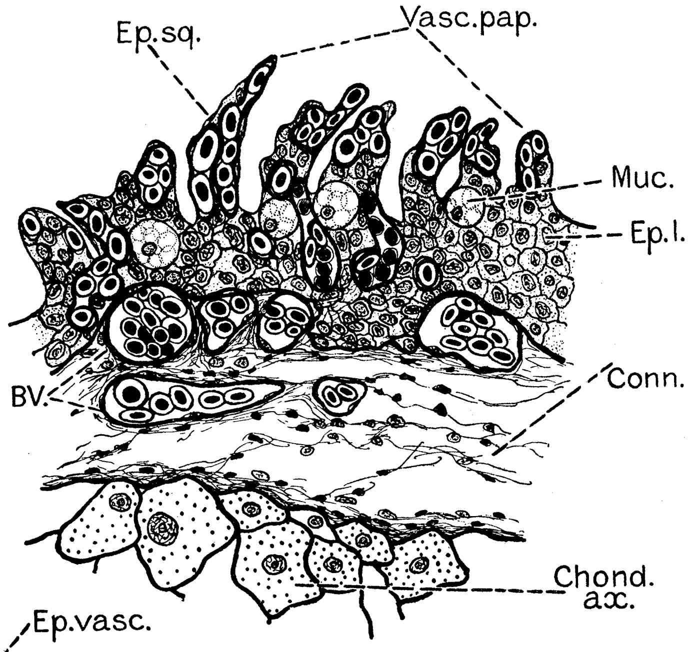
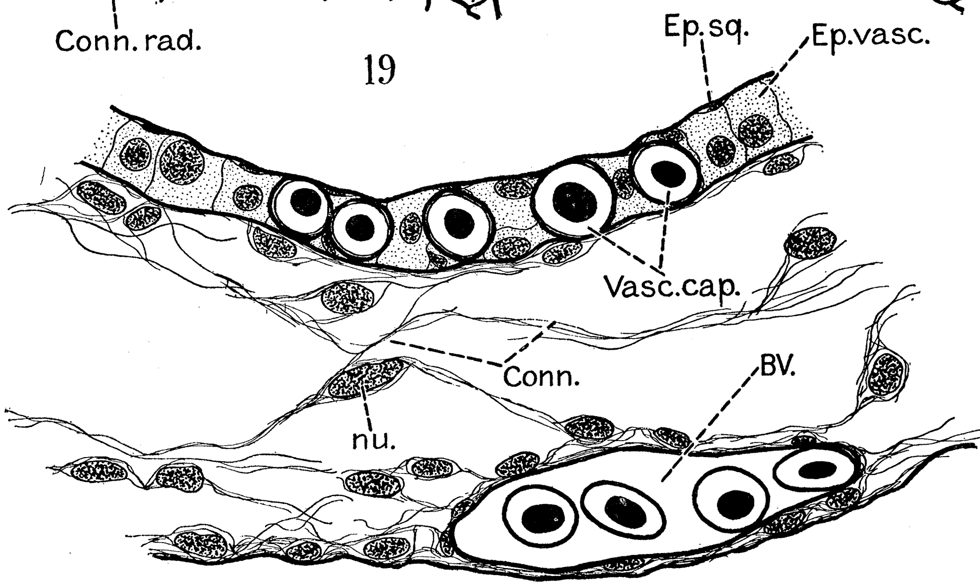

Ep.sq.
Ep.l.
ul.
Chond.
Vasc. cap.
Conn.
Chond. ax.
Conn. rad.

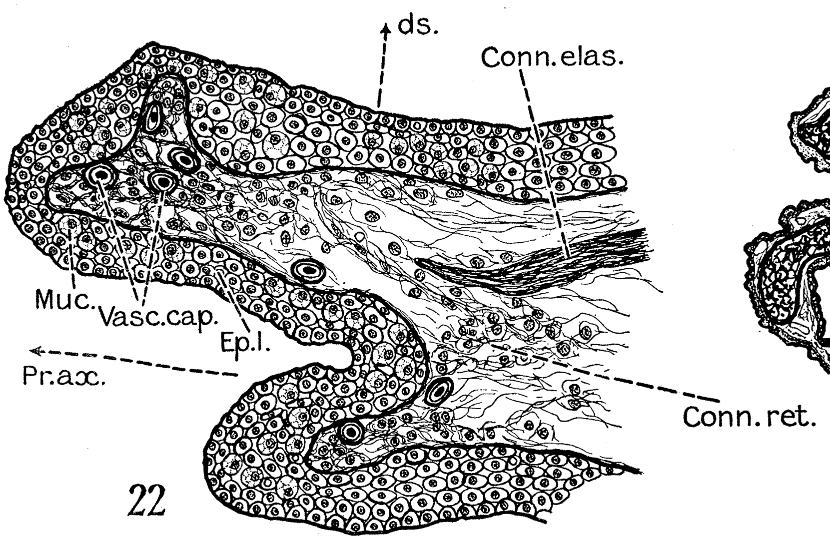
19


Ep.sq.
Vasc.pap.
Muc.
Ep.l.
BV.
Conn.
Chond. ax.

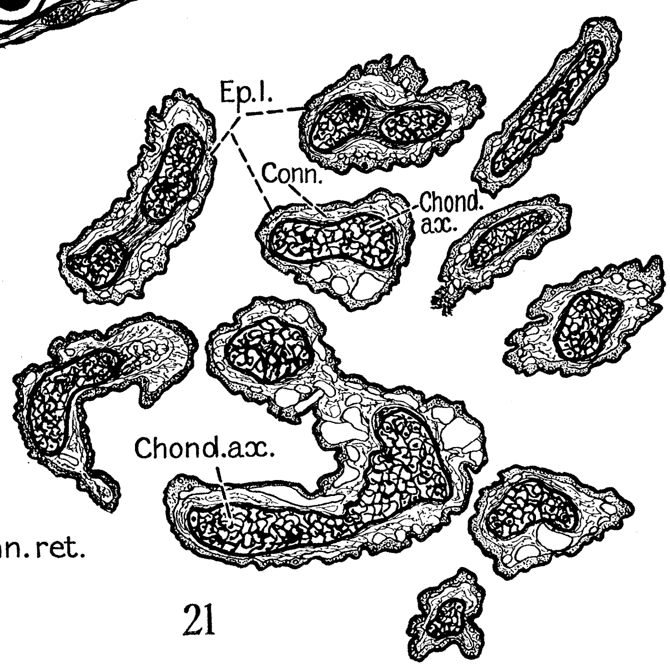
20


Ep.sq.
Ep.vasc.
Vasc.cap.
Conn.
BV.
nu.

