

VIII.—*The Development of the Auditory Apparatus in Sphenodon punctatus; with an Account of the Visceral Pouches, Aortic Arches, and other Accessory Structures.*

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I. INTRODUCTION.

An investigation of the development of the inner ear of *Sphenodon* was suggested to me by Prof. DENDY during the spring of 1913, and the present paper records the results of the consequent research begun at King's College in the summer of the same year.

At an early stage of the work it became evident that a study of the inner ear, isolated from the structures intimately associated with it, would be neither conclusive nor complete. The scope of the investigation was therefore extended to include the development of the pharynx, the auditory capsule, the middle ear, and the nerves and blood vessels of the auditory region.

In this paper the term “auditory region” is used to denote that region lying between, but exclusive of, the roots of the Trigeminal and Hypoglossal nerves.



While a detailed examination of structures outside the auditory region thus defined was not attempted, I did not hesitate to extend my investigations beyond its limits wherever such a course appeared desirable.

Although for the space of half a century *Sphenodon*, the "living fossil" as it has been called, has proved a constant stimulus to research and discussion, our knowledge of its anatomy is by no means complete, and we are still more ignorant of the details of its development. Apart from the vexed question of its exact position in the line of vertebrate evolution, to the consideration of which question a fuller knowledge of its embryology may perhaps provide a valuable contribution, a detailed investigation of the life-history of this reptile appears desirable. Its primitive structure, its very limited distribution, and its obviously imminent extinction, render this a matter of some urgency. The present paper is one of a series dealing with the organogeny of this reptile, and based upon material collected in New Zealand by Prof. DENDY. The papers already published are included in the bibliography (Appendix I).

In August, 1914, my work was, unfortunately, interrupted by the war, and was not resumed until February, 1918. During this interval there appeared an important paper by Mr. E. S. GOODRICH (1915) on the "Chorda Tympani and Middle Ear of Reptiles, Birds, and Mammals," in which the author discusses the development and structure of the middle ear of *Lacerta*. He states that examination of *Sphenodon* embryos selected from Prof. DENDY's collection shows, as regards the development of the middle ear, a substantial agreement between *Lacerta* and *Sphenodon*. His brief observations concerning the latter reptile are in entire agreement with the conclusions I had already reached as a result of my previous examination of the same and similar embryos, and I have not found necessary any subsequent modification of my views. The numerous monographs describing the anatomy of adult *Sphenodon* and discussing its phylogeny need not here be considered. A list of the earlier of these is given by HOWES and SWINNERTON (1901), while the more recent publications, together with any of the earlier ones to which I have found it necessary to refer, are enumerated in Appendix I of the present paper.

As regards the region with which this research is concerned: In no case has any attempt hitherto been made to do more than give an account of its condition in the adult, or to describe, at most, a few outstanding embryonic features.

A systematic account of the development of the auditory organ and its associated structures is now attempted for the first time. The long anatomical dissertation of OSAWA (1897) contains a description of the middle ear, the auditory capsule, the cranial nerves, and the chief blood vessels of this region, together with a careful, but incomplete, account of the inner ear of adult *Sphenodon*. VERSLUYS (1898, 1903) has described the adult middle ear, while GISI (1907) gives an account of the brain and cranial nerves.

Almost simultaneously with the commencement of the present research there appeared a memoir by Dr. A. A. GRAY (1913), on the "*Comparative Anatomy of the Middle Ear*," which contains a description of that structure in adult *Sphenodon*. This interesting and suggestive paper supplements and confirms my observations, which have necessarily been limited to the conditions obtaining in the embryo.

Papers supplementing DENDY'S work on the early stages of development are few, the supply of embryonic material being very limited. SCHAUINSLAND (1900) describes certain phases of development, discusses the origin and relationships of the *Columella auris*, and gives a very accurate account of the cranial nerves and principal blood vessels of the auditory region of an embryo of a late stage. HOWES and SWINNERTON (1901) include in their treatise on the skeletogeny of *Sphenodon* a very brief account of the developing auditory capsule, and the hyoid-columella complex, and they discuss the homology of the latter. GOODRICH (1915), as already stated, refers to *Sphenodon* in his account of the development of the *Chorda tympani* and middle ear of *Reptilia*. It is evident, therefore, that ample scope still remains for further investigation.

Where a consideration of the embryology or of the adult anatomy of the auditory region of animals other than *Sphenodon* is germane to the present discussion, the authorities whose works are consulted are mentioned in the text, and a list of these is given in Appendix II.

I wish gratefully to acknowledge my indebtedness to Prof. DENDY, under whose supervision and in whose laboratory this work has been carried out. In addition to his kindness in placing at my disposal his extensive collection of *Sphenodon* embryos, he has given me invaluable advice and guidance during every stage of the investigation.

## II. MATERIAL AND METHODS.

### (a) *Material.*

The available embryonic material comprised several early embryos, stained, cleared, and mounted for examination as transparent objects, a very large and representative collection of serial sections prepared and used by earlier workers, and a number of uncut embryos specially selected for the purpose of this research.

The subjoined list of embryos examined contains references to the memoirs in which may be found details of the methods employed in their preparation, the absence of a reference indicating an embryo sectioned during the progress of the present investigation.

For these a uniform method of treatment was adopted. Fixation of the embryo was effected by *Kleinenberg's picric acid*, it was then preserved in *alcohol*, stained in bulk with *Grenacher's borax-carmin*, embedded in paraffin-wax, and cut into serial sections 10  $\mu$  thick.

These sections were provided with "*Richtleisten*," and counter-stained on the slide with *picro-indigo-carmin*e, cleared with *clove oil*, and finally mounted in *Canada balsam*.

Each embryo is identified by its number in Prof. DENDY's collection, and the stage of development it has attained is denoted by a letter. The system of lettering is that first proposed for *Sphenodon* by Prof. DENDY (1899), and now generally adopted by British zoologists.

In addition to the microscopic examination of these specimens, a number of wax reconstructional models were made in order to demonstrate the principal anatomical features of the auditory region during the different stages of development. Embryos employed in the construction of these models are marked by an asterisk.

*List of Embryos Examined.*

Stage of development.	No. of embryo.	Plane of section.	Reference.
H	78	Mounted whole	DENDY, 1899.
J (early)	44	Transverse	DENDY, 1899.
J (late)	79	Transverse	
K	39*	Transverse	DENDY, 1899.
K	80	Longitudinal	
L	50*	Longitudinal	DENDY, 1899.
M	51*	Transverse	DENDY, 1899.
M	81	Longitudinal	DENDY, 1899.
N	14a*	Transverse	DENDY, 1899.
N	96	Longitudinal	DENDY, 1899.
N-O	24a	Longitudinal	
O	32*	Longitudinal	
O-P	35a*	Transverse	
P	45a*	Transverse	
P-Q	51a	Transverse	DENDY, 1910.
Q	52a*	Longitudinal	HOWES and SWINNERTON, 1901.
R	141*	Transverse	DENDY, 1910.
	142	Longitudinal	HOWES and SWINNERTON, 1901.
S	11*	Longitudinal	HOWES and SWINNERTON, 1901.
	9a*	Transverse	

Specimens of the skull of adult *Sphenodon*, as occasionally noted in the subsequent sections of this paper, were examined in order to determine the persistence, or otherwise, of certain embryonic features.

(b) *Methods.*

In addition to microscopic examination of sections—camera lucida drawings of some of which are reproduced—a detailed investigation of embryos of each stage of development was made by means of projection drawings (*projektive konstruktion of His*), and

for most stages of development wax models of typical embryos were constructed according to the methods of PETER and BORN.

For the purpose of plotting reconstruction drawings and making wax models, the best results were obtained by selecting as a "zero," or "base-line," an imaginary antero-posterior axis traversing the mid-ventral surface of the brain. The general outline of the head of the selected embryo of any given stage, first was drawn under a low power, and by this means, together with the use of "*Richtleisten*," the form of the "zero-line," usually more or less curved, was accurately determined. Reconstruction drawings then were made by the projection, in the horizontal and sagittal planes, of the salient points of each section, the "zero-curve" being used as a base-line. The drawings thus obtained constituted a series of plans and elevations of the auditory region of the different embryos.

In all cases the drawings were made with the camera lucida, the magnifications employed for those used in the projections and models being 33, 50, 60 or 100 diameters, according to the age of the embryo and the nature of the structures under examination. Drawings of sections, at regular intervals dependent upon the degree of magnification employed, were traced on thin wrapping paper, schematically coloured with waterproof liquid pigments and outlined in Indian ink. A molten mixture of beeswax and turpentine was then run on the back of each drawing, and adhering to the paper produced a plate 1 mm. thick.

In cutting out the sections outlined on the wax plates trabeculæ were left, in order to hold together the various structures shown in the drawings. The wax plates were laid upon glass, and for the purpose of cutting out a sharp straight-bladed scalpel or tenotomy knife was used. The trabeculæ were cut away as early as possible during the process of building up of the model.

The superposed wax sections were fastened together by running a slightly heated metal modelling tool along their edges. In a few cases more secure fixation was ensured by means of heated pins driven through the plates.

For the final colouring of the models two very thin coats of a mixture of *Maurice's porcelaine enamel* with *xylol* were used.

Drawings of the actual models accompany this paper. These were found to be preferable to photographs since a greater wealth of detail could thereby be displayed.

The models have been deposited in the Zoological Laboratory at King's College, where, by kind permission of Prof. DENDY, they are available for examination.

### III. THE TOPOGRAPHY OF THE AUDITORY REGION.

A due appreciation of the topographical relationships of the auditory organ must necessarily precede a detailed study of its embryogeny. In order that this condition may be satisfied, a preliminary brief account of the development of the structures lying immediately adjacent to the auditory organ is now given.

These, for the present purpose, are considered to be :—

- (A) The *Pharynx* and its derivatives.
- (B) The *Head Cavities*.
- (C) The *Blood Vessels*.
- (D) *Cranial Nerves VI, VII (VIII), IX, X, XI, XII*.

The development of the auditory nerve (VIII) is most conveniently considered in connection with that of the inner ear, and it is therefore included in the account of the latter structure given in Section IV of this paper.

In all cases, only those portions of the above-named structures which lie within the auditory region, as previously defined, are now considered.

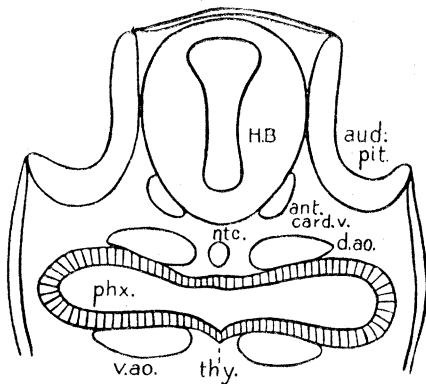
#### (A) THE PHARYNX AND ITS DERIVATIVES.

The earliest stages of the development of the *pharynx* have been briefly described by DENDY (1899), and exhibit no features of special interest.

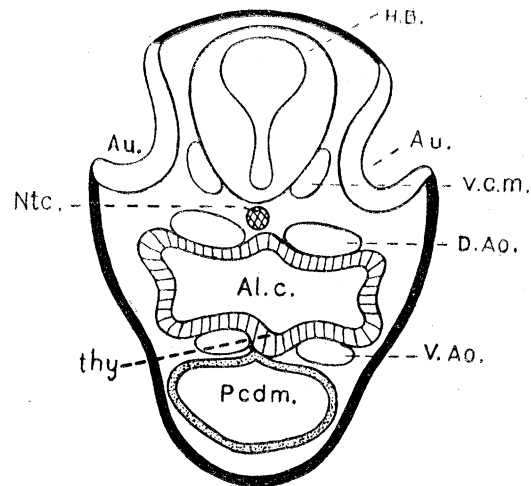
In *Stage H* (Embryo 78, fig. 1), the *pharynx* is seen as a wide tube filled with yolk granules, the anterior extremity of which terminates somewhat abruptly about midway between the anterior border of the heart and the head end of the embryo, while in a posterior direction the enclosed portion of the alimentary canal extends to a point just behind the heart. The wall of the pharynx is composed of a single layer of columnar epithelial cells.

In *early Stage J* (Embryo 44, fig. 2), the anterior end of the pharynx lies in the angle included between the floor of the mid-brain and that of the ventrally directed fore-brain. It terminates in a small bluntly-conical diverticulum with a circular lumen. This is the rudimentary *Seessel's pouch* which grows out from the pharynx in an anterior and slightly dorsal direction until it comes in contact with the floor of the mid-brain. Below the hind-brain the pharynx for some distance in a posterior direction is expanded transversely, and the lateral "wings" thus formed, having displaced most of the intervening mesoblast, extend almost to the epiblast of the body wall. A cross-section of the pharynx in this region exhibits a nearly semi-lunar lumen but there is as yet no sign of the formation of definite visceral pouches. Immediately anterior to this region, the hypoblast of the floor of the pharynx is in contact with the epiblastic wall of the stomodæum over a somewhat transversely elongated elliptical area. The wall of this area ultimately becomes thinned, forming the *Bucco-pharyngeal membrane*; its ultimate perforation results in the formation of the "mouth." In a posterior direction the lumen of the pharynx gradually assumes a circular form and its diameter simultaneously undergoes considerable diminution until it reaches the post-cardiac region. Here the alimentary canal opens to the exterior by the *anterior intestinal portal*; this opening still persists owing to the fusion of the folds of the *splanchnopleure* having as yet failed to extend posteriorly to this region.

In a slightly older embryo referred to *late Stage J* (Embryo 79, fig. 3, text-fig. 1) there are present the rudiments of *two pairs of visceral pouches*. The wing-like lateral expansions of the pharynx have been considerably flattened in a dorso-ventral direction except at two pairs of points at which bulbous enlargements are formed, and where the walls of the pharynx have continued to extend laterally, and having completely pushed aside the intervening mesoblast have fused with the epiblast of the body wall. These paired bulbous enlargements, the rudimentary 1st and 2nd pairs of visceral pouches, are thus separated from the exterior by a comparatively thin epiblastic membrane. The Bucco-pharyngeal membrane is now much thinned preparatory to its imminent perforation by the mouth, which occurs during the interval between Stages J and K.



TEXT-FIG. 1.



TEXT-FIG. 2.

TEXT-FIG. 1.—Stage J. Embryo 79. Diagrammatic transverse section through the auditory pits. ( $\times 100$ .)

TEXT-FIG. 2.—Stage K. Embryo 39. Diagrammatic transverse section through the auditory pits. ( $\times 100$ .)

(For explanation of lettering see pp. 367–368.)

As in Stage H, the alimentary canal contains a large number of oval yolk-granules. Its wall consists of a single layer of somewhat low columnar epithelial cells which are somewhat flattened in the mid-dorsal and mid-ventral regions of the anterior portion of the pharynx.

*The thyroid rudiment* appears as a slightly evaginated nearly circular patch of tall columnar epithelium in the floor of the pharynx between the rudiments of the 2nd pair of visceral pouches.

*Stage K* (Embryo 39, figs. 4 and 5, and text-fig. 2).

The 1st and 2nd pairs of visceral pouches are now well developed and the epiblastic membrane which separates their distal extremities from the exterior is very thin.

The 1st visceral pouch of either side has undergone considerable flattening, and its long axis, previously vertical, is now directed forwards, outwards, and upwards at an angle of about  $45^\circ$  from the floor of the pharynx.

It has a well developed dorsal angle, and a more acute ventro-lateral angle from which there runs along the under surface of the pouch a distinct ridge or crest terminating near the mid-ventral line of the pharynx. This ridge results from the evagination of a radially directed groove-like pocket in the floor of the pouch. It is the rudiment of the ventral diverticulum of the pouch, and reaches its maximum development during Stage N.