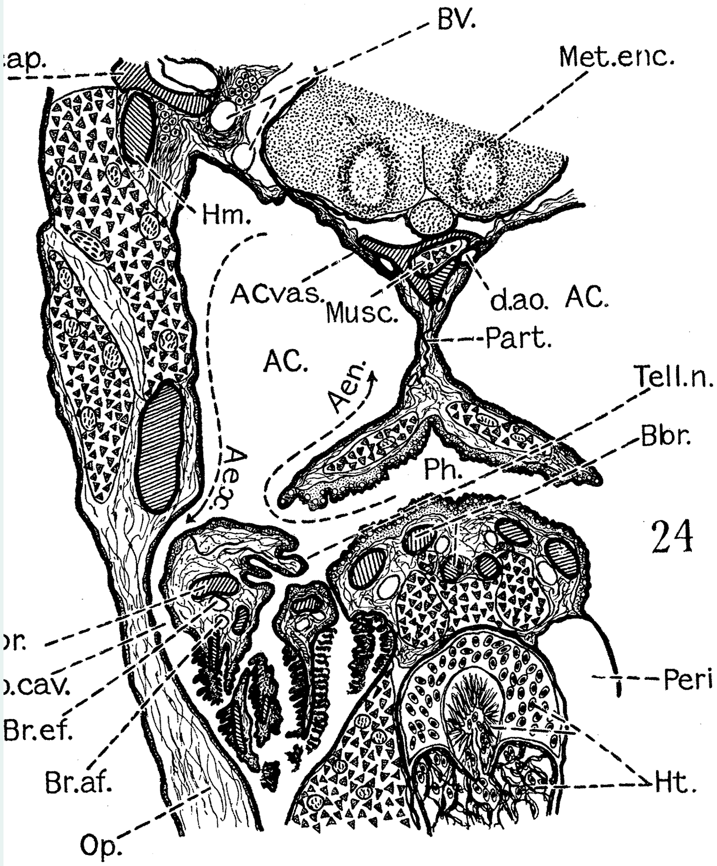
23


ds.
Conn.elas.
Muc.
Vasc.cap.
Ep.l.
Pr.ax.
Conn.ret.

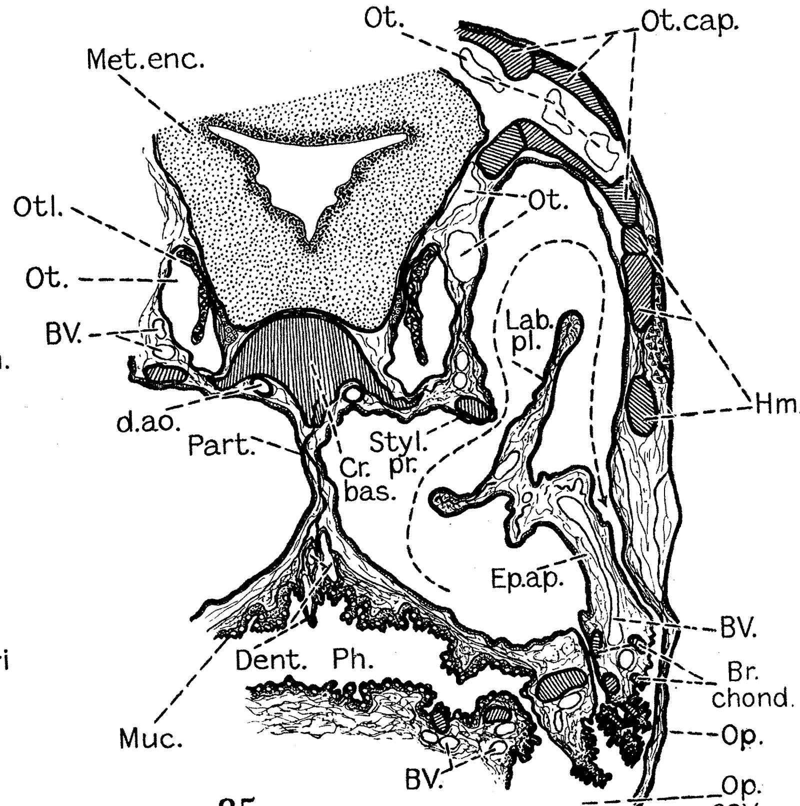
22


Ep.l.
Conn.
Chond. ax.
Chond.ax.

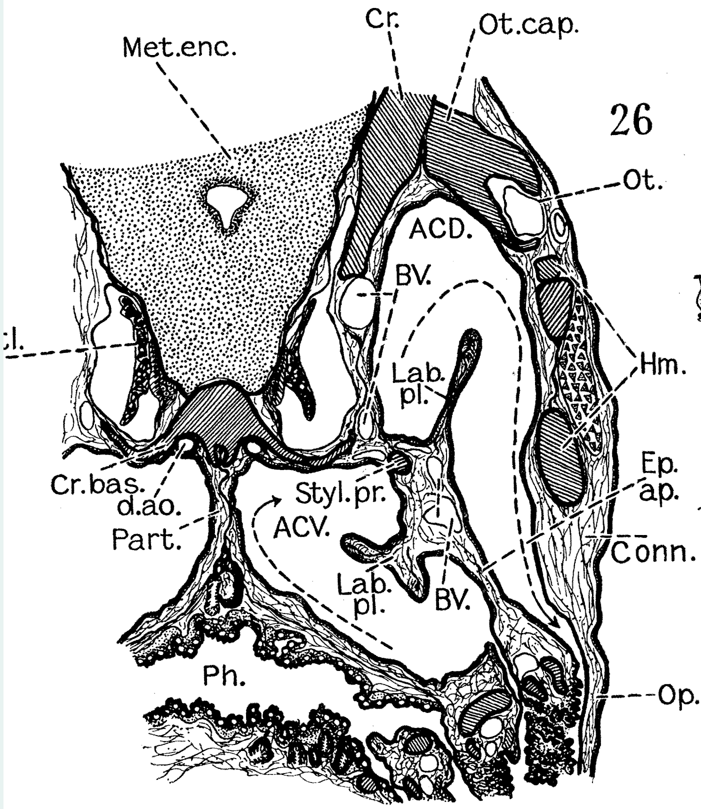
21


BV.
Met.enc.
Hm.
ACvas.
Musc.
d.ao.
AC.
Part.
AC.
Aen.
Tell.n.
Bbr.
Ph.
Aec.
Br.ef.
Br.af.
Op.
Peri
Ht.

24

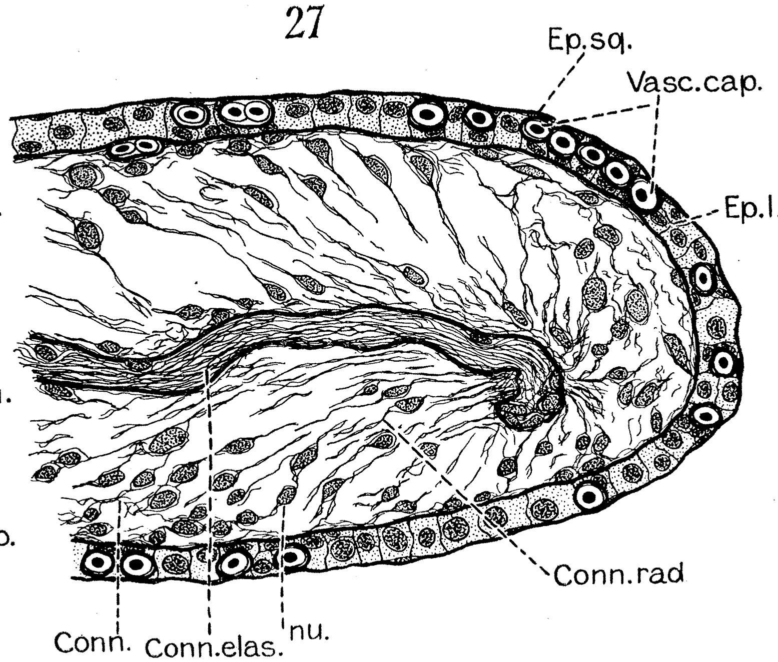

Ot.
Ot.cap.
Met.enc.
Otl.
Ot.
Ot.
BV.
Lab.
pl.
Hm.
d.ao.
Part.
Styl.
pr.
Cr.
bas.
Ep.ap.
BV.
Br.
chond.
Dent.
Ph.
Muc.
Op.
BV.
Op.
cav.

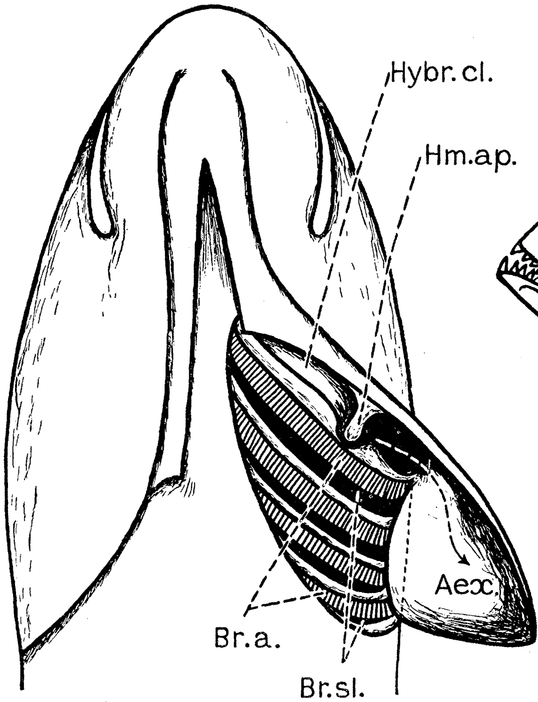
25


Cr.
Ot.cap.
Met.enc.
Ot.
ACD.
BV.
Hm.
Lab.
pl.
Ep.
ap.
Cr.bas.
d.ao.
Styl.pr.
ACV.
Part.
Conn.
Lab.
pl.
BV.
Ph.
Op.

26

27


Ep.sq.
Vasc.cap.
Ep.l.
Conn.rad
Conn.
Conn.elas.
nu.



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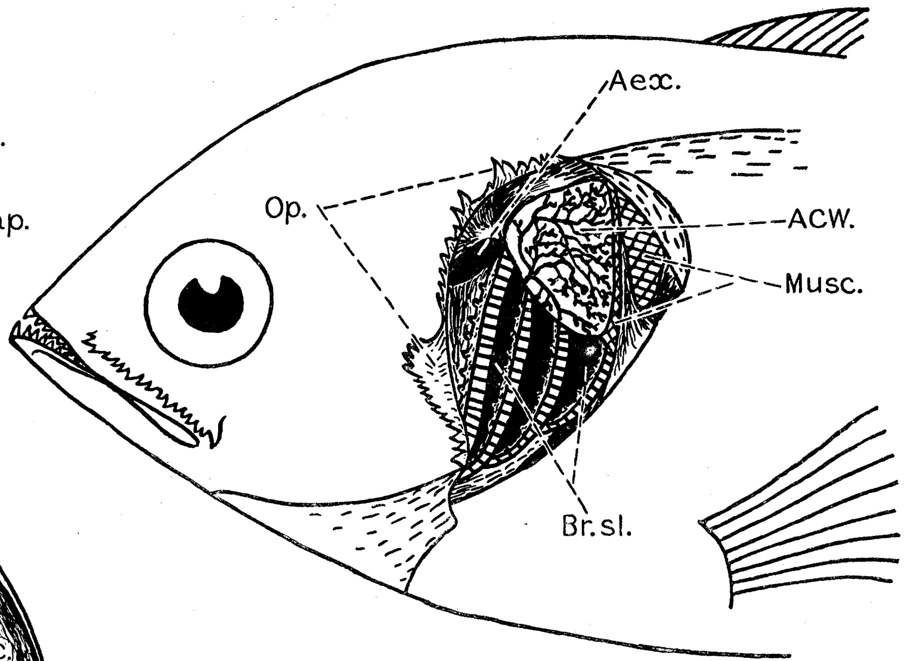