Each of the 2nd pair of visceral pouches is an ovoid outgrowth of the pharynx, with a nearly vertical long axis and a somewhat short acute dorso-lateral extremity and somewhat elongated and bluntly conical in a ventral direction. The distal wall of each pouch is fused with the epiblast of the adjacent body wall and the membrane closing the pouch is still imperforate.

The Bucco-pharyngeal membrane is perforated, the Stomodæum having an oval lumen with its long axis set transversely to that of the embryo. The *Thyroid gland* is now a deep hemispherical evagination, the lumen of which opens into the pharynx by a wide circular aperture.

*Stage L* (Embryo 50, fig. 6).

A considerable advance in development has taken place during the period that has elapsed since Stage K. Four pairs of visceral pouches are now developed, of which only the two anterior pairs open to the exterior. The lumen of the pharynx has assumed the form of a much flattened crescent and simultaneously the visceral pouches have become much flattened in an antero-posterior direction, while their dorso-ventral axes have undergone a corresponding elongation. While the long axis of each of the 2nd and 3rd pairs of visceral pouches is nearly vertical, that of each of the 1st pair is directed forwards and in a dorsal direction at an angle of about  $45^\circ$ . The clefts of the 1st and 2nd pairs of visceral pouches are long narrow slits, those of the 1st pair extending the whole length of the dorso-ventral axis of the pouches, whilst the cleft of each of the 2nd pair does not quite reach either extremity of the pouch. Each of the 3rd pair of pouches is a vertically elongated elliptical evagination of the wall of the pharynx, similar in shape to the second pouch, but closed, as yet, by a thin epiblastic membrane.

Immediately behind the 3rd pair of pouches the pharynx bears on either side a pyriform evagination, the more acute end of which is directed ventrally and slightly forwards, and whose long vertical axis is equal to only about one-third of that of each of the other pouches. These evaginations are the rudimentary 4th pair of visceral pouches.

The Thyroid is now connected with the ventral wall of the pharynx by a very short and narrow *Thyroglossal duct* (HIS), the circular lumen of which



establishes communication between the nearly spherical lumen of the gland—the wall of which still consists of a single layer of columnar epithelium—and that of the pharynx. The pharynx between the posterior border of the 1st and the anterior border of the 2nd visceral pouch has extended almost to the body wall. The lateral ridge or wing thus formed, which considerably reduces the latero-medial diameter of the central portion of the 2nd visceral arch, is present in Chick embryos (LILLIE) and has also been demonstrated in the embryo Ferret (RADFORD).

The Stomodæum is much narrowed in an antero-posterior direction and is somewhat wider transversely than during the preceding stage of development. Seessel's pocket has undergone considerable reduction, its lumen now being almost obliterated.

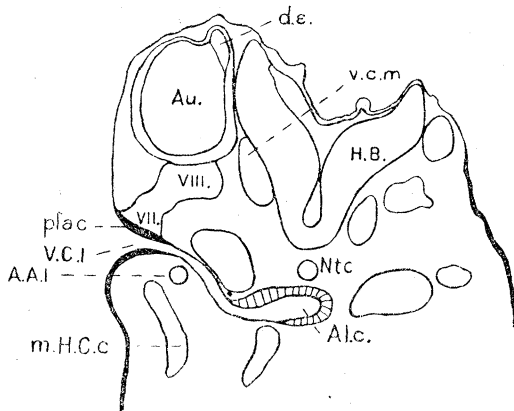
In front of this structure, and apparently immediately anterior to the position formerly occupied by the forward boundary of the Bucco-pharyngeal membrane there is a conical evagination of the roof of the oral cavity. It extends towards the infundibulum, and between it and the anterior end of the notochord. This is *Rathke's pocket*, from which is developed the dorsal portion of the pituitary complex. Its wall consists of columnar cells, those at its distal extremity being considerably elongated. Its epithelium merges into the ordinary buccal epithelium suddenly on the pharyngeal, and less suddenly on the buccal side of the pouch. Its further development is not considered, as the structure eventually lies entirely anterior to the region with which this paper is concerned.

*Stage M* (Embryo 51, figs. 7, 23, 24, and text-fig. 3).

The cranial flexure, which was well marked in Stage L, has somewhat increased and has also involved the auditory region, with the result that the posterior wall (floor) of the buccal cavity, and the ventral extremities of each of the 1st and 2nd pairs of visceral pouches have become somewhat approximated. The 1st visceral pouch of either side now opens to the exterior by a large widely open, vertically elongated, elliptical cleft, which terminates ventrally in a somewhat elongated, conical pocket or angle, which is apparently a rudimentary structure representing the ventral diverticulum of the visceral pouch observed in Mammalian embryos by Fox (1908). Each of the 2nd pair of visceral pouches opens by a single vertically elongated elliptical 2nd visceral cleft, somewhat narrower but longer in a dorso-ventral direction than that of the 1st pouch. Below and slightly medial to the cleft, the floor of the pouch has developed a conical evagination or rudimentary ventral diverticulum, which forms the ventral extremity of the pouch.

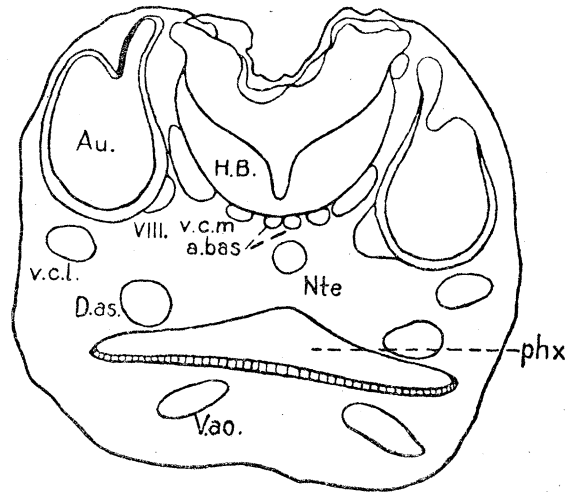
It appears probable that the condition now described is more primitive than that obtaining in the embryo chick, in which both the 2nd and 3rd pairs of visceral pouches develop separate dorsal and ventral divisions of their visceral clefts, the latter being somewhat the better developed (LILLIE). The exact significance of

the separate dorsal and ventral divisions of the visceral clefts is unknown, although it has been suggested that—since the branchial sense organs are developed at the dorso-lateral extremity of the visceral pouches—the dorsal diverticula may originally have had some special function in connexion with these (LILLIE).



TEXT-FIG. 3.

TEXT-FIG. 3.—Stage M. Embryo 51. Diagrammatic transverse section through the otocysts. ( $\times 50$ .)



TEXT-FIG. 4.

TEXT-FIG. 4.—Stage N. Embryo 14a. Diagrammatic transverse section through the otocysts. ( $\times 50$ .)

(For explanation of lettering see pp. 367–368.)

The 3rd visceral pouch of either side is similar in shape to those just described, but is much smaller and perforated only by a small vertically elongated and very narrow cleft, which at this stage is confined to the dorsal third of the pouch. Each of the 4th pair of visceral pouches is a small vertically ovoid evagination of the pharyngeal wall, and it bears at the junction of its posterior curvature with the wall of the pharynx a small hemispherical outgrowth, which apparently represents a rudimentary 5th visceral pouch (post-branchial body, auctorum) (fig. 7).

From the region of the 4th pair of visceral pouches there extends in a posterior direction in the mid-ventral line a long and somewhat shallow depression or furrow in the floor of the pharynx, deepening somewhat as it passes backwards beyond the posterior boundary of the auditory region to end blindly in a rounded pocket. This is the rudimentary *laryngo-tracheal groove*, from the proximal extremity of which is formed the larynx, while the trachea, bronchi, and lungs are developed from its distal portion.

During this stage there is developed a *facial placode* in connexion with the distal extremity of the facial portion of the *acustico-facialis neurencytium* (text-fig. 3). The placode of each side appears as a thickened, latero-medially elongated, elliptical patch of proliferating epiblast, the cells of which are continuous with the undifferentiated  $\alpha$ -*neuroblasts* of the neurencytium. It is situated at the posterior border of the junction of the dorso-lateral wall of

the 1st visceral pouch with the epiblast of the body wall, and extends into a visceral furrow of the latter, situated just posterior to the cleft.

A similar, but considerably smaller, *glosso-pharyngeal placode* occurs in a similar position relative to the 2nd visceral pouch of either side and in connexion with the developing glosso-pharyngeal nerve. These placodes are transitory structures, usually considered to be vestiges of a superficial sensory canal system similar to that of the head of aquatic vertebrates.

*Stage N* (Embryo 14*a*, text-fig. 4, and figs. 8, 13, 25, 26 and 35).

The visceral pouches and clefts are now very conspicuous, the 1st and 2nd visceral pouches of each side being separated by a very much antero-posteriorly elongated 2nd visceral arch which has also begun to extend laterally, so that it is much more prominent than the visceral arches posterior to it. Owing to its encroachment upon the posterior border of the 1st visceral pouch, the cleft of the latter has become a narrow vertical slit, opening into the much wider cavity of the pouch.

The 2nd visceral pouch is narrow, its long axis is nearly vertical, and its cleft extends from the dorsal to the ventral extremity of the pouch, its aperture being narrow and triangular, with well marked acute dorsal and ventral angles, and an obtuse antero-ventral angle. The 3rd visceral arch is deep, narrow, and somewhat wider in an antero-posterior direction, at its dorsal than at its ventral extremity.

The 3rd visceral pouch is much elongated ventrally, its cleft being triangular, similar in shape to, and somewhat larger than, the 2nd visceral cleft. The 4th visceral arch is about as wide as, but otherwise rather smaller than, the 3rd visceral arch. The 4th visceral pouch is imperforate, oval in shape, with a long dorso-ventral axis, and bears the rudimentary 5th pouch (post-branchial body) as a hemispherical prominence on its posterior wall near the junction of the latter with the wall of the pharynx. All the pouches are much narrowed at their proximal extremities, suggesting an incipient conversion into the pharyngo-branchial tubes (*canales pharyngo-branchiales*) of Mammalian embryos.

Both KASTSCHENKO (1887) and LILLIE (1908) note in Chick embryos an antero-posterior extension of the 2nd visceral arch similar to that described above, while a lateral thickening of this structure is found in Human and other Mammalian embryos referred to a stage of development corresponding to this now being considered. The significance of the lateral thickening becomes evident in the immediately ensuing phases of development (*cf.* figs. 28, 36).

The *laryngo-tracheal groove* is considerably deeper than during the preceding stage of development. A transverse section of the pharynx in the region of the 4th pair of visceral pouches exhibits a T-shape, the ends of the limbs of the latter

being somewhat swollen and rounded. The horizontal transverse limb represents the cross-section of the pharynx, while the ventrally directed vertical limb represents that of the laryngo-tracheal groove. Just behind the 6th pair of aortic arches the groove terminates in a postero-ventrally directed and slightly bifurcated pocket, from which are developed the rudimentary "lung buds."

The *thyroid gland* is now a nearly spherical, but slightly asymmetrical, thick-walled structure, with a small spherical lumen, and almost completely shut off from the pharynx. The lumina of the two structures communicate by means of a very narrow and short *ductus thyroglossus*.

The stomodæum is very narrow in an antero-posterior direction, but much elongated transversely. The lumen of *Seessel's pouch* is obliterated, and the pouch itself is reduced to a small, inconspicuous prominence situated just posterior to the developing *pituitary body*. In a slightly older embryo (Embryo 96), also referred to Stage N, the pouch has completely disappeared, and its lumen is represented by a hardly perceptible "notch" in the columnar epithelium of the dorsal wall of the pharynx—and visible only in one or two median longitudinal sections of this embryo.

#### *The Placodes.*

Well developed placodes are now present in connexion with the 1st, 2nd and 3rd visceral pouches and their respective visceral furrows. The placodes of the 1st pair of visceral pouches are much larger than the others, elliptical in shape and transversely elongated, while those of the 2nd and 3rd pairs of visceral pouches are nearly circular. Their thickened epiblast is continuous respectively with the distal extremities of the ganglionic masses (neurencytia) of the developing facial, glosso-pharyngeal and vagus nerves.

#### *Stage O* (Embryo 32a, figs. 9, 10, 27, 28 and 36).

The *visceral pouches* and *clefts* having attained their maximum degree of development during the immediately preceding embryonic phase now begin to undergo a series of changes which results in the closure of the visceral clefts and the eventual obliteration of the 3rd, 4th, and rudimentary 5th pairs of visceral pouches. Certain parts only of the 1st and 2nd pairs of visceral pouches persist and contribute to the formation of the tympanic cavity of each side.

The *pharynx* is now a very wide tube, occupying nearly the whole width of the head in the auditory region, but its dorsal and ventral walls have so closely approached one another that the lumen of the tube is a much flattened crescent, of which the cornua are dorso-laterally directed. The 1st and 2nd visceral arches have undergone considerable lateral thickening, and this has extended to the regions immediately dorsal and ventral to the corresponding extremities of the respective visceral clefts. Since, however, the lateral extension of the more posterior arches

has not kept pace with that of the 1st and 2nd visceral arches, the former now lie in a somewhat depressed area on the side of the head, the anterior, antero-dorsal and antero-ventral borders of this area being somewhat overlapped by the hinder margin of the thickened 2nd visceral arch, while in front of the latter the thickened ventral portion of the 1st visceral (mandibular) arch grows forwards and downwards to form the rudiment of the lower jaw. The 1st visceral cleft is now a very narrow vertically elongated aperture, which has undergone a certain amount of closure from below upwards owing to the upward growth of the junction of the thickened postero-ventral extremity of the 1st visceral arch and the antero-ventral border of the 2nd visceral arch. This becomes more marked in the immediately succeeding stages of development, and is in agreement with the observations of GOODRICH (1915), who notes that the closure of the 1st visceral cleft, and the consequent reduction of the distal portion of the 1st visceral pouch of *Lacerta* embryos, is effected by a similar process.

The characteristic feature, however, of both this and the immediately succeeding stage of development is the practical closure of the 2nd and 3rd visceral clefts by the very extensive lateral and posterior growth of the 2nd—and to a less extent of the 3rd—visceral arch (fig. 36).

The laterally thickened 2nd visceral (hyoid) arch grows backwards and downwards, thus closing the 2nd visceral cleft, except at its extreme postero-ventral angle (*cf.* shape of this cleft in Stage N, Embryo 14*a*, fig. 8). The backwardly growing border of the arch passes into the general surface of the head dorsal to the cleft, but is, at first, free at its ventral border, so that the cleft opens by a postero-ventral aperture. The posterior margin of the backwardly growing arch now meets and fuses with the anterior border of the less prominent 3rd visceral arch. The growth continues backwards across, and closes the 3rd visceral cleft, and the fold (“*operculum*”) of mesoblast—to which, apparently, both 2nd and 3rd visceral arches contribute—fuses with the anterior border of the 4th visceral arch. The 3rd visceral cleft now opens to the exterior by a small ventral aperture. The distal portion of the lumen of each pouch has therefore been converted into a nearly vertical tubular space, flattened latero-medially. That of the 2nd visceral pouch is directed postero-ventrally, while that of the 3rd visceral pouch is directed antero-ventrally, their ventrally placed apertures being confluent and opening into the dorsally placed apex of a pyramidal pit, the triangular base of which is ventrally directed. The sides of this pit are formed by the head wall ventral to the clefts, really the unthickened ventral region of the 3rd visceral arch, the overgrowing posterior fold of the 2nd visceral arch, and the downwardly growing border of the thickened portion of the 3rd visceral arch. The angles of the pit are situated antero-ventrally, laterally, and postero-ventrally.