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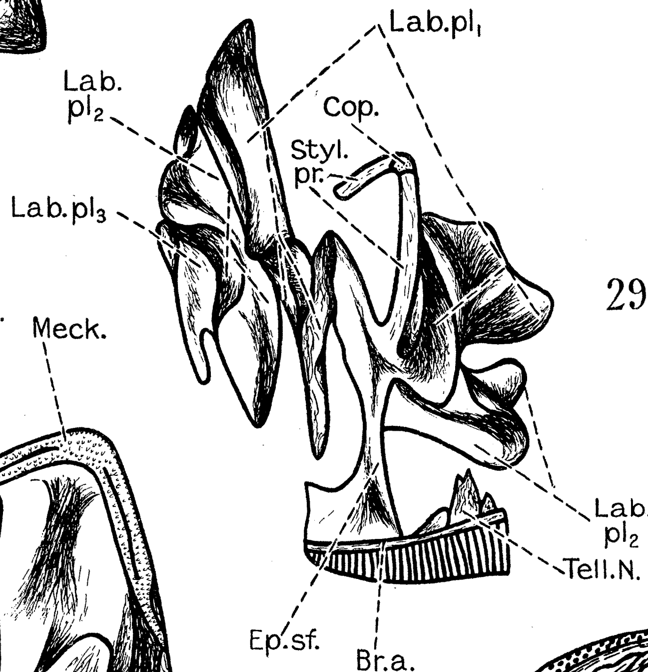

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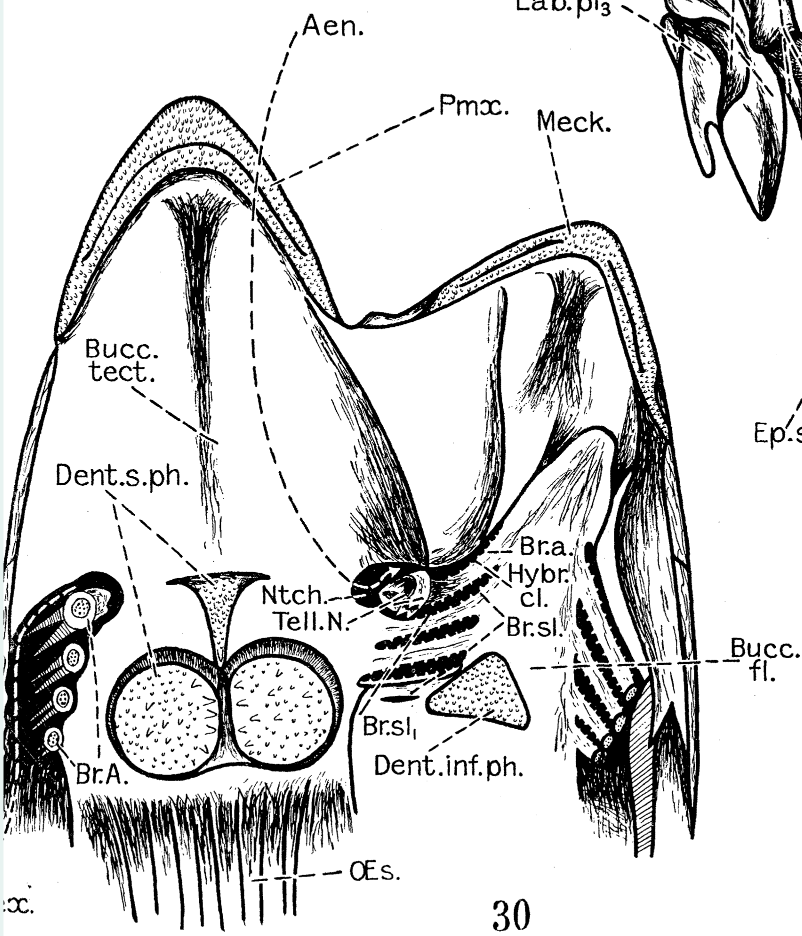

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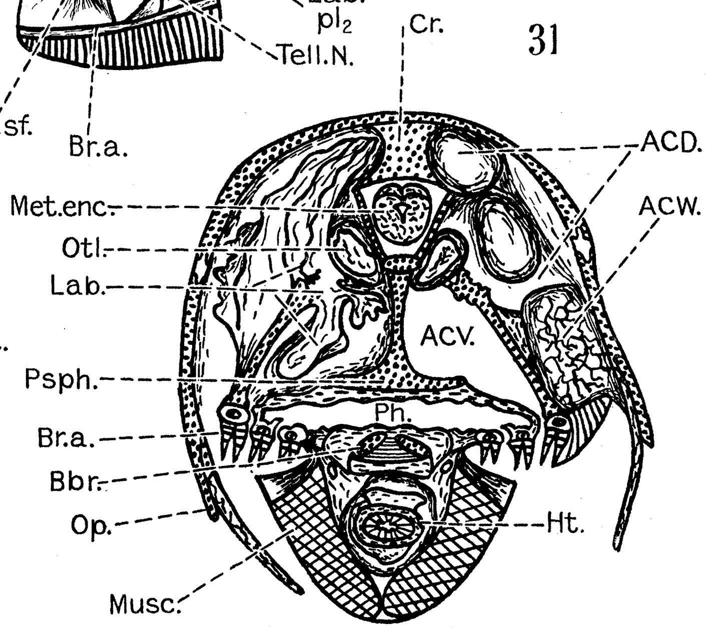
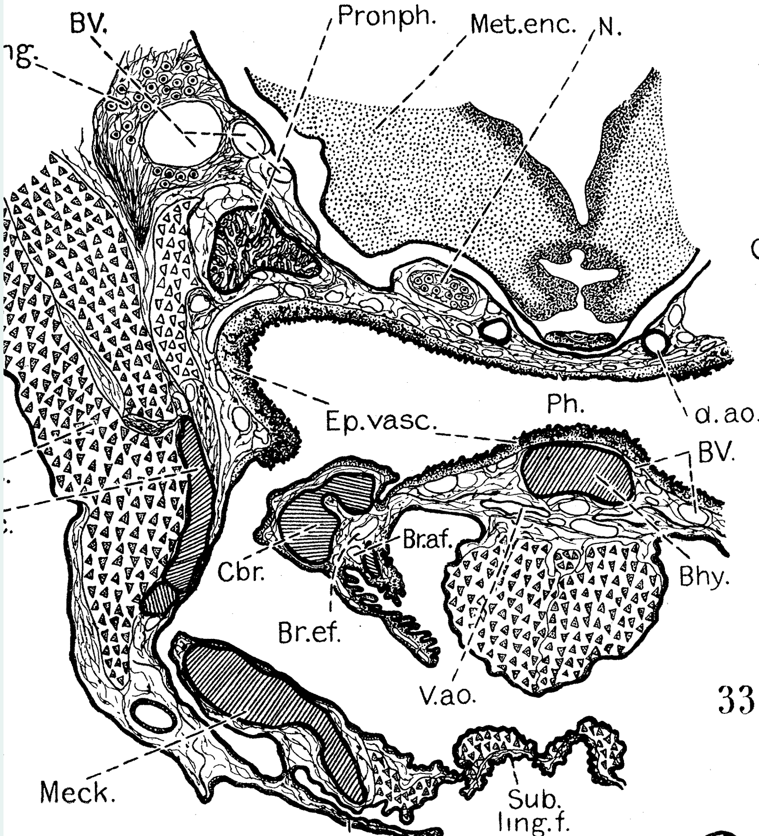
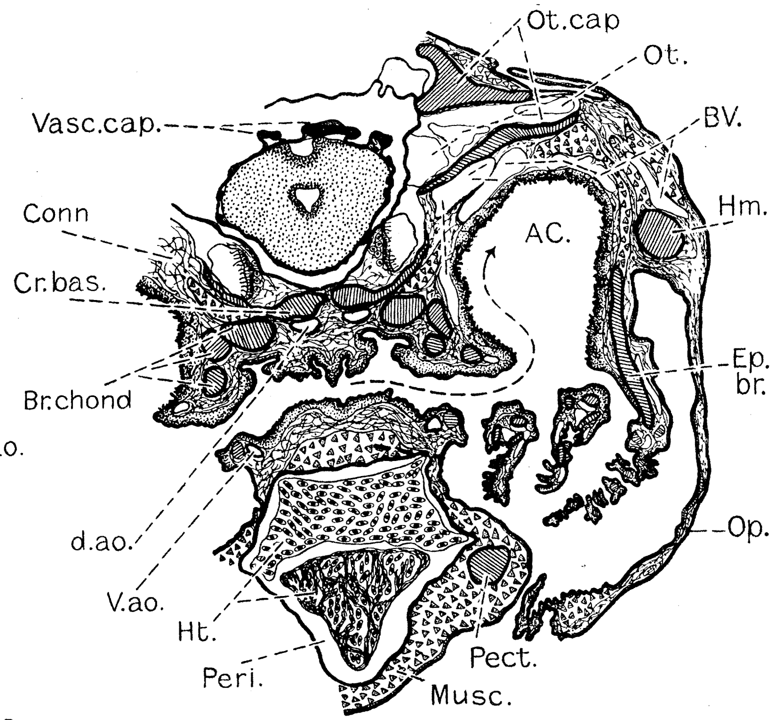


31

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

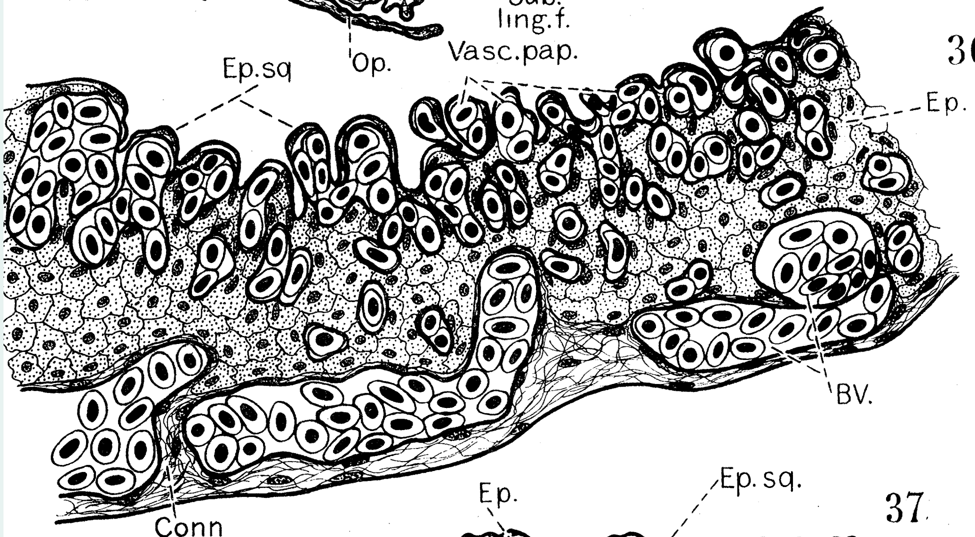


33

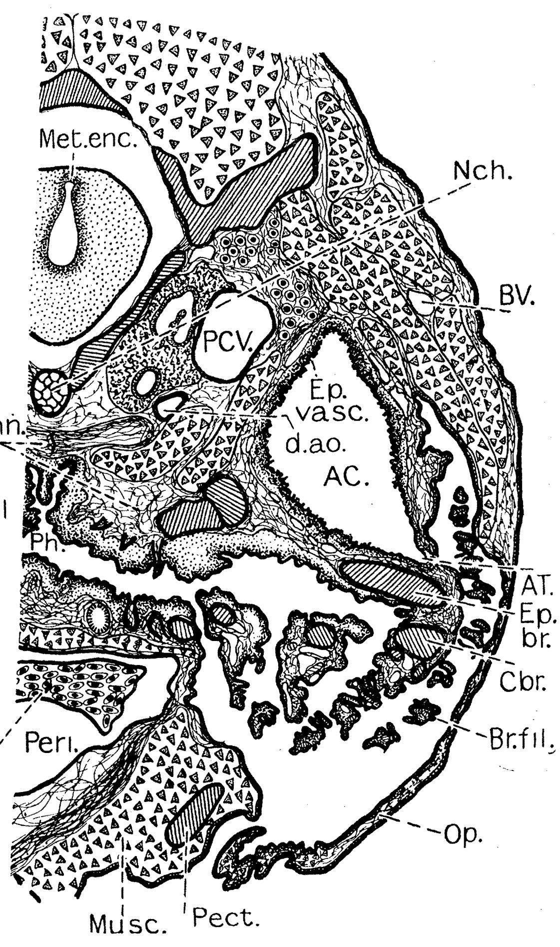


34

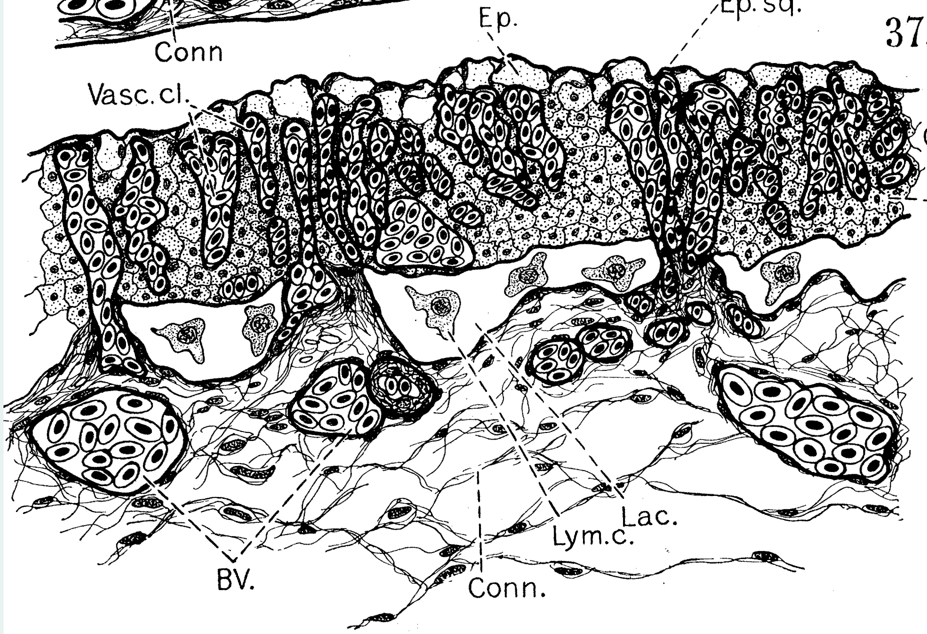
36



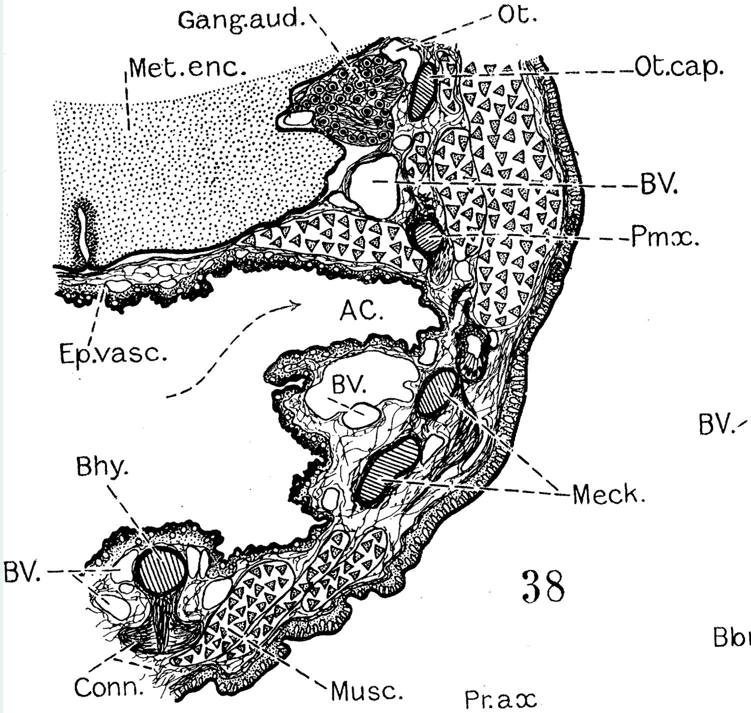