It is possible that the whole of the “*operculum*” is derived from the 2nd visceral arch, but a consideration of the transverse sections of Stage O-P, Embryo 35*a*, and

the models of Stage O, Embryo 32*a*, and O-P, Embryo 35*a*, appears to favour the assumption that both 2nd and 3rd visceral arches take part in the process of closure, each perhaps being mainly responsible for the closure of its own cleft. This stage of the process of closure of the 2nd and 3rd visceral clefts is diagrammatically represented in figs. 36(A) and 36(B), and the presence of a somewhat similar backwardly growing fold or "operculum" closing the 2nd and 3rd visceral clefts has been observed in Human and some other Mammalian embryos.

The 4th visceral pouch of each side is a small ovoid evagination of the pharynx similar in general appearance and size to that found in the embryo of Stage N previously described, but exhibiting a somewhat constricted proximal neck at its junction with the pharynx. The rudimentary 5th visceral pouch has become a narrow oval protrusion from the posterior wall of the 4th pouch elongated in a posterior direction and apparently about to become detached from the latter, a constriction between the structures being already visible. The lumen of the thyroid gland is now practically obliterated, the lumen of the thyroglossal duct alone persisting and being apparently about to disappear as the separation of the gland from the pharyngeal wall becomes complete.

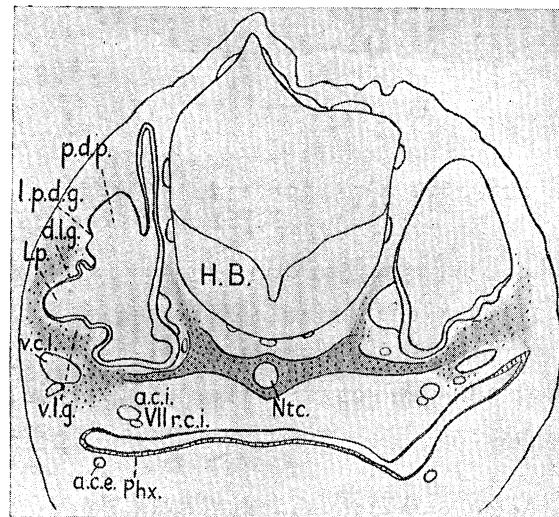
The laryngo-tracheal groove is similar to that already observed in Stage N, but the bifurcation of its posterior (distal) extremity is slightly more obvious, and the separation of the dorsal surface of the pocket-like posterior terminal region of the groove from the ventral wall of the pharynx is extending in an anterior direction.

*Stage O-P* (Embryo 35*a*, text-figs. 5 and 11, also figs. 29, 30, 31, 32 and 37).

The pharynx has become still more dorso-ventrally flattened, and its lumen is now a horizontal, transverse slit extending across and reaching almost to the lateral walls of the head in the auditory region (text-fig. 5).

The 1st visceral cleft is a small, very narrow, vertically elongated aperture which shows signs of impending closure owing to the upward and lateral extension of the ventral portions of the 1st and 2nd visceral arches (fig. 28). The vertically triangular distal portion of the lumen of the pouch opens at its proximal apex into the general lumen of the pharynx, the connecting portion of the pouch being reduced to a very short narrow tube (*canalis pharyngo-branchialis*). The 2nd visceral pouch is a latero-medially flattened tube, its dorsal extremity forming a blunt conical pouch terminating blindly just above the level of the lateral border of the pharynx. Its long axis is directed in a postero-ventral direction, and the lumen of the tube appears in horizontal section as a narrow ellipse with a long antero-posterior major axis. The ventral extremity of the pouch fuses with the body wall, which here exhibits a deep antero-posterior groove, at the posterior and deeper end of which the lumen of the 2nd visceral pouch communicates with the exterior by a small and narrow elliptical aperture common to itself and to the 3rd visceral pouch. The ventral extremity of

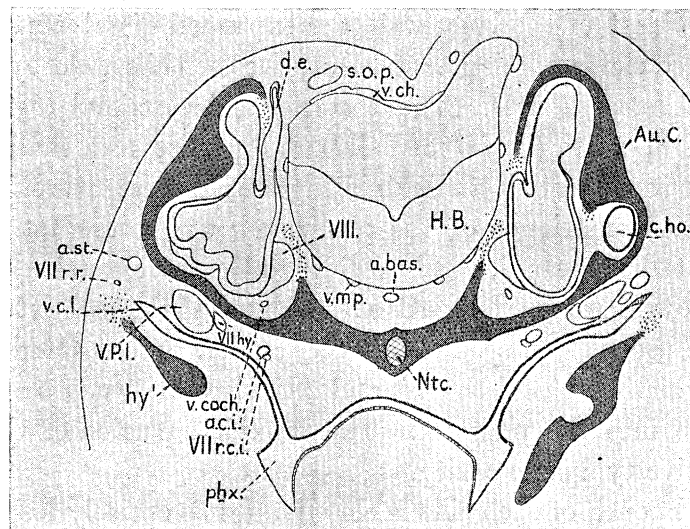
the lateral wall of the 2nd visceral pouch fuses with the body wall above the lateral groove while that of the medial wall unites with the body wall below the groove. Between the 2nd and 3rd visceral pouches the transverse diameter of the pharynx is



TEXT-FIG. 5.—Stage O-P. Embryo 35*a*. Diagrammatic transverse section through the otocysts.

( $\times 33$ .)

(For explanation of lettering see pp. 367-368.)



TEXT-FIG. 6.—Stage P. Embryo 45*a*. Diagrammatic transverse section through the auditory capsules and otocysts [developing membranous labyrinths]. ( $\times 33$ .)

(For explanation of lettering see pp. 367-368.)

somewhat diminished, and a similar further diminution occurs between the 3rd and 4th pouches. The 2nd, 3rd and 4th visceral arches thus form a series, each of the two posterior members of which lies postero-medially to the arch in front of it.

Similarly the 3rd visceral pouch lies postero-medial to the 2nd pouch and the 4th pouch is similarly placed relatively to the 3rd. The 3rd visceral pouch is shorter than, but similar in shape to, the 2nd pouch, the ventral extremities of both are fused and they open to the exterior by a common aperture (fig. 37). The dorso-medial extremity of the 3rd visceral pouch is united with the pharynx by a comparatively narrow and short tubular junction (rudimentary *canalis pharyngo-branchialis*). The 4th visceral pouch is an oval structure, now united to the pharynx by a comparatively narrow antero-medial neck. The rudimentary 5th visceral pouch has now lost its lumen, and is a dense antero-posteriorly elongated mass of tissue, extending in a posterior direction from the junction of the 4th visceral pouch with the wall of the pharynx. It ultimately becomes detached, suffers displacement in a posterior direction, and forms a portion of the bilobed *thymus gland*. It appears probable that persistent portions of the epithelium of the closed 3rd and 4th pouches also contribute to the formation of this gland. The consideration of this process is, however, outside the scope of the present paper.

*Stage P* (Embryo 45a, text-figs. 6 and 12, figs. 11, 12, 14, 15, 38, 39 and 40).

The 1st visceral pouch of each side is now much reduced (fig. 31). Its cleft is closed and the proximal portion of the pouch remains as a conical diverticulum, from which there extends laterally a stalk of dense tissue which represents the walls of the closed distal region of the pouch. This expands somewhat at its outer end and blends with the epiblast of the body wall, the expanded distal portion occupying the position of the closed cleft. A similar structure has been observed by VERSLUYS (1903) in an embryo of *Calotes jubatus*. The posterior and proximal regions of the pouch are much reduced in width (latero-medially) and persist as a shallow pouch, nearly rectangular in transverse section, and exhibiting a wide crescentic outline when viewed from the side. The constriction of the pharynx between the 1st and 2nd visceral pouches has almost disappeared, partly owing to the retrogression of the 1st visceral pouch and partly owing to the forward extension of the dorsal extremity of the 2nd visceral pouch. The condition produced is very similar to that noted by KASTSCHENKO in the Chick, in which he states the 1st and 2nd visceral pouches eventually open by a common aperture into the pharynx. The proximal portion of the common cavity he calls the primitive tympanic cavity.

The 2nd visceral pouch of each side is closed and has entirely lost any vestige of its former connection with the cleft common to itself and to the 3rd visceral pouch, by which it formerly opened to the exterior. It is a much elongated and narrow pyriform pouch, the rounded dorsal extremity of which is directed somewhat forward immediately behind, and rising towards the dorsal surface of, the developing *columella auris*. Its ventral extremity is somewhat pointed and recurved in a slightly anterior direction (figs. 38, 39).

Behind the 2nd visceral pouch the latero-medial diameter of the pharynx is



considerably reduced and its lumen is now a horizontal slit, occupying little more than half the width of the head. Behind the 3rd pair of visceral pouches it undergoes a further diminution of width and its transverse section exhibits a crescentic form, the convexity of which however is now dorsally directed, whereas in the anterior part of the auditory region the dorsal surface of the pharynx is still concave.

The 3rd visceral pouch of either side is a nearly horizontal, somewhat elongated small pyriform closed sac, the blunt anterior extremity of which lies behind and slightly below the ventral extremity of the 2nd visceral pouch of the same side, while its conical hinder end is directed laterally and somewhat dorsally.

It is evident from a comparison of these pouches with those of the embryos representing the three preceding stages of development, that the closure of the 1st visceral cleft of each side and the reduction of the 1st visceral pouch has proceeded upwards, inwards, and in a posterior direction. The corresponding process in the 2nd visceral pouch has taken place upwards and has not proceeded so far, while there has been a simultaneous upward (dorsal) and forward extension of the dorsal extremity of the pouch. Similarly, the 3rd visceral pouch has closed from below upwards and in a posterior direction.

The 4th visceral pouch is reduced to a small spherical sac attached to the posterior extremity of a narrow canal jutting out from the pharynx in a lateral and posterior direction, while the vestige of the rudimentary 5th visceral pouch is quite detached and appears as a solid mass of cells posterior to the former structure.

The conversion of the laryngo-tracheal groove into a tube by the fusion in the middle line of its dorso-lateral walls has extended forward to the level of the 3rd pair of visceral pouches, while the solid thyroid gland has been displaced in a posterior direction and now lies in the middle line, just ventral to the underside of the pharynx behind the 2nd, and just in front of the 3rd, pair of visceral pouches (fig. 38).

In the immediately subsequent stages of development (Stages Q, R, S) all traces of the 3rd and 4th pairs of visceral pouches have disappeared.

The further developmental changes undergone by the persistent vestiges of the 1st and 2nd pairs of visceral pouches are discussed below (*vide Section VI, MIDDLE EAR AND CHORDA TYMPANI*).

With the fate of the other pharyngeal diverticula the present paper is not concerned.

The position and appearance of the thymus and thyroid glands, the trachea, and the pharynx of the auditory region during Stages R and S are shown in figs. 17, 18, 44, 45, and text-fig. 16.

In conclusion, it may be observed that the apparent absence of separate dorsal and ventral divisions of the visceral clefts, whereby all or any of the first three pairs of visceral pouches of the embryo *Sphenodon* communicate with the exterior, would

seem to be an indication of the primitive nature of this reptile. If such separate divisions of the visceral clefts occur they must be of very transitory duration, and no positive evidence of their existence has yet been adduced. With this possible exception, the present observations do not reveal any abnormalities in the developmental changes undergone by the pharynx, or by such of its derivatives as have now been considered.

#### (B) THE HEAD-CAVITIES.

These transitory structures, of which neither the significance nor the ultimate fate is accurately known, persist but a short time, and disappear at a comparatively early stage of development.

In *Reptilia* the existence of three pairs of *pre-otic somites*, each of which gives rise to a cavity, presumably a *myocoel*, is generally accepted. HOFFMANN (1890) has stated that four pairs of cavities sometimes exist, but he does not appear to postulate the existence of a fourth pair of pre-otic somites. The presence of first one pair, and ultimately two pairs, of head-cavities in early embryos of *Sphenodon* was discovered by DENDY (1899). He concluded that the appearance of the second pair is the result of a constriction and ultimate transverse division of the pair already existing, and this is confirmed by the present investigation.

*Stage J.*—In an embryo of early Stage J (Embryo 44, fig. 2) a single pair of pyriform head-cavities are present. These are preoral, lying one on either side of the floor of the mid-brain and antero-lateral to the dilated medial portion of the 1st aortic arch. The more acute extremity of the cavity is directed postero-ventrally, and lies parallel to the aortic trunk in the dorsal region of the mandibular arch.

In a slightly older embryo (*late Stage J*, Embryo 79) each head-cavity shows a constriction which, as DENDY found in an embryo of Stage K, ultimately divides it transversely into an antero-ventral and a postero-dorsal cavity.

The walls of these cavities consist of a single layer of flattened mesoblast cells, the cytoplasm of which is so scanty that the wall appears, at first sight, to consist only of a single layer of closely set oval nuclei.

*Stage K.*—In Embryo 39 (figs. 4 and 5) of this stage, the two pairs of head-cavities are well developed. Of the posterior pair, which appear to be those originally present, one is situated in the dorsal region of the early mandibular arch, lateral to the 1st aortic arch and immediately in front of the antero-dorsal extremity of the 1st visceral pouch. It is pyriform in shape, its long axis being directed ventrally and slightly backwards, and terminating in a well developed conical diverticulum which invades the dorsal third of the mandibular arch.

It is impossible to determine from an examination of the available material, which of the three pairs of head-cavities, usually accepted as existing in the *Reptilia*, are represented by those just described. It is proposed, therefore, to name them—

on topographical grounds only—the “*mandibular head-cavities*,” and to apply the term “*pre-mandibular*” to the pair lying immediately anterior to them.

Each of the paired pre-mandibular head-cavities is ovoid in shape and rather less than half the size of the corresponding mandibular head-cavity, immediately antero-ventral to which it is situated. From its dorso-medial surface it gives off a long conical diverticulum which passes first dorsally and then medially, just anterior to the middle of the loop of the 1st aortic arch. It approaches, but does not at this stage unite with, its fellow on the opposite side of the head, but terminates just in front and to the side of the anterior extremity of the preoral gut (Seessel's pocket).\*

*Stage L.*—In Stage L (Embryo 50, fig. 6) the two pairs of head-cavities are still very conspicuous. Owing to the very marked cranial flexure which is characteristic of this stage of development, each of the mandibular head-cavities is so distorted that it appears to have become elongated in an antero-posterior direction; this process, to a slight extent only, having really taken place dorso-ventrally. The pre-mandibular head-cavity of either side lies in front of the region affected by the cranial flexure and has retained its original shape.

The postero-ventral diverticulum of the mandibular head-cavity of either side has now developed into a canal, circular in cross-section, traversing the mandibular arch and extending into the region immediately in front of the antero-dorsal boundary of the pericardium, the wall of which it closely approaches. Here it turns abruptly in a medial direction, and passing immediately in front of the thyroid diverticulum (developing thyroid gland) it unites in the middle line, ventral to the pharynx, with its fellow of the opposite side.

The pre-mandibular head-cavity of either side has undergone considerable enlargement, its size now exceeding that of the mandibular head-cavity. A narrow tubular connection between the two pre-mandibular head-cavities passes immediately in front of the anterior extremity of the notochord and between it and Seessel's pocket.

In *Stage M* (Embryo 51, fig. 7 and text-fig. 3) the structures described above remain practically unaltered, only two or three minor differences being observed. The mandibular head-cavities appear to be less distorted and have assumed a more regularly ovoid shape, while there is a slight proliferation of the mesoblast cells in the regions immediately surrounding the walls of the various head-cavities.