35



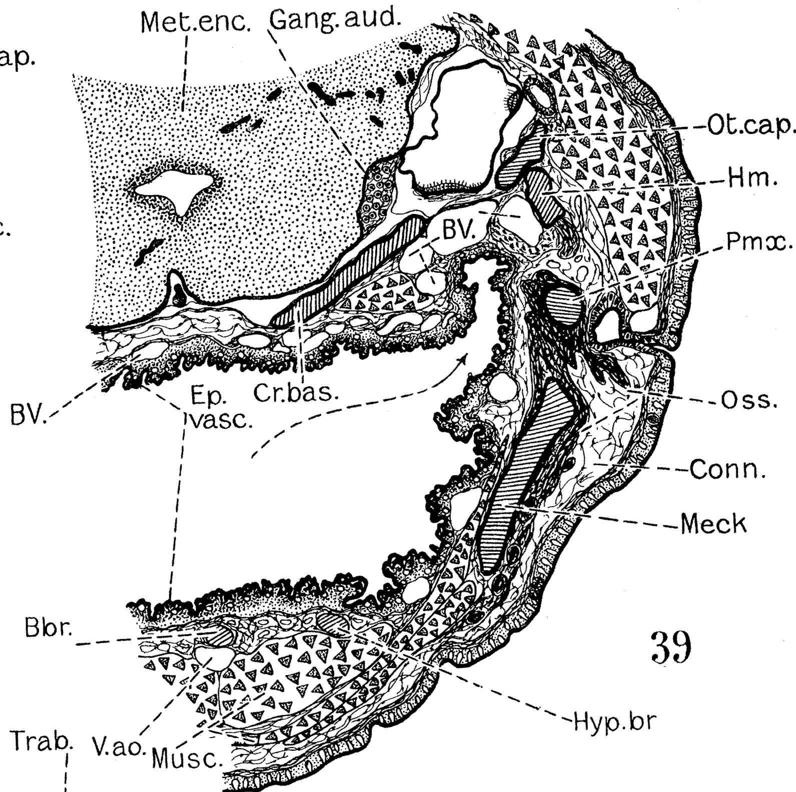
37



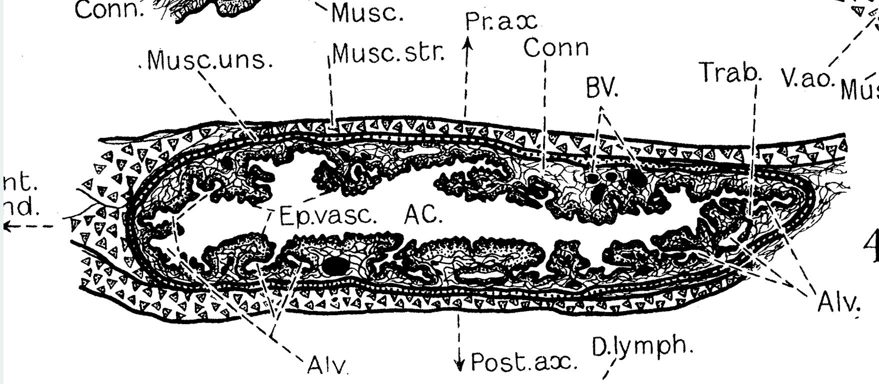
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES


Gang.aud.
Ot.
Met.enc.
Ot.cap.
BV.
Pmx.
AC.
Ep.vasc.
BV.
Bhy.
Meck.
BV.
Conn.
Musc.

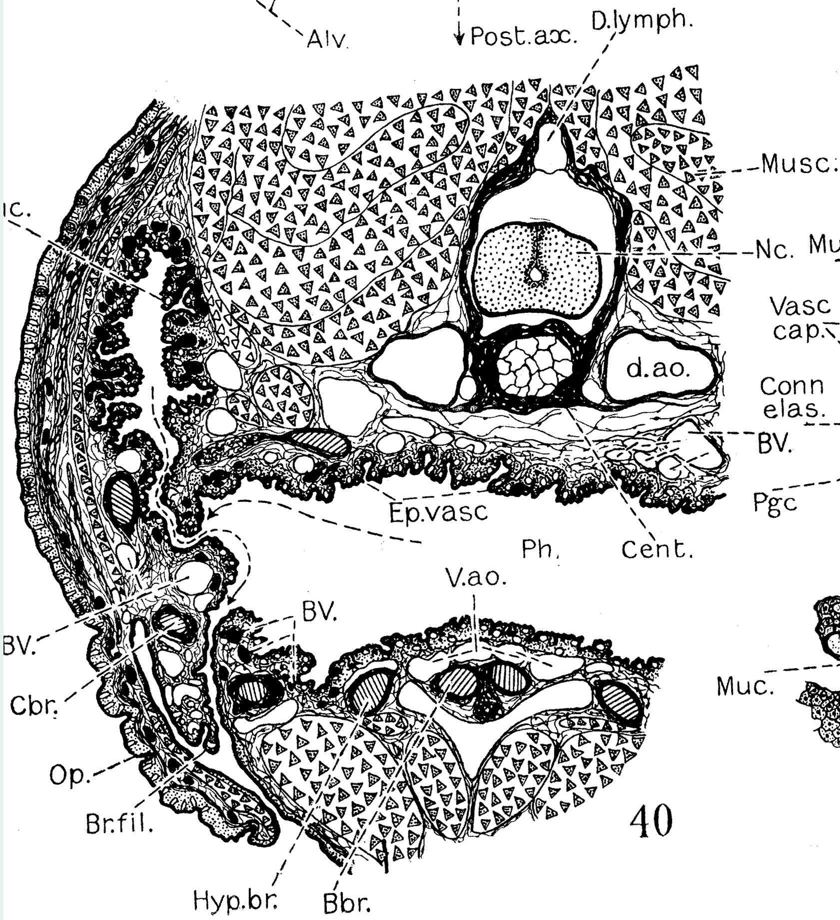
38


Met.enc.
Gang.aud.
Ot.cap.
Hm.
BV.
Pmx.
BV.
Ep. vasc.
Cr.bas.
Oss.
Conn.
Meck
Bbr.
V.ao.
Musc.
Hyp.br

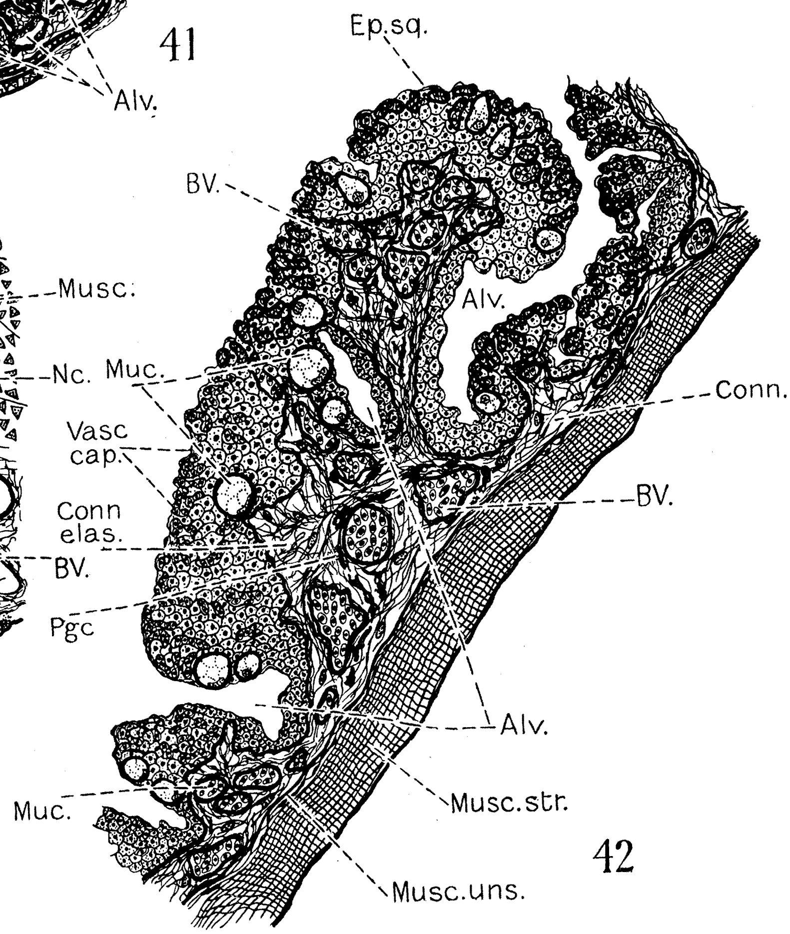
39


Musc.uns.
Musc.str.
Pr.ax
Conn
BV.
Trab.
nt.
nd.
Ep.vasc.
AC.
Alv.
Alv.
Post.ax.