The proximal portion of the canal of the mandibular head-cavity of either side is more dorso-ventrally directed and appears to be relatively shorter than in the preceding stage of development. This is evidently due to the more vertical (dorso-ventral) position of the 1st visceral cleft and pouch, both of which are less elongated in an antero-posterior direction than has been previously the case (*cf.* Stage L). In other respects the conditions during this stage resemble those of that immediately preceding it.

\* Further examination of this embryo, and other embryos of late Stage J, leads me to believe that the transverse canals exist in these stages as in Stage L.

*Stage N* (fig. 8).—In Embryo 14*a* of this stage the only change to be observed in the relationship of the *head-cavities* to the surrounding structures is due to the marked development in an antero-posterior direction of the *hyoid arch*, which thus interposes as a wide dorso-ventrally directed wedge of mesoblast between the 1st and 2nd visceral pouches, and which has been described elsewhere (*vide Section 3 (A)*, Stage N). As a result of this excessive development of the hyoid arch a considerable distance now intervenes between the thyroid gland, which is still directed in the mid-ventral line, at the level of the anterior border of the 2nd pair of visceral pouches, and the transverse portion of the canal joining the paired mandibular head-cavities. This canal passes ventral and slightly medial to the 1st visceral cleft and crosses the head as described in the immediately preceding stages of development.

The increased density of the mesoblast immediately surrounding the *head-cavities*, which has already been noticed in the preceding stage, is now somewhat more marked.

In embryos of all stages, subsequent to Stage N, the head-cavities are absent.

In *Stage N-O* (Embryo 24*a*) a dense mass of mesoblast is apparent in each of the regions formerly occupied by the head-cavities. The significance of these rounded masses of mesoblast is uncertain, but it suggests that they are rudiments of the musculature of these regions and that each head-cavity should be regarded as a *myocoele*. It has generally been assumed that the orbital muscles arise from the anterior head-somites, although the latter have never been identified. The head-cavities certainly exist where, later, the orbital muscles are developed, but that they represent the cavities of the head-somites is uncertain, as is also their suggested connection with the orbital muscles. REUTER (1897) in the Pig embryo and LEWIS (1910) in the Human embryo have shown that the orbital muscles arise from "pre-muscle masses" which lie dorsal to the optic nerve, postero-medial to the optic cup, and anterior to the *Gasserian ganglion*. It is possible that the above-described mesoblastic proliferations represent these pre-muscle masses.

It must, however, be concluded that both the nature and the ultimate fate of the head-cavities still remain uncertain.

REESE (1910) found in embryos of the American alligator two pairs of head-cavities almost identical in situation and appearance with those now described.

### (C) THE BLOOD VESSELS.

A detailed study of the development of the blood vessels of *Sphenodon* at stages earlier than the first appearance of the auditory primordium was not made, as this subject has been worked out in detail in some other vertebrate embryos by a number of investigators (EVANS, 1909, GÖPPERT, 1909, BREMER, 1908). Some earlier embryos of *Sphenodon* were examined, but owing to the indifferent state of preservation of the material the results obtained were by no means decisive, although nothing was

observed which could be regarded as conflicting with the current view concerning the origin of the blood-vessels from the embryonic mesoblast.

#### *Arteries.*

*Stage J.*—During early Stage J (Embryo 44, fig. 2) the single wide *ventral aorta* runs forward from the heart to a point immediately posterior to the oral sinus, where it bifurcates, and the *paired ventral aortæ*, separated by the stomodæum, pass forward to the anterior end of the alimentary canal, where each bends sharply in a dorsal direction, forming the 1st aortic arch, the lumen of which is considerably dilated.

Dorsal to the pre-oral gut, the *aortic arch* of either side turns abruptly in a posterior direction, undergoes considerable reduction of calibre, and continues in a posterior direction along the dorso-lateral wall of the pharynx, as the right or left *dorsal aorta*.

*Stage K.*—The only further development to be noted during this stage (Embryo 39, figs. 4, 5, and text-fig. 2) is a lateral dilatation of each dorsal aorta in the region lying between the developing 1st and 2nd visceral pouches, and a more marked lateral diverticulum of each ventral aorta in the same region. These are the rudiments of the 2nd aortic arch.

*Stage L.*—A marked development of the aortic arches occurs in Stage L (Embryo 50, fig. 6). The 1st, 2nd, 3rd, and 4th aortic arches are now complete, while posterior to the 4th aortic arch are two small and narrow vessels, representing respectively the ventral and dorsal portions of the developing 6th aortic arch. The 2nd and 4th are of considerably smaller calibre than the 1st and 3rd aortic arches.

*Stages M-N.*—The 6th aortic arch soon becomes complete (Stage M, Embryo 51, figs. 7 and text-fig. 3), but the 5th aortic arch is, as usual, very transitory, and appears first during Stage N (Embryo 14a, figs. 8 and 13), in which embryo it exists as a short narrow vessel of ventral origin, arising from the junction of the 4th and 6th aortic arches and running dorsally and then posteriorly towards the dorsal portion of the 6th aortic arch. In this embryo the two ventral aortæ diverge immediately anterior to the heart and each passes forwards and obliquely outwards along the ventral surface of the pharynx, passes ventral to the 1st visceral pouch, and traverses the mandibular arch as the stout 1st aortic arch, from the ventral portion of which springs the *arteria lingualis*, a fairly stout, ventrally and anteriorly directed vessel, distributed to the wall of the stomodæum. The dorsal aorta of either side passes back immediately above the pharynx, tending slightly towards the middle line as it pursues its posterior course. It will be remembered that characteristic features of this embryo are the great width of the shallow 2nd visceral arch and the depth of the narrow 3rd and 4th visceral arches. These features are accompanied by corresponding modifications of the aortic arches, the 3rd and 4th of which are well developed and deeply seated, while the 2nd is a very slender vessel, which on both sides of the embryo appears already to have become incomplete at the middle of the

arch. Further, the dorsal and ventral aortæ very closely approach each other at the level of the 2nd visceral arch, so that the arterial trunk of this arch is not only very slender but is very much reduced in length as compared with the other aortic arches.

The *arteria pulmonaris* of either side runs in a posterior and slightly medio-ventral direction from the ventral portion of the 6th aortic arch. The *arteriæ basiliares* now make their first appearance as a pair of small vessels originating from a dorsally directed branch of the anterior extremity of the dorsal aorta (*arteria carotis interna*).

*Stage O.*—Of the 1st and 2nd aortic arches only the ventral portions persist in Stage O (Embryo 32, figs. 9 and 10) as short latero-dorsal branches of the ventral aorta, which terminates anteriorly as the *arteria lingualis*, as already noted. The persistent portion of the ventral aorta will in future be referred to as the *arteria carotis externa*, and the anterior portion of the dorsal aorta as the *arteria carotis interna*. A stout artery—now evident for the first time—has developed from the dorsal root of the disappearing 2nd aortic arch and takes an antero-dorsal course, lateral to the *vena capitis lateralis*, anterior to the otocyst, and is eventually distributed to the tempero-facial region. This is the *arteria stapediales* (*a. facialis*, auctorum).

The 3rd, 4th, and 6th aortic arches are still complete, but the 5th has aborted.

*Stages P–S.*—At and after late Stage P (Embryo 45, figs. 11, 12, 14, 15) the arrangement of the arteries and veins closely approximates to that obtaining in the adult.

(i) *Extra-cranial arteries.*—

The arterial system of the auditory and adjacent regions may briefly be summarised as follows:—The 1st and 2nd aortic arches have aborted, but the anterior extremity of the ventral aorta persists as the *arteria lingualis*, the anterior extremity of the dorsal aorta as the *arteria maxillaris*, the dorsal vestige of the 1st aortic arch as the *arteria palatina* (*arteria palatino-nasalis*, VERSLUYS, 1898), while the dorsal root of the 2nd aortic arch gives off the *arteria stapediales* (*a. facialis*, auctorum).\*

TANDLER (1902) has demonstrated a similar blood supply in a Bat embryo.

GROSSER (1901) states that in a Bat embryo the *arteria infra-orbitalis*, instead of being a branch of the *arteria stapediales*, and therefore belonging to the 2nd aortic arch—as in the Human embryo—arises as a separate branch of the *arteria carotis interna* (dorsal aorta). He found also that it “accompanied medially the vidian nerve.” It is obviously equivalent to the *arteria palatina* of *Sphenodon*, both as regards its origin and distribution. These facts suggest that the

\* It appears probable that the *Arteria thyroidea* is derived from a persistent vestige of the ventral portion of the 2nd aortic arch.

condition obtaining in *Sphenodon* embryos is primitive, while that found in Man is a secondary development. It will be seen below (*vide arteria stapediales*) that in considering the fate of the 2nd aortic arch this inference receives additional support.

The 3rd aortic arch may be regarded as the proximal portion of the *arteria carotis interna* of the adult, while the 4th becomes the systemic arch and the 5th has aborted.

The trunk of the dorsal aorta included between the 3rd and 4th aortic arches persists in the adult as the *ductus caroticus*, from which is given off a fair sized artery, which runs in an antero-lateral direction, and is distributed to the muscles of the neck. This is the *arteria muscularis cervicis* (O'DONOGHUE (1917)) (fig. 16). From the ventral portion of the persistent 6th aortic arch arises the *arteria laryngealis*, which runs in an anterior, and the *arteria pulmonalis*, which passes in a posterior direction, the remaining portion of the arch, which connects this artery to the dorsal aorta, being known as the *ductus arteriosus* (*ductus Botalli*). The *arteria carotis externa* (ventral aorta) is now a comparatively small vessel pursuing a postero-anterior course along the latero-ventral wall of the pharynx (figs. 16, 17, 18). After passing just ventral to the thymus gland and *vena capitis lateralis*, it crosses medially the hypoglossal nerve, and runs parallel to and between this nerve and the main trunk of the glosso-pharyngeal, passing forward latero-dorsally across the 2nd cornu of the hyoid cartilage. It gives off a small branch to the thyroid gland—the *arteria thyroidea*, which is apparently to be regarded as the persistent ventral portion of the 2nd aortic arch. On the side of the trachea and dorsal to the thyroid gland is the small *arteria laryngealis*, which lies medial to the more conspicuous *vena laryngealis*. This small artery, as already stated, springs from the ventral portion of the 6th aortic arch, and has been already noted in adult *Sphenodon* by O'DONOGHUE (1917).

The *arteria carotis interna* crosses obliquely in an antero-dorsal direction the medial surface of the thymus gland, passes ventral to the glosso-pharyngeal-vagus ganglion and the *vena jugularis interna*, then bending forward resumes a horizontal course, passing ventro-medially of the *vena capitis lateralis* to a point immediately ventral of the columella (stapes), at which level it bifurcates. The main trunk, which is considerably the smaller of the two branches, then bends away sharply in a ventro-medial direction, lying in close proximity to the latero-ventral surface of the *basis cranii* (parachordal plate) and between it and the pharynx. The second, or dorsal, branch is the *arteria stapediales*, a wide vessel which passes anterior to the columella, crosses laterally the *vena capitis lateralis*, and then, lying close to the surface of the cartilaginous auditory capsule, runs in a bold curve, first dorsally, and then in an anterior direction, into the temporo-facial region. During and after Stage R (Embryo 141, figs. 48, 50) this artery is protected by the overlying squamosal bone (*cf.* Stage S, Embryo 9a, fig. 45).

Immediately dorsal of the point at which the *arteria stapediales* passes medial to the ventral margin of the squamosal bone, a strong arterial branch leaves the anterior surface of the vessel. This artery passes in an anterior direction between the squamosal bone and the auditory capsule, crosses dorso-laterally the third ramus of the trigeminal nerve, and closely accompanied by the *ramus mandibularis* is finally distributed to the lower jaw (figs. 16, 17). It is present also in Stage S (Embryos 11 and 9a), and its origin and distribution indicate that it is the *arteria dentalis inferior*, and must be considered as the homologue of the *arteria mandibularis* of the Human embryo. VERSLUYS (1898) remarks that in adult *Sphenodon* the *arteria facialis (arteria stapediales)* "does not give off an *arteria dentalis inferior* in the tympanic region." I am unable to say whether his statement is correct, but the artery certainly exists in the four embryos of Stages R and S which I examined.

The exact point of origin of this artery appears to be somewhat variable. In *Chameleo vulgaris* (VERSLUYS, 1898), and in the adult *Chameleo vulgaris*, and in a *Lacerta* embryo (GOODRICH, 1915, Plate 11, fig. 8), the *arteria dentalis inferior* originates as a branch of the *arteria stapediales*, but in an adult *Pachydactylus bibronii* (VERSLUYS, 1898) figures but does not describe an *arteria dentalis inferior*, which appears to be a branch of the *arteria carotis interna*.

At about the middle point of its ascent into the temporal region the *arteria stapediales* gives off a branch which runs in a posterior direction, and terminates at a point immediately dorsal to the *foramen jugulare*. This artery is probably to be considered equivalent to the *arteria temporalis posterior* of Man, which identification is rendered more probable by the presence of a dorsally directed branch, leaving it just anterior to the hinder margin of the squamosal bone, and which is evidently the *arteria auricularis posterior*.

These three arteries have not been described or figured by earlier investigators, and their presence affords confirmation of the view expressed below concerning the homology of the *arteria stapediales*.

From the posterior surface of the *arteria stapediales* there arises at a point, slightly anterior and dorsal to the level of the upper surface of the stapes, a small artery, which passes in a posterior direction, crossing dorsally the surface of the stapes, at which level it bifurcates, giving off one branch, which runs parallel with and close to the *chorda tympani*, and is finally distributed to the medial surface of the *tympanic aponeurosis*. A second branch of this artery runs in a slightly postero-ventral direction, and supplies the dorso-lateral wall of the *tympanic diverticulum* of the pharynx. I propose to call this artery the *arteria tympanica* (fig. 16).

Immediately posterior to the point at which the *arteria stapediales* leaves the *arteria carotis interna* there originates from the dorsal surface of the latter a small artery (*arteria hyomandibularis*). This artery first appears at Stage P (Embryo 45a),



in which, leaving the *arteria carotis interna* just posterior to the point of origin of the *arteria stapediales*, it runs in a dorso-lateral direction, being distributed to the mesoblast surrounding the procartilaginous rod which represents the developing stapes. On the right side of the head of this embryo the artery enters the mesoblast and terminates within it, but on the left side the corresponding vessel only comes in contact with, but does not penetrate, the tissue.

In Stage R this artery runs in a postero-dorsal direction, and finally terminates on the wall of the tympanic diverticulum posterior and ventral to the stapes (figs. 11, 14, 16).

In Stage S (Embryos 11 and 9a) this artery is much more conspicuous. In each of these embryos it leaves the dorsal surface of the *arteria carotis interna*, and almost immediately curves in a posterior, and then in a ventral, direction. About midway between the posterior surface of the stapes and the anterior border of the thymus it bifurcates, one branch continues its course in a posterior direction, and reaching the thymus gland, runs in a medial direction across its anterior surface, and is finally distributed to the glandular tissue. The second branch traverses the dorsal and posterior wall of the tympanic diverticulum, and leaving this, runs almost parallel to the muscle branch of the posterior main stem of Nerve VII, and terminates in the *musculus depressor mandibulae*.

In this connection it may be noted that SCHAUINSLAND (1900), in an embryo of approximately Stage R, finds the same artery passing with the muscle branch of the posterior main stem of Nerve VII to the *musculus depressor mandibulae*. He identifies it with a similar artery which VERSLUYS (1898) finds in adult *Varanus*. The former investigator notes that he found this artery "as a single exception in a great number of cases, passing through the stapes directly above the base-plate of the latter; the round hole thus caused in the cartilage made the stapes look singularly similar to the stirrup of the Mammalia." He suggests, therefore, that "this artery is rather to be compared to the *arteria stapediales* of the Mammalia than is the large *arteria facialis*." He considers that a penetration of the stapes by the *arteria facialis* is highly improbable, since the diameter of that vessel is usually greater than that of the cartilage. This latter statement I found to be correct for every embryo I have examined, but the evidence adduced above from my Embryo 45a, Stage P, while at first it may appear to support, does not really confirm, the contention of SCHAUINSLAND that this small artery is homologous with the *arteria stapediales* of the Mammalia. I would rather suggest that the function of this small artery is to ensure the blood supply of the posterior wall of the tympanic cavity, the thymus gland, and the *musculus depressor mandibulae*. I have called it, therefore, the *arteria hyomandibularis*. The *arteria stapediales* (*arteria facialis*) frequently shows a constriction as it passes the stapes (Stage P, Embryo 45a), and it is occasionally somewhat sunken in a groove on the anterior surface of this cartilage (Stage P, Embryo 45a, Q. 51a, and R. 141). These facts

may possibly be adduced as additional evidence in favour of the generally accepted homology between the *arteria stapediales* (*arteria facialis*) of the Reptilia and the *arteria stapediales* of the Mammalia.

The presence of an artery piercing the stapes in many Mammalian embryos was demonstrated by SALENSKY (1880), and although the vessel usually atrophies in Man, it persists in many other Mammals. GOODRICH (1915) records the chondrification of the developing stapes around the *arteria stapediales* in an embryo *Trichosurus*.

All these facts appear sufficiently conclusive to justify the assumption that the *arteria facialis*, or *arteria stapediales* of *Sphenodon* is the homologue of the Mammalian *arteria stapediales*, and I suggest therefore that the latter name for this artery is to be preferred.

In some adult Reptilia (*e.g.*, *Pachydactylus bibronii*), a branch of the *arteria carotis interna* pierces the columella (VERSLUYS, 1898), and in an embryo, *Platydictylus mauretanicus*, the *arteria stapediales* leaves the *arteria carotis interna* posteriorly to the stapes, penetrates this cartilage nearly horizontally, and passes in an antero-dorsal direction into the temporal region (VERSLUYS, 1903). In the different species of Reptilia, in which the *arteria stapediales* does not penetrate the stapes, its position relative to the latter appears to be subject to some variation. In *Sphenodon*, *Chamaeleo* and *Uroplatus*, the course of the artery is ventral and anterior to the stapes, while in *Amphisbæna* and *Lacerta* it passes posterior and dorsal to the cartilage.

I have shown that the *arteria stapediales* is developed from a persistent dorsal vestige of the second aortic arch, and it has been stated (TANDLER, 1902) that the Mammalian *arteria stapediales* is of identical origin. It may here be noted that, in common with the other reptiles, *Sphenodon* retains the primitive condition in which the *arteria stapediales* persists in adult life as a branch of the *arteria carotis interna*, whereas in man a secondary connection is established between its branches (*arteria supra* and *infra-orbitales* and *mandibularis*) and the *arteria carotis externa*, while the main stapediales trunk atrophies.

(ii) *Intra-cranial arteries*.—

I have been able to confirm, and in one or two respects add to, the account previously given by DENDY (1909) of the intra-cranial blood vessels.

The *arteria basilaris*, which appeared at Stage N as a paired structure, undergoes in the auditory region a degree of fusion which increases as development proceeds. This points to the imperfectly fused condition of the *arteria basilaris* persisting in *Sphenodon* being a primitive feature.

HOFFMANN (1900), in *Testudo græca*, and BEDDARD (1905), in *Testudo vicina*, found a completely paired condition of the *arteriae basilares*. The latter observer appears to consider this a divergence from the primitive condition, but as DENDY

(1909, p. 410) points out, the double condition of this artery is more likely to be primitive, which suggestion the present observations strongly support.

At Stage P (Embryo 45*a*) the anterior bifurcation of the *arteria basilaris* occurs just in front of the anterior boundary of the root of Nerve VII; in Stage R (Embryos 141, 142) the fusion has extended to the level of Nerve V, while in the adult DENDY finds it almost midway between the level of the roots of Nerves III and V. In all cases the angle of divergence of the limbs of the bifurcated artery is very acute. Just posterior to the point of bifurcation there is given off at right angles on either side the *arteria medullaris posterior*, which runs in a dorsal and slightly posterior direction, passing immediately in front of the root of Nerve VI (fig. 11), and then to the ventral surface of the anterior ramus of Nerve VIII, and traversing in an antero-posterior direction the ventral surface of the sacculus terminates near the posterior curvature of this structure. This artery corresponds in origin and distribution with the *arteria auditiva* of *Rana temporaria* (GAUPP and WIEDERSHEIM). Just before reaching the root of Nerve VI the artery gives off a small branch which runs obliquely in a postero-dorsal direction over the floor and side of the mid-brain, while a small branch running in an anterior direction is given off just after the main trunk of the artery has passed the root of Nerve VI.

The undivided trunk of the *arteria basilaris* is continued in a posterior direction to bifurcate at an acute angle at a point slightly anterior to the roots of Nerve IX (Stage P), where the diverging limbs form the anterior portion of a narrow and elongated *circus arteriosus spinalis*. In Stage R the fusion has extended in a posterior direction to the level of the roots of Nerve X, while in the adult the point of bifurcation has moved still further backwards and is now found opposite the middle of the group of roots of Nerve XII.

On the roof of the brain are found for the first time at Stage P the paired *arteriæ choroideæ posteriores*, which are the posterior continuation of the *arteriæ bigeminiles*. Each runs along a dorso-lateral angle of the brain tending obliquely towards the mid-dorsal line, passes ventral to the junction of the *sinus transversalis* and the *vena cephalica media*, and terminates just posterior to the *saccus endolymphaticus*. At Stage R, as also in the adult, the artery passes ventromedially of the *saccus endolymphaticus* along the anterior wall of the 4th ventricle to terminate in the region of the posterior choroid plexus.

#### VEINS.

The development of definite venous trunks in the cephalic region occurs considerably later than the appearance of the primitive aortæ, the venous function doubtless being at first performed by a system of lacunæ in the mesoblast.

*Stage J.*—During the earlier period of this phase of development (Embryo 44, fig. 2) no definite venous sinuses or trunks are demonstrable, but in a later embryo

(Embryo 79, figs. 3, 4) there is on either side of the brain near the mid-ventral line a narrow irregular sinus originating in the region of the fore-brain and running in an antero-posterior direction. This is apparently the primitive head-vein (*vena capitis medialis*), less accurately termed *vena cardinalis anterior*, into which vessel however it really passes laterally in the region of the second post-otic somite.

*Stage K.*—In Embryo 39 (figs. 4, 5 and text-fig. 2) this vein is a much more clearly defined trunk although somewhat irregularly dilated and sinus-like from the region of the cranial flexure forwards along the base and side of the fore-brain.

*Stage L.*—In Embryo 50 (fig. 6), the *vena capitis medialis* of either side has become a large vein of fairly uniform calibre pursuing a more directly axial course.

*Stage M* (Embryo 51, fig. 7 and text-fig. 3).—The venous system at this stage exhibits its first considerable increase in complexity. From the dorsal surface of the mid-brain a pair of narrow longitudinal sinuses, apparently connected by a series of small lacunæ, pass in a posterior direction and traverse the dorsal surface of the hind-brain. These represent the developing posterior limb of the *sinus longitudinalis* of adult *Sphenodon*. GRÖSSER (1901) found similar paired venous trunks in an embryo Bat, and these persist in the adult as the *venæ longitudinales mesencephali*. SALVI (1897) found similar veins in *Cavia* and *Lepus*, and it seems probable that a homologue of the *sinus longitudinalis* of Reptilia makes a transitory appearance in all vertebrate embryos. A small vein, apparently the rudiment of the *vena occipitalis communicans*, runs in a longitudinal direction along either side of the mid-brain close to its dorso-lateral angle—which in this stage of development is very conspicuous. The *vena capitis medialis* of either side receives just posterior to the otocyst a vein which runs nearly vertically downwards on the side of the brain. This is the *vena cephalica posterior* now making its first appearance. From the junction of this vessel with the *vena capitis medialis* there curves in a lateral direction a vein the calibre of which soon becomes greater than that of the *vena capitis medialis* itself, and which passing just medial of the glosso-pharyngeal and vagus-accessorius nerve trunks runs in a posterior direction parallel to, but lateral of, the *vena capitis medialis*. This is the *vena capitis lateralis*, which soon extends ventrally and laterally of the otocyst—beyond the posterior border of which it is not yet apparent—into the region of the fore-brain. GRÖSSER and BREZINA (1895) found a generally similar arrangement of the cephalic veins in Reptilia, while a mode of development of the *vena capitis lateralis* identical with that now described, was found in Chick embryos by EVANS (1909) and WILLIAMS (1910).

*Stage N* (Embryo 14*a*, text-fig. 4 and figs. 8 and 13).—From this stage of development onwards the venous system of the auditory region exhibits the main features characteristic of the adult condition. This is described in detail below (Stages R and S) and it is necessary here to note only those vessels in which developmental changes are proceeding.

The *vena capitis lateralis* has now extended into the region of the fore-brain where

it receives, antero-ventrally of the *Gasserian ganglion* a large *sinus post-orbitalis*, while just posterior to the ganglion the vertically descending *vena cephalica media* places it in communication with the *sinus transversalis* which occupies the whole width of the roof of the brain in the region immediately anterior to the otocyst. The *vena capitis lateralis* which hitherto has passed medial to the trunks of Nerves IX and X–XI now proceeds to assume its final position lateral to these. The transition is first effected relative to Nerve IX, by means of a growth of the vein outwards around the nerve trunk which in Stage N, Embryo 14*a*, is seen to be encircled by it. The original, or medial limb of the bifurcated vein then aborts leaving the new venous trunk lying lateral to the nerve. A repetition of this process then ensues in connection with the relation of the vein to the vagus-accessorius trunk before Stage O–P (Embryo 35*a*) is reached, although a slightly younger embryo (Stage O, Embryo 32, figs. 9, 10) still shows the vein lying medially of this nerve trunk. Anterior and posterior to the nerve the *vena capitis lateralis* is slightly dilated, the two lateral diverticula thus produced indicating an approaching envelopment of the nerve trunk. Meanwhile the *vena capitis medialis* has undergone some retrogression and persists as a comparatively slender vein pursuing a course slightly lateral of, and parallel to, the *arteria basilaris*.

*Stage P.*—Before this stage (Embryo 45*a*, figs. 11, 14, 15) is reached this vein appears to undergo a further reduction, the medial portion of the trunk having aborted, the vessel posterior to the level of the root of Nerve VIII persisting as the *vena medullaris posterior*, while the persistent portion anterior to the root of Nerve VI becomes the *vena medullaris anterior*.

On either side of the mid-ventral line a *vena jugularis externa*, which has previously been represented by a small and somewhat irregular antero-posteriorly directed sinus, first appears as a well defined venous trunk at Stage O, its course being approximately parallel to and ventral of that of the *arteria carotis externa*.

*Stages R–S.*—The arrangement of the cephalic veins in embryos of these stages (Stage R, Embryos 141 and 142, Stage S, Embryo II, figs. 16, 17, 18, 45) is practically identical with that obtaining in adult *Sphenodon* (OSAWA (1897), VERSLUYS (1898), DENDY (1909)).

The *vena capitis lateralis* has developed a marked dorso-lateral curvature in the post-otic region. It passes ventral of the thymus and pharynx, crosses the lateral wing of the latter, and runs forward immediately below the parotic process, across the dorsal surface of the stapes and between the *arteria stapediales* and the lateral wall of the auditory capsule. Keeping close to the surface of the latter, the vein passes forward between the *Geniculate* and *Gasserian ganglia* and enters the region of the fore-brain. Immediately posterior to the *Gasserian ganglion* the *vena capitis lateralis* receives the *vena cephalica media*, which, leaving the ventro-lateral surface of the *sinus transversalis*, runs in an antero-ventral direction between the medial wall of the anterior sinus of the auditory capsule and the side of the brain, and,

bending sharply outwards, crosses the postero-dorsal surface of the *Gasserian ganglion*, to enter the *vena capitis lateralis*. It receives at different points of its course a number of small venous branches, which form part of a network on the lateral surface of the brain—in some cases uniting with the *vena choroidea lateralis* or the *vena occipitalis communicans*. The results now recorded confirm the observations of SCHAUINSLAND (1900) and DENDY (1909), the latter of whom found in an embryo of Stage S a communication between the *sinus transversalis* and the *vena cephalica media*. While he did not trace the course of the latter vessel beyond the *Gasserian ganglion*, he accepts as correct SCHAUINSLAND'S statement that in *Sphenodon* embryos he has traced back the *vena capitis lateralis* from this region, and suggests that the *vena cephalica media* may open into the *vena capitis lateralis*. I have verified the presence of this junction between the two veins in embryos of Stages N to S inclusive, and there is no reason to doubt its persistence in adult *Sphenodon*.

The *sinus transversalis* is a large venous sac—somewhat resembling in shape a depressed and truncated pyramid—lying above the roof of the brain below the middle third of the *supra-occipital cartilage*, its apex being dorsally directed, and opening somewhat widely into the *torcular Herophili* (RATHKE). Its base and sides are somewhat hollowed posteriorly by the convex surfaces of the cerebellum and auditory capsule respectively. From the sides of the *sinus transversalis*, just above the base, open the right and left *venæ cephalicæ mediæ*, as already described.

From the *choroid plexus* of the 4th ventricle arise a number of small veins, which unite to form a large sinus-like medial vessel, the *vena choroidea posterior* (sive, *magna*), which in embryos of all stages of development subsequent to Stage O passes forward between and slightly ventral to the *sacci endolymphatici* and above the roof of the brain to enter the torcular region of the *sinus transversalis*. On either side of this vein, and approximately parallel to it, there runs just medial to the dorso-lateral angle of the brain a small and somewhat sinuous vein, which enters the *sinus transversalis* immediately lateral to the point of entry of the *vena choroidea posterior*. These are the right and left *venæ choroideæ laterales* (sive, *parvæ*). As previously stated, there is in all embryos subsequent to Stage O a venous network on the sides of the brain, some branches from which enter the *venæ choroideæ laterales*, some pass forward more medially to enter the *sinus transversalis*, and others communicate with the *vena occipitalis communicans*, *vena cephalica posterior*, or *vena cephalica media* of either side. From the postero-dorsal, or torcular region of the *sinus transversalis*, the *sinus longitudinalis posterior* (*sinus occipitalis posterior*) extends backwards in the *dura mater* immediately below the antero-medial limb of the supra-occipital cartilage, being separated from the *venæ choroideæ* by the extensive sub-dural space. Between, and slightly dorsal to, posterior surface of the *sacci endolymphatici*, the *sinus occipitalis posterior* bifurcates into a right and left *vena cephalica posterior*. Each of these veins curves outwards

and downwards, lying against the surface of the medial wall of the posterior sinus of the auditory capsule. It then turns sharply in a lateral direction, traversing the *foramen jugulare*, through which it leaves the skull, together with, and antero-ventrally to, the proximal portion of the trunks of Nerves IX, X and XI. Remaining closely in contact with the inferior surface of the posterior convexity of the auditory capsule, it passes, first laterally and then ventrally, to enter the *vena capitis lateralis* at a point just anterior to the thymus and postero-ventral to the parotic process. The extra-cranial portion of the *vena cephalica posterior* is evidently equivalent to, and may be called, the *vena jugularis interna*.

With reference to the *vena capitis lateralis* and the *vena cephalica posterior*, it may here be noted that in Man the anterior portion of the former vessel atrophies, and the venous drainage of the entire brain takes place by means of the *vena cerebialis posterior* (= *vena cephalica posterior* of *Sphenodon*), which emerges through the *foramen jugulare* and passes into the *vena jugularis interna*. In some Monotremes the *vena capitis lateralis* persists, that of *Echidna* draining the anterior portion of the brain, while in *Ornithorhynchus*, although the vessel persists, the main drainage is effected by the *vena jugularis interna*. VERSLUYS (1898) has stated that adult *Sphenodon* possesses no *vena jugularis interna*, but this statement is incorrect. SCHAUINSLAND (1900), who appears to have examined an embryo of approximately the same stage of development as DENDY's Stage R, describes such a vein lying in the *foramen jugulare*, and I have now demonstrated its existence in embryos of Stages M to S inclusive. Although the vein (*vena cephalica posterior*) first appears at Stage M, and soon becomes an important trunk (Stage N), both it and the *foramen jugulare* are somewhat less conspicuous at Stage S than in the immediately preceding stages of development. No extensive retrogression of either the vein or the foramen, however, has occurred at this stage, such as VERSLUYS asserts to take place before the adult stage of development is reached. On the contrary, the *vena cephalica posterior* persists, traverses the *foramen jugulare*, and enters the *vena capitis lateralis*. It is therefore an indubitable *vena jugularis interna*. DENDY (1909) affirms its presence in adult *Sphenodon*, and (pp. 420-424) gives, in addition, a comparative account of the intra-cranial venous system of Reptilia, including the observations of earlier investigators concerning this vein.

On either side of the brain a second channel of communication between the torcular *Herophili* and the *vena cephalica posterior* is found in the *vena occipitalis communicans*. This vein leaves the torcular region of the *sinus transversalis*, and, passing in a latero-ventral curve along the superior lateral surface of the brain, unites with the *vena cephalica posterior* just below its point of junction with the *sinus occipitalis posterior*. Its earliest appearance in connexion with the *vena cephalica posterior* is during Stage N, and it persists in the adult, in which it was first described by DENDY (1909).

Immediately posterior to the point of junction of the *vena occipitalis communicans*

and the *vena cephalica posterior* the latter vein receives a large *vena spinalis*, which traverses the ventral surface of the medulla and, pursuing an antero-dorsal course between the roots of Nerve X, unites with the *vena cephalica posterior*. DENDY (1909) has shown that in adult *Sphenodon* the paired *venæ spinales* are continuous posteriorly with the single median and ventral *vena spinalis inferior*.

At Stage P there appears on either side of the roof of the medulla a small unnamed vein (*v.x.*), described by DENDY (1909) in adult *Sphenodon*, which runs in an anterior direction to enter the *vena cephalica posterior* of the same side just posterior to its point of origin from the *sinus occipitalis posterior*.

In Stages R (Embryo 141) and S (Embryos 11 and 9a) there arises in the loose connective tissue dorsal to the supra-occipital cartilage in the region of the *foramina endolymphatica*, and slightly to the right side of the mid-dorsal line, a narrow venous sinus, which runs in a posterior direction. Immediately dorsal to the posterior margin of the supra-occipital cartilage it undergoes considerable dilation into an irregularly oval sinus, which lies in the supra-occipital connective tissue. From the ventral surface of this saccular sinus a narrow vein passes antero-ventrally to open into the right *vena cephalica posterior* just posterior to its junction with the *sinus occipitalis posterior*. This small vein is obviously the anterior branch of the *vena supra-occipitalis* described and figured by DENDY (1909, pp. 414-5, figs. 4, 5). In the three embryos examined I failed to identify the posterior branch of this vein, which is present in adult *Sphenodon* and, like DENDY, I found no supra-occipital foramen in Stages R and S. The *vena supra-occipitalis* lies in contact with the posterior margin of the developing supra-occipital cartilage, which as yet has failed completely to surround it. The *vena medullaris anterior* of either side arises on the floor of the brain just anterior to the root of Nerve VI, and after receiving several small branches, runs nearly parallel to the *arteria basilaris*, finally passing in an antero-lateral direction in front of the root of Nerve V to unite with the corresponding *vena post-geminalis*.

The *vena medullaris posterior* of either side appears on the ventral surface of the brain midway between the posterior root of Nerve VIII, and the *arteria basilaris* runs in a posterior direction, passing between the roots of Nerves X and XII, finally to unite with its corresponding *vena spinalis* just posterior to the roots of the latter nerve in Stage P, but anterior to them in adult *Sphenodon* (DENDY, 1909).

A small *vena cochlearis* runs in an antero-posterior direction along the medio-dorsal surface of the cochlea (*lagena*), and emerges (Stages P-S, figs. 11, 14, 15, 16, 40) through the *foramen rotundum*, uniting with the *vena cephalica posterior* just as it enters the *foramen jugulare*. This vein was first observed in Stage O-P (Embryo 35a), its exit from the developing auditory capsule being noted as occurring at the region in which the *foramen rotundum* ultimately appears. The vessel here penetrates a considerably thinned area of the blastema which is not involved in the ensuing chondrification. The *vena facialis* (*vena mandibularis*, BRUNER) coming from the



mandibular region passes between the quadrato-jugal and quadrate, and runs in a posterior direction ventral and lateral to the lateral tympanic diverticulum, and, passing medially the anterior cornu of the hyoid, enters ventrally the *vena capitis lateralis* opposite the point at which the *vena jugularis interna* enters it dorsally. In the tympanic region the *vena capitis lateralis* receives a small vein, which I propose to call the *vena tympanica*. This vein, which, during and after Stage P, is found in the region of the anterior tympanic diverticulum, traverses *Huxley's foramen* (Stages R and S), and, running almost parallel to the *chorda tympani*, finally unites with the *vena capitis lateralis* just dorsal to the base of the stapes. This is obviously the "*vena comes*" of that branch of the *arteria stapediales* which I have called the *arteria tympanica* (figs. 11, 14, 15, 16).

The *vena jugularis externa* of either side pursues in the auditory region a slightly sinuous course along the dorso-lateral surface of the trachea, passes dorsally and slightly medially to the thyroid gland and receives from it a *vena thyroidea superior*. The latter vein runs obliquely forward from the anterior surface of the gland to enter the ventral side of the *vena jugularis externa* (figs. 16, 17, 18).

Parallel and just dorso-medial to the *vena jugularis externa*, with which it exhibits several anastomoses, is the *vena laryngealis*, a small vein which lies on the dorsal surface of the trachea and between it and the mid-ventral surface of the pharynx.

In conclusion, attention may be directed to the primitive features exhibited by that portion of the vascular system which has now been considered.

The commonly accepted view that the *arteria basilaris* originates as a pair of completely separated vessels (HOFFMANN, 1900, and DE VRIESE, 1905) is confirmed in the case of embryo *Sphenodon*. The progressive fusion subsequently undergone by these primitive arteries also supports the suggestion advanced by DENDY (1909), that the condition of the *arteria basilaris* of adult *Sphenodon* being reminiscent of an ancestral paired condition is a primitive feature. In general, it may be remarked, the results now recorded confirm, and to some extent supplement, those obtained by the latter investigator. The persistence of the *ductus caroticus* and *ductus arteriosus* now noted has already been recorded in adult *Sphenodon* by O'DONOGHUE (1917), as has also the presence of the *arteria laryngealis*, *pulmonalis* and *cervici muscularis* of either side. The progressive reduction and ultimate fate of the 1st and 2nd aortic arches has already been noted, and it is now necessary only to recall the presence of the newly-identified branches of the *arteria stapediales* (the *arteria tympanica*, *dentalis inferior*, *temporalis posterior* and *auricularis posterior*), and to record the fact that *Sphenodon* is similar to other Reptilia in respect of the persistence and primitive nature of the *arteria stapediales*, which has been shown to be derived from a persistent dorsal vestige of the 2nd aortic arch.

As regards the venous trunks of the auditory region the work of earlier observers has been generally confirmed and, in certain respects, considerably supplemented.

The persistence of the *vena cephalica media* and *cephalica posterior* are obviously primitive features.

The observations of DENDY (1909) on the intra-cranial venous system have been confirmed, and in addition the presence of the *venæ facialis, tympanica* and *cochlearis* has been recorded.

It is evident that the arrangement of the blood-vessels in the auditory region of *Sphenodon* is very similar to that found in Lacertilia, but that it exhibits several primitive features—notably as regards the *venæ cephalicæ* and *arteria basilaris*.

#### (D) THE CRANIAL NERVES OF THE AUDITORY REGION.

It has already been stated that the present research does not include a detailed study of the development of these nerves. Their salient features only are described, since some knowledge of these appears to be a desirable supplement to the study of the topographical relationships of the auditory apparatus.

(i) *The Sixth Cranial Nerve, or Nervus Abducens* of each side appears at a comparatively late stage of development. It is first distinguishable in Stage N (Embryo 14a) where it occurs as a slender root attached to the latero-ventral surface of the hind-brain between the *vena capitis medialis* and the mid-ventral line. It lies below the proximal portion of the *acustico-facialis ganglion* at the level of the vestige of the 2nd aortic arch. The slender nerve trunk leaves the surface of the brain in a ventral direction, then turns sharply forward parallel to the mid-ventral line and soon disappears in the mesenchyme below the ventral surface of the hind-brain.

In all subsequent stages it can be identified (as shown in Stage P, Embryo 45a, fig. 11) as a slender nerve arising by a number of fine rootlets which at once unite to form a single root, leaving the ventro-lateral surface of the hind-brain immediately posterior to the *arteria medullaris posterior* and about midway between the *arteria basilaris* and the roots of Nerves VII–VIII. The nerve trunk turns sharply forwards, crossing the ventral surface of the artery and, running somewhat ventrally and laterally, passes ventral to the *arteria carotis interna*, and leaves the auditory region immediately medial to the ventral surface of the Gasserian ganglion.

The late appearance of this nerve has also been noted in the embryo Chick, in which it first occurs during the 4th day of incubation (LILLIE).

(ii) *The Seventh Cranial Nerve, or Nervus Facialis*.—The common rudiment of the facial and auditory nerves (*acustico-facialis neurencygium*) of each side first appears during Stage J (Embryo 79, fig. 3) as a somewhat ill-defined oval mass of periaxial tissue, distinguishable from the surrounding (axial) mesenchyme only by its greater density and the more rounded form of its constituent cells. The *neurencygium*\* lies against the wall of the hind-brain immediately in front of the auditory pit and passes

\* This may be defined as a nucleated tract of cytoplasm, by means of which the auditory end-organ is brought into direct anatomical continuity with the hind-brain (auditory synectium, CAMERON and MILLIGAN, 1910).

antero-dorsally into the inconspicuous preotic neural crest, while its ventral extremity is in contact with the dorso-lateral wall of the pharynx, which structure is, in this region, somewhat laterally expanded to form the rudimentary 1st visceral pouch.

During *Stage K* (Embryo 39*a*, figs. 4 and 5) the neurencytium has assumed a somewhat conical form, and while it still consists of a single undifferentiated mass of cells of the  $\alpha$ -*neuroblast* type, there is a trace of impending differentiation into an antero-ventral (distal) facial, and a postero-dorsal auditory region. A portion of the latter is expanded to embrace the convex anterior wall of the deep auditory pit. The distal extremity of the facial region of the neurencytium is somewhat expanded and is in contact with the dorsal wall of the developing 1st visceral pouch. Here it gives off antero-ventrally along the antero-dorsal surface of the pouch a short blunt outgrowth which is evidently a rudiment of the *pre-trematic ramus* of the *nervus facialis*, and postero-ventrally a well-developed cylindrical rudimentary *post-trematic process* which runs along the postero-dorsal surface of the 1st visceral pouch and passes into the rudimentary 2nd (hyoid) visceral arch.

*Stages L and M* (Stage L, Embryo 50, fig. 6, and Stage M, Embryo 51, figs. 7, 24, and text-fig. 3).

Early during the first of these stages of development a horizontal constriction appears in the middle region of the *acustico-facialis neurencytium*. The portion of the nerve mass lying ventral to this constriction may now definitely be identified as the developing *ganglion geniculatum* and rudimentary nerve trunks. At the constricted neck the nervous tissue of the ganglion geniculatum is continuous with that of the auditory ganglion, and both are still united with the brain by a common root. The developing ganglion geniculatum is a nearly conical mass, the expanded ventral base of which, in contact with the dorsal wall of the 1st visceral pouch, is divided into a short, somewhat broad cylindrical pre-trematic outgrowth, and a more distinctly trunk-like conical post-trematic branch which now extends for some distance in a ventral direction along the posterior wall of the 1st visceral pouch.

In *Stage N* (Embryo 14*a*, figs. 8, 26) the facial portion of the *acustico-facialis* complex is more clearly differentiated into an oval, somewhat vertically elongated geniculate ganglion, and a well developed conical pre-trematic branch which is evidently the developing trunk of the *ramus palatinus facialis*. At the point where this outgrowth leaves the ventral border of the ganglion geniculatum a postero-medially directed short conical branch lies across the dorsal wall of the 1st visceral pouch. This is the rudimentary *ramus communicans internus*. Still more posterior is the post-trematic branch which, at first, is a stout conical outgrowth from the underside of which a thin nerve trunk (the rudimentary *chorda tympani*) passes in a ventral direction, ultimately curving forward below the 1st visceral pouch to terminate in the mesenchyme of the ventral portion of the mandibular arch. The proximal region of the post-trematic branch of the *facialis*

portion of the neurencygium now gives rise to the hyomandibular trunk, or posterior main stem of the *nervus facialis*, together with its branches, all of which are found to be fully developed during the immediately succeeding stages of development.

The uniformity of the conditions obtaining during this period is shown for Stages O (Embryo 32*a*, figs. 9, 10, 35) and O-P (Embryo 35*a*, fig. 32), and the anatomy and distribution of the *nervus facialis* during late Stage P will be now described, the subsequent relationship of the *chorda tympani* to the tympanic diverticula being further discussed in connection with the development of the middle ear.

That the distribution and state of development of the *nervus facialis* remains substantially unchanged subsequent to late stage P, is rendered evident by a comparison of the account now given with the somewhat more brief description of the adult nerve given by OSAWA (1898) and VERSLUYS (1899).

A few minor changes in the topographical relationships of the nerve occur owing to the development of the cartilaginous and bony elements of the cranial skeleton during stages Q, R and S, and these are duly recorded below.

During late Stage P (Embryo 45*a*, figs. 11, 14) the large *acustico-facialis* nerve-root is situated at the middle level of the side of the hind-brain, and is clearly differentiated into an anterior and a posterior portion. From the antero-medial region of the anterior division of the nerve mass the *nervus facialis* is given off in an antero-ventral direction, and at once gives rise to a large bilobed ganglion geniculatum. During Stage P this proximal portion of the *nervus facialis* lies between the side of the hind-brain and the medial side of the antero-ventral wall of the developing pro-cartilaginous auditory capsule, and the ganglion geniculatum lies in a large notch situated at the junction of the parachordal plate with the antero-ventral border of the auditory capsule.

During Stages R and S the *nervus facialis* leaves the *ramus acusticus anterior* at the *foramen acusticum anterior* and enters the *canalis* (or *foramen*) *facialis*, traversing in an antero-lateral direction the medial wall of the pro-otic region of the auditory capsule, finally emerging from the lateral orifice of the *canalis facialis* on the lateral wall of the cranium just ventral and anterior to the anterior sinus of the auditory capsule. Here the large bilobed ganglion geniculatum lies against the orifice of the canal, immediately ventral to the *vena capitis lateralis*, and dorsal to the *arteria carotis interna*.

From the ventral surface of the ganglion geniculatum are given off three stout rami faciales (figs. 11, 14, 17, 18, 41).

*Ramus I* (or *ramus palatinus*) passes in an anterior and slightly ventral direction lying on the dorso-lateral surface of the *arteria carotis interna*, and, lying close to the lateral surface of the *arteria palatina*, passes with this vessel in a ventral direction and so leaves the auditory region. An account of the ultimate distribution

of this nerve is given by OSAWA, and, so far as it has now been followed beyond the auditory region, its course was found to be identical with that described by this observer.

*Ramus II (ramus hyomandibularis)* is the stout main posterior stem of the *nervus facialis* which leaves the postero-ventral border of the ganglion geniculatum and runs in a posterior direction, lying against the ventro-medial surface of the *vena capitis lateralis*. Some distance anterior and ventral to the stapes the *ramus hyomandibularis* divides into two fairly stout and two more slender branches:—

(a) A slender *ramus recurrens*, which passes in a dorsal direction lateral to the *vena capitis lateralis* and assuming a position close to the medial surface of the *arteria stapediales*, passes in a dorsal and anterior direction with this vessel, ultimately lying on the dorso-lateral wall of the auditory capsule slightly ventral to the forwardly directed artery which it accompanies into the temporal region.

(b) After the *ramus recurrens* has left the main posterior stem of the *nervus facialis* there is given off ventrally a second slender branch, the *ramus communicans externus*, which passes in a ventral and posterior direction. It crosses the medial surface of the *arteria stapediales* and passes immediately ventral to the stapes, and lying on the dorso-medial surface of the *arteria carotis interna*, pursues its course in a posterior direction, ultimately to unite with the medial limb of the loop formed by *Ramus III* (the *ramus communicans internus* described below) around this vessel, with which it enters the *ganglion petrosum*.

The stouter third and fourth branches of the *ramus hyomandibularis* remain closely united, and run in a posterior direction passing slightly in a lateral direction and lying latero-ventrally to the *vena capitis lateralis*, accompanying this vessel as it crosses the dorsal surface of the stapes. The two branches separate above the anterior border of the stapes.

(c) The third (or latero-ventral of the two branches) is the *chorda tympani*. This passes parallel to, and above, the dorsal surface of the developing stapes in Stage P until it reaches the lateral extremity of this structure, at which point it turns abruptly in an antero-ventral direction, then turns in a ventral direction, passes slightly backwards, and then in an anterior direction, to terminate in the proliferating procartilaginous posterior portion of the developing Meckel's cartilage. A detailed account of the course of this nerve during the stages of development subsequent to late Stage P is deferred, and is included in the description of development of the middle ear.

(d) The fourth, or postero-dorsal branch, is the *ramus muscularis*. This continues in a posterior and slightly lateral direction, passing ventro-lateral to the parotic process and dorso-medial to the dorsal extremity of the 1st cornu of the hyoid, at which point it divides into two branches. Of these, one (which ultimately divides into two smaller rami) is distributed to the *musculus depressor mandibulae*, and the other passes still further in a posterior direction medial to the descending

region of the *vena jugularis interna*. Its ultimate distribution was not determined.

*Ramus III (ramus communicans interna).*

This nerve leaves the ventral surface of the ganglion geniculatum just posterior to the origin of the *ramus palatinus*, and runs in a posterior direction. Its course is at first latero-dorsal and then medio-ventral of the *arteria carotis interna*. In the tympanic region, as SCHAUINSLAND (1900) remarks, this nerve lies approximately parallel to, but always ventral of, Ramus II, and it thus avoids the stapes, ventral to which it passes, being separated from it by the *arteria carotis interna*. Just posterior to the point at which the latter vessel gives off the *arteria stapediales*, the nerve divides into two branches, which run respectively in a dorso-medial and a dorso-lateral direction, forming a loop around the artery, the branches ultimately uniting with one another and with the *ganglion petrosum*, and finally leave the latter in a posterior direction as a portion of the superficial trunk of the *nervus sympatheticus* (fig. 41).

In addition to these main rami of the *nervus facialis*, there are found during Stages R and S two fine connecting branches, one of which unites the *ramus communicans interna* with *Ramus II (ramus hyomandibularis)*, or main posterior-stem of the *nervus facialis*. It leaves the latter nerve just posterior to the ganglion geniculatum, and runs in a postero-ventral direction along the cranial wall, passing medial to the *arteria carotis interna*, to unite with the *ramus communicans interna*. A second similar fine connecting branch unites the same two nerve trunks at a point some distance in front of and ventral to the stapes. VERSLUYS (1899) finds these two fine connecting branches in adult *Sphenodon*, and notes that neither he nor FISCHER (1852) found any similar nerve connections in *Lacertilia*.

(iii) *The Ninth Cranial Nerve (Nervus Glossopharyngeus).*

The *nervus glossopharyngeus* of each side first appears during Stage J as a mass of periaxial tissue of very indefinite outline, and situated immediately behind the auditory pit (*Stage J*, Embryo 79, fig. 3). In *Stage K* (Embryo 39, figs. 4 and 5) the rudimentary neurencygium is more clearly defined, and is then seen to originate dorso-medially to the auditory pit as a very thin strand of dense tissue, which curves backwards and in a ventral direction posterior to the auditory pit, its expanded ventral extremity lying in contact with the dorsal surface of the developing 2nd visceral pouch.

Little change in the appearance of this primitive nerve-tract occurs in *Stage L*, although it assumes a more definitely cylindrical form with a distal enlargement, which is apparently a rudimentary ganglion petrosum, situated immediately dorsal to the 2nd visceral pouch (fig. 6).

In *Stage M* (Embryo 51, figs. 7, 24) the developing nerve tract shows distinct

differentiation into three regions, a swollen proximal portion consisting of a number of incompletely differentiated roots attached to the medial surface of the hind-brain, a medial narrow cylindrical nerve trunk, and distally an oval developing *ganglion petrosum*, the ventral surface of which passes into the "placode," situated postero-dorsally to the 2nd visceral cleft, and gives off a short conical postero-ventral outgrowth, which passes into the 3rd visceral arch immediately posterior to the 2nd visceral pouch.

In *Stage N* (Embryo 14*a*, fig. 8) the nerve trunk is seen to be encircled by the two limbs of the bifurcated *vena capitis lateralis*, which vessel is now in process of taking up a position lateral to the nerve, on the medial side of which it originally appeared. A more definite downward growth of the nerve trunk into the 3rd visceral arch has also taken place.

In *Stage O* (Embryo 32*a*, figs. 9, 10) the *nervus glossopharyngeus* is seen to possess two stout roots, by which it is connected with the lateral surface of the hind-brain. The *ganglion petrosum*, which lies medio-ventral to the *vena capitis lateralis* and dorso-lateral to the *arteria carotis interna*, is now more conspicuous than during the immediately preceding stage of development.

In *Stage P* (Embryo 45*a*, figs. 11, 14) the proximal portion of the *nervus glossopharyngeus* lies in the anterior portion of the inner space between the auditory capsule and the developing exoccipital cartilage. The stout nerve trunk is seen to leave the lateral wall of the hind-brain by three roots, the most anterior of which is the largest, and is somewhat widely separated from the other two. The main trunk of Nerve IX enters the anterior portion of a ganglionic mass, the main portion of which is contributed by Nerves X and XI. Immediately on leaving this, it again swells out into the rounded *ganglion petrosum*, into the anterior portion of which enters the *ramus communicans interna facialis*, and which lies between the *arteria carotis interna* and the *vena capitis lateralis*.

During *Stages Q, R, and S* the condition of the nerve is similar to that described by OSAWA (1897) and VERSLUYS (1899) for the adult condition, and in greater detail by SCHAUINSLAND (1900) for a later embryo. The nerve now enters, and forms the anterior portion of, a large bilobed ganglion which lies between the brain and the proximal portion of the *foramen jugulare* (figs. 17, 18, 41). The nerve trunk then traverses the foramen, the anterior portion of which it occupies, and swells up into the rounded *ganglion petrosum*. It then passes between the medial surface of the *vena capitis lateralis* and the antero-lateral border of the thymus gland, and runs ventrally to emerge below the *vena capitis lateralis*. It continues its course ventrally and slightly laterally, passing between the posterior surface of the dorsal portion of the 2nd cornu of the hyoid and the *nervus hypoglossus* (Cranial Nerve XII). It then crosses lateral to the cornu, and reaching the posterior surface of the 1st (anterior) cornu of the hyoid passes downwards and forwards in contact with it, and finally leaves the auditory region.

(iv) *The Tenth (Vagus), Eleventh (Spinalis accessorius), and Twelfth (Hypoglossus) Cranial Nerves.*

Since a considerable portion of each of these nerves lies outside the auditory region, none of them is exhaustively described, and owing to the circumstances of their origin, it is convenient to include in a single statement the early stages of their development.

The rudiments of these nerves appear somewhat later than those of Nerves V, VII-VIII, and IX. At *Stage K* the periaxial tissue from which the rudiment of the *nervus glossopharyngeus* is formed is very ill-defined at its posterior end, and cannot clearly be distinguished from the surrounding mesenchyme. The formation of the 3rd visceral pouch appears to be followed by a splitting-off of the posterior portion of the periaxial tissue, and from the dorso-ventrally elongated, ill-defined mass of tissue thus partly isolated presumably originate the rudiments of Cranial Nerves X, XI, and XII.

Only an ill-defined tract of tissue, the ventral extremity of which is in contact with the dorsal wall of the 3rd visceral pouch, is evident in *Stage L* (Embryo 50, fig. 6), but an extension of this mass into the dorsal region of the 4th visceral arch is evident in *Stage M* (Embryo 51, fig. 7). This is the first unmistakable sign of the presence of a definite rudimentary vagus trunk. This consists proximally of a mass of partly divided strands of developing nerve tissue arising from the lower portion of the dorsal third of the lateral wall of the hind-brain immediately posterior to the root of the developing *nervus glossopharyngeus*. A cylindrical trunk extends to a point just dorsal to the 4th visceral arch, where it ends in a swollen distal extremity, which shows incipient bifurcation into a short conical antero-ventral limb, which terminates in the placode situated on the postero-dorsal wall of the 3rd visceral pouch, and into a somewhat longer and more slender branch, which passes backwards and in a ventral direction over the dorso-lateral surface of the 4th visceral pouch into the rudimentary 5th visceral arch.

In *Stage N* (Embryo 14a, fig. 8) there appear posterior to the roots of this nerve a network of fine roots, from which the rudiments of Nerves XI and XII appear to grow in a ventral and slightly posterior direction. The anterior surface of the ventral region of Nerve X is still in contact with the postero-dorsal wall of the 3rd visceral pouch, the terminal ganglion (rudimentary ganglion nodosum) is well developed and is united dorsal to the 4th (and rudimentary 5th) visceral pouch with an irregular ganglionic mass, which extends in a posterior direction beyond the limits of the auditory region and into which pass the rootlets mentioned above. These rootlets and the ganglion evidently represent respectively the roots of Nerves XI and XII and the posterior portion of the bilobed ganglion, which is ultimately found in the *foramen jugulare* during Stages R and S and in the adult condition. Apparently, Nerve IX does not enter this ganglion until its trunk and those of Nerves X and XI approach one another at this point subsequent to the obliteration of the 3rd visceral pouch, by which structure they are now separated.



In *Stage O* (Embryo 32*a*, figs. 9, 10) the *nervus vagus* is a stout cylindrical trunk, leaving the brain by two of the most anterior of a number of interlacing roots, and passing lateral to the *vena capitis lateralis* (which partly encircles it), and dividing into three stout branches, of which the anterior passes into the 4th visceral arch, the central and much stouter ganglionic mass gives off a short branch into the 5th visceral arch and a posterior trunk leaves the dorsal region of the ganglionic mass and runs in a postero-dorsal direction across the lateral surface of the descending *vena capitis lateralis* to leave the auditory region. Posterior to the roots of Nerve X occur several fairly stout roots, from the more anterior of which is given off the proximal portion of the trunk of Nerve XI, which immediately passes from the auditory region in a posterior direction. Apparently, the roots lying behind those just mentioned give rise to Nerve XII, the course of which was not followed in this embryo.

The conditions obtaining in *Stage P* (Embryo 45*a*, figs. 11, 14) are generally similar to those described. Subsequent to the assumption by the *vena capitis lateralis* of a position lateral to the trunk of Nerve X, and the reduction of the 3rd visceral pouch, the trunks of Nerves IX, X, and XI now enter a large incompletely trilobed ganglion, situated ventro-medially to the *vena capitis lateralis* and dorso-medially to the *arteria carotis interna*. This ganglion, which persists in the adult, is more fully described below. Nerve XII is now seen to leave the undersurface of the hind-brain by a series of five fine roots, situated ventro-medially to the roots of Nerve X and between the *vena medullaris posterior* and the bifurcated *arteria basilaris*. These roots leave the cranial cavity by an antero-posteriorly arranged series of four small foramina in the exoccipital region of the parachordal cartilage. So few changes in the appearance and extent of distribution of these nerves occur subsequent to late Stage P that only a description of their relationships during Stages R and S need here be given for the purpose of comparison with SCHAUINSLAND'S account of their distribution in a late embryo and with the condition described by OSAWA in adult *Sphenodon*.

*The 10th, 11th and 12th Cranial Nerves during Stages R and S.* (Stage R, Embryo 141, figs. 17, 18, 41.)

Within the *foramen jugulare* lies the conspicuous, incompletely trilobed ganglion, into which enter the numerous roots of Nerves IX, X, and XI. The two roots of Nerve IX unite to form a single strong cord which enters the ganglionic mass of which Nerve IX forms the anterior portion. Immediately posterior to these, first a dorsal group of rootlets, and then a similar ventral group, pass into the ganglion, each group as a stout nerve-cord. These are the roots of Nerve X. Still more posterior, there leaves the brain another group of rootlets somewhat dorsal to those last mentioned, and these are joined by a nearly horizontally and anteriorly directed group of filaments, which unite into a single root which can be traced backwards to its origin from the wall of the cervical spinal cord by a number of fine rootlets situated between the roots of cervical (spinal) Nerves II and III.

Examination of transverse sections of the above-mentioned ganglion shows it to be composed of three component parts—slightly differentiated externally—and between which the passage of few communicating fibres can be observed. These component parts are a small anterior portion derived from the *nervus glossopharyngeus*, a large central portion composed of *vagus* elements and a small postero-ventral mass derived from the *nervus spinalis accessorius*. The *nervus vagus* leaves the ganglion, and passes in a caudal and ventral direction over the dorso-lateral surface of the thymus gland, and then forms a large oval *ganglion nodosum*. The further course of this nerve trunk lies outside the auditory region. It is described by OSAWA (1897).\*

In figs. 17, 18, of Embryo 141, Stage R, are shown those portions of the superior laryngeal and inferior laryngeal branches of Nerve X which lie within the auditory region. These branches here run almost parallel to one another. The *ramus laryngeus superior* passes in a postero-anterior direction along the ventral wall of the pharynx, just dorso-lateral to the thyroid gland and dorsal to the posterior extremity of the 3rd cornu of the hyoid, crosses medial (dorsal) to the 2nd cornu, and runs forward parallel and medial to the *arteria carotis externa*. The *ramus laryngeus inferior* pursues a nearly parallel course along the dorso-lateral surface of the trachea in contact with the dorso-medial wall of the *vena jugularis externa*.

*Nerve XI.*—The *nervus spinalis accessorius* leaves the postero-lateral surface of the ganglion, crosses dorso-laterally to the main trunk of Nerve X just above and anterior to the *ganglion nodosum*, and, running in a postero-ventral and slightly lateral direction, leaves the auditory region.

*Nerve XII.*—The roots of the *nervus hypoglossus* originate on the ventral surface of the hind-brain immediately ventral and posterior to the roots of Nerve X. In Stages R and S these roots are reduced to four in number, and they leave the cranial cavity by an antero-posteriorly arranged series of three small foramina, the most anterior of which perforates the basal region of the pleurooccipital cartilage immediately ventral to the posterior boundary of the *foramen jugulare*. In the adult condition only two foramina persist (HOWES and SWINNERTON, 1901). These roots unite to form one main nerve-trunk which passes between Nerves X and XI, where they separate immediately posterior to the root-ganglion of Nerves IX, X and XI. The nerve trunk then passes in an antero-ventral direction, traversing the latero-dorsal surface of the thymus gland, and runs parallel and medio-ventral to the *nervus glossopharyngeus* to reach the lateral surface of the 2nd cornu of the hyoid, which it crosses immediately ventral to the *arteria carotis externa*, closely parallel and ventral to which it runs along this cornu, together with which it finally leaves the antero-ventral of the auditory region.

\* Professor DENDY kindly permitted me to dissect the neck region of an adult *Sphenodon*, and I was thus able to verify OSAWA'S account of the distribution of the branches of this nerve.

It is obvious that the distribution of the nerves is practically identical during Stages R and S with that in the adult condition as described by OSAWA.

#### IV. THE INNER EAR AND THE AUDITORY NERVE.

In the Introductory Section of this paper it was noted that, except for passing references in the papers of DENDY (1899) and SCHAUINSLAND (1900), current Zoological literature contains practically nothing concerning the Embryology of either the Inner Ear or the Auditory Nerve of *Sphenodon*. The auditory organ and nerve of the adult have been briefly described by GÜNTHER (1867), RETZIUS (1881), and in greater detail by OSAWA (1898), while GISI (1907) includes the Auditory Nerve in her paper on the Brain and Cranial Nerves.

The development of the Inner Ear of Reptiles other than *Sphenodon* has received but little more attention. The embryogeny of that of *Tropidonotus* was investigated by RATHKE (1842) and by HOFFMANN (1889), who also described the development of the Inner Ear of *Lacerta*.

The more recent researches of VILLY (1890), KRAUSE (1890, 1901), AYERS (1892), C. HILL (1900), RÖTHIG and BRUGSCH (1902), STREETER (1906, 1915), LILLIE (1908), and CAMERON and MILLIGAN (1910), while adding much to our knowledge of the development of the Inner Ear of other classes of Vertebrates, contribute but little to that of Reptilia.

A list of the works of these, and of other investigators referred to in the text, is given in Appendix II.

#### *Stage H.*

The earliest rudiment of the auditory organ can first be identified in an embryo of Stage H. Unfortunately no sections of an embryo of this stage of development are available for examination, the single specimen having been mounted whole (fig. 1).

Paired *epiblastic patches*, which evidently constitute the *primitive auditory epithelium*, are situated one on either side of the head, on the dorso-lateral surface in the posterior region of the hind-brain, and just anterior to the somewhat ill-defined 2nd pair of mesoblastic somites. Comparison of this embryo with a Chick embryo of approximately the same stage of development reveals remarkable similarities between them in all important features, and since in such an embryo C. HILL (1900) locates the rudimentary auditory organ between Neuromeres IX and X, while LILLIE (1908) places it opposite to Neuromere X, it appears probable that a similar position should be assigned to this structure in the *Sphenodon* embryo.

So far as can be ascertained, the auditory epithelium consists at this stage of a single layer of columnar cells, each of which contains a single large oval nucleus. No rudiment of the auditory nerve can be identified in this embryo.

*Stage J.*

An embryo, only slightly older than the foregoing, has been assigned to early Stage J (Embryo 44, fig. 2). In this embryo the central portion of the auditory epithelium of either side has become slightly sunken, the shallow depression thus produced forming the rudiment of an auditory pit. This is nearly circular, and has a diameter of 0.32 mm. and a maximum depth of approximately 0.08 mm. It is now possible to state that the single layered auditory epithelium consists of tall columnar cells with scanty cytoplasm. The basal third of each cell contains a single large, oval, finely granular nucleus. The existence of any connection between the auditory organ and the brain cannot definitely be affirmed, although in several transverse sections a thickening of the tissue immediately underlying the auditory epithelium is apparent, and suggests the approaching formation of a neurencytium. It is impossible, therefore, to postulate the existence of any rudiment of an auditory nerve, although both VILLY (1890) and KELLICOTT (1913) state that *Frog* embryos of approximately the same stages of development as those (H and early J) above described exhibit a strand of cells uniting each of the auditory epithelial patches with the latero-dorsal surface of the brain. They regard each of these cell-strands as a developing auditory neurencytium, and KELLICOTT in particular holds that the auditory epithelial patch is a placode similar to those which are formed during later stages of development as transitory superficial epiblastic structures in connection with Nerves V, VII, IX and X.

In an embryo of late *Stage J* (Embryo 79, fig. 3 and text-fig. 1) each of the paired auditory pits is much deeper—especially in the anterior and ventral regions—than the shallow depressions in the auditory epiblast of the earlier embryo described above. The antero-posterior axis of the auditory pit, approximately 0.28 mm. in length, is slightly longer than the dorso-ventral (0.25 mm.), and the maximum depth of the interior concave surface of the pit below the general surface of the head is approximately 0.11 mm. A transverse (dorso-ventral) section through the middle of the auditory pit shows it to be shaped like a letter J, with its longer limb slightly inclined in a dorso-medial direction and the extremities of the letter representing the lateral and latero-dorsal boundaries between the epiblast of the auditory pit and that of the surface of the head. The columnar epiblast cells are slightly more elongated in the ventral than in the medial anterior or posterior walls of the auditory pit, but in no other respect does its structure differ from that of the earlier embryo of the same stage.

The *auditory neurencytium* can be identified for the first time during late Stage J (Embryo 79, fig. 3 and text-fig. 1). No neural crest can be distinguished in the auditory region, but there occurs, just anterior to each of the auditory pits, an ill-defined ovoid mass of tissue, slightly more dense than the adjacent axial mesenchyme, with its longer axis directed antero-ventrally. It is presumably to be

considered as derived from the "periaxial layer," and consists of a mass of large, finely granular nuclei, surrounded by very scanty cytoplasm. The nuclei near the centre of the mass are nearly spherical, while those more superficially situated are oval, and gradually merge into the axial mesenchyme, which consists of more sparsely scattered elongated and fusiform cells. This dense mass is evidently the primordium of the *acustico facialis neurencytium* (Nerves VIII and VII), the cells of which, at this stage, appear to be of the  $\alpha$ -type of neuroblast (CAMERON and MILLIGAN, 1910).

*Stage K* (Embryo 39, figs. 4, 5, and text-fig. 2).

*The Auditory Pit.*—At this stage the auditory pit of either side is found to have undergone slight displacement in a latero-ventral direction, its ventral border extending very slightly below, instead of being somewhat above, that of the brain. Its anterior and posterior surfaces have become considerably more convex, as has also, to a lesser degree, its medial surface. While the antero-posterior axis of the auditory pit, now 0.22 mm. in length, is but little greater than that of the above-described embryo of late Stage J, there has been a considerable increase in its dorso-ventral diameter, the length of which is now 0.35 mm., while the depth of the pit has doubled, and is at present 0.25 mm. Owing to a marked overgrowth from both the anterior and the posterior margin of the originally shallow auditory pit it has now become more nearly hemispherical, and an ultimate closure of the existing aperture, and consequent conversion of the pit into a sac (otocyst) is clearly indicated. As a result of these marginal overgrowths the auditory pit has, at this stage, an elliptical and vertically elongated lateral aperture occupying the dorsal third of the lateral surface of the auditory region of the head. The ventral lip of the pit also exhibits a tendency to grow vertically upwards. All these changes obviously presage an early closure of the pit, the antero-posterior diameter of which is about two-thirds of the length of its dorso-ventral diameter, while a median transverse section of the pit is nearly semi-circular in shape.

The nuclei of adjacent epithelial cells of the wall of the auditory pit, especially those of its ventral region, are situated at different levels, although almost invariably remaining in the basal half of the cells. Thus in a typical section several rows of nuclei appear and a multi-layered condition is sometimes suggested, although the auditory epithelium consists of a single layer of cells closely packed, much elongated, and frequently tapering.

*The Auditory Nerve (nervus acusticus).*—Owing to the increasing convexity of the auditory pit only about one-third of its antero-medial wall is in contact with the posterior surface of the *acustico facialis neurencytium*. The latter appears to taper off antero-dorsally into the periaxial layer, and the neuroblasts of its dorsal region are apparently continuous with those of the hind-brain, although the state

of preservation of the available embryos does not justify a definite assertion of such continuity. The neurencygium still consists of a dense mass of tissue, the cells being of the undifferentiated  $\alpha$ -neuroblast type. It is more clearly defined than was that of the above-described embryo of late Stage J. It has now assumed an elongated figure-of-eight (8) shape, the upper half of the figure representing the dorsally situated auditory portion of the neurencygium, while below the shallow constriction lies the ventral or *Facialis* portion of the neural mass, the ventral surface of which fuses with the epiblast of the dorsal extremity of the 1st visceral pouch.

*Stage L* (Embryo 50, fig. 6).

The *otocyst* which has resulted from the almost complete closure of the original aperture of the auditory pit is now open to the exterior by only a small aperture situated on the dorso-lateral surface of the head, and occupying the position of the upper part of the original opening. The main portion of the *otocyst* is approximately spherical, but is somewhat flattened latero-medially, while on its dorsal surface there is a small ovoid prominence the height of which is equal to about one-sixth of that of the main sac. There is still a small circular aperture at the more acute and laterally directed extremity of this prominence, by which its lumen communicates with the exterior, and at the circumference of which the cubical epithelium (epiblast) of its wall is continuous with the flattened epithelium (epiblast) of the surface of the head. The dorsal prominence, which is the rudimentary *ductus endolymphaticus*, extends inwards from the surface of the head to open into the cavity of the *otocyst* by a large aperture on the dorsal surface of the latter.

In this embryo the measurements of the *otocyst* (exclusive of the endolymphatic duct) are: Dorso-ventrally, 0.33 mm.; antero-posteriorly, 0.37 mm.; and latero-medially, 0.22 mm.

It is obvious that the marked change in shape of the *otocyst* during the transition period between Stages K and L is due to rapid antero-posterior extension unaccompanied by appreciable growth in any other direction, whereby the antero-posteriorly flattened auditory pit of the previous stage has become almost spherical. The process appears to have been most active in the middle region of the lateral wall, where it has resulted in the closure of the ventral part of the previously existing aperture, thus converting the auditory pit of Stage K into the auditory sac of Stage L.

A comparison of the Embryos of Stages J, K and L, above described, indicates that the sequence of events resulting in the closure of the auditory pit is as follows:—During late Stage J the anterior and antero-ventral regions of the margin of the shallow auditory pit extend in a posterior and postero-dorsal direction respectively. This process is immediately followed by a corresponding forward growth of the

posterior margin of the pit. During the earlier phases of Stage K a considerable lateral convexity is developed and the ventral margin of the pit commences to grow in a dorsal and slightly lateral direction. This upward growth of the ventrolateral margin of the auditory pit continues during the later period of Stage K. By the time Stage L is reached the overgrowths above described have resulted in the reduction of the wide lumen characteristic of the earlier stages of development (e.g., Stages H-J) to a narrow circular dorsal aperture, whereby the lumen of the newly-formed otocyst remains in connection with the exterior.

The wall of the rudimentary *ductus endolymphaticus* and that of the extreme dorsal region of the otocyst consists of a single layer of cubical epithelial cells, each of which contains a single large and nearly spherical nucleus. This cubical epithelium is evidently derived from the columnar cells more nearly resembling those of the early auditory epithelium which still constitute the greater portion of the lateral wall, and the middle third of the medial, anterior, and posterior walls of the otocyst. A transitional epithelium intermediate in character between these two types is found in the wall of the lower part of the upper third of the otocyst, while the basal region is occupied by much elongated and tapering columnar cells, exhibiting several rows of oval nuclei.

*The Auditory Nerve.*—The *acustico facialis neurencygium* is now divided by a well-marked constriction into an antero-ventral or facial portion (developing geniculate ganglion) and a postero-dorsal auditory portion. The latter is a large pyriform ganglionic mass with its long axis lying in an antero-posterior and slightly medial direction. Its posterior surface is hollowed to receive the antero-ventral convexity of the wall of the otocyst, immediately anterior and slightly central to which it lies. Dorso-medially a short cylindrical outgrowth unites the developing auditory ganglion with the brain.

#### *Stage M.*

*The Otocyst.*—A further change in the shape of the otocyst is observed in Stage M (Embryo 51, figs. 7, 23, 24, and text-fig. 3). While the dorso-ventral axis of the otocyst remains practically unchanged (0.35 mm.), the antero-posterior diameter of the structure has undergone considerable reduction, and there is a corresponding increase in its latero-medial axis, these being respectively 0.22 mm. and 0.31 mm. in length.

It is obvious, therefore, that there has been no appreciable growth of the otocyst during the interval between Stages L and M, and the change of shape it has undergone appears to have resulted from the backward extension of the cranial flexure which is to be noted at this stage, and has apparently involved that part of the auditory region within which the otocyst is situated. This has caused an antero-posterior flattening and a corresponding latero-medial expansion of the developing auditory organ.

The *ductus endolymphaticus* is now more clearly defined as a tubular connection between the otocyst and the surface of the head, whereby the cavity of the former still communicates with the exterior. The proximal portion of the tube opens into the otocyst by an oval aperture, which, since Stage L, has shifted somewhat in a medio-ventral direction, and is therefore situated on the dorso-medial, instead of the dorsal, surface of the otocyst. The tube, after running first dorsally and then laterally, opens to the exterior by a small nearly circular distal aperture on the dorso-lateral surface of the head.

The structure of the walls both of the otocyst and of the *ductus endolymphaticus* is similar to that observed during Stage L, but the outline of the thickened epithelium occupying the nasal portion of the otocyst is now somewhat more clearly defined (fig. 23).

It forms a cup-like patch which includes the whole of the ventral region, together with about one-sixth of the lateral and nearly one-half of the medial wall of the otocyst, lining in all about one-third of its interior surface. The multi-layered appearance previously noted is particularly conspicuous in the medio-ventral region, and there is no clear delimiting surface separating the basal nuclei of this primitive sensory epithelium from those of the neurencytium which is in contact with it, although doubtless a *membrana limitans* similar to that found by CAMERON and MILLIGAN (1910) in Human, Frog, and Rabbit embryos is present. LILLIE (1908) proposes for this primitive sensory epithelium the name "*neuro-epithelium*," and this term will henceforth be applied to such sensory (auditory) epithelium until it differentiates into "hair" cells and "supporting" (interstitial) cells.

The *Auditory Nerve*.—The auditory portion of the *acustico facialis neurencytium* is an approximately hemispherical mass of undifferentiated neuroblasts continuous dorso-medially with the wall of the brain. The somewhat constricted neck of tissue connecting the neurencytium with the brain joined the latter at the junction of the middle and dorsal thirds of its lateral wall. The postero-dorsal surface of the auditory neurencytium is hollowed to receive the antero-ventral convexity of the wall of the otocyst, while antero-ventrally a well marked constriction separates the facial from the auditory portions of the neurencytial complex.

*Stage N* (Embryo 14a, figs. 8, 25, 26 and text-fig. 4).

Attention has already been directed to the very considerable antero-posterior thickening of the 2nd visceral arch