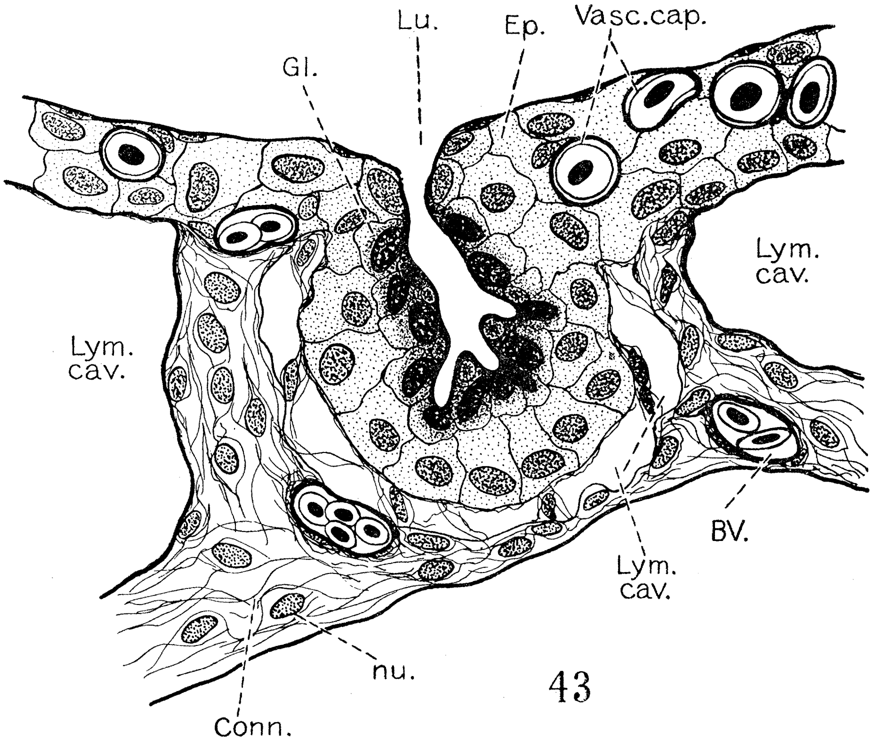
41


D.lymph.
Musc.
c.
Nc.
d.ao.
BV.
Ep.vasc
Ph.
Cent.
V.ao.
BV.
BV.
Cbr.
Op.
Br.fil.
Hyp.br.
Bbr.

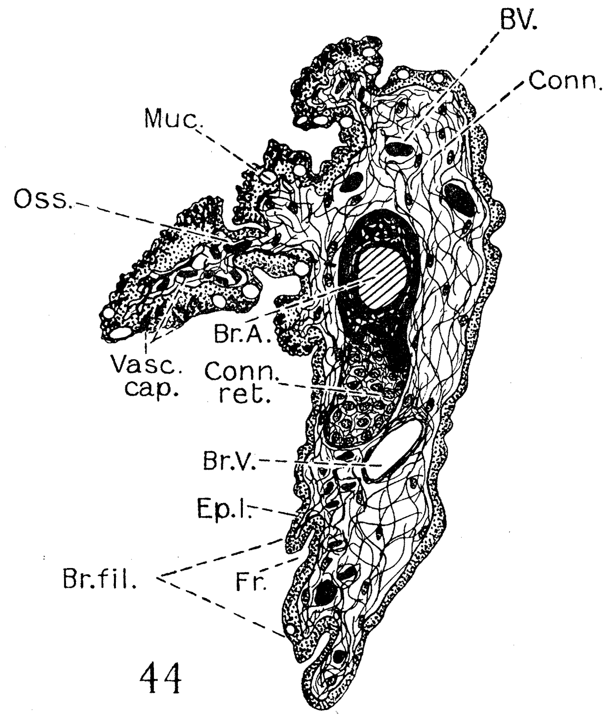
40


Ep.sq.
BV.
Alv.
Muc.
Conn.
Vasc cap.
BV.
Conn elas.
Pgc
Alv.
Muc.
Musc.str.
Musc.uns.

42

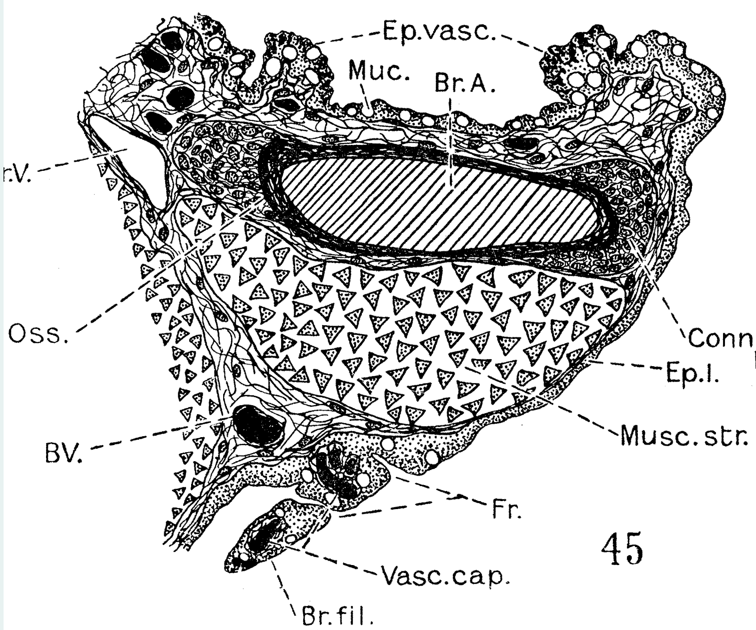

Lu.
Ep.
Vasc.cap.
Gl.
Lym. cav.
Lym. cav.
BV.
Lym. cav.
nu.
Conn.

43

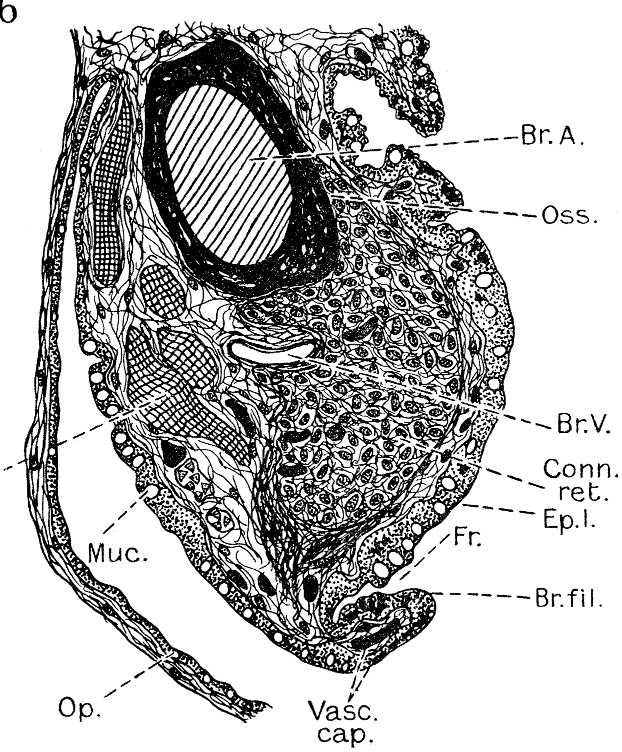

BV.
Conn.
Muc.
Oss.
Br.A.
Vasc. cap.
Conn. ret.
Br.V.
Ep.l.
Br.fil.
Fr.

44

46


Ep.vasc.
Muc.
Br.A.
r.V.
Oss.
Conn.ret.
Ep.l.
Musc.str.
BV.
Fr.
Vasc.cap.
Br.fil.

45


Br.A.
Oss.
Br.V.
Musc.
Conn. ret.
Ep.l.
Fr.
Muc.
Br.fil.
Op.
Vasc. cap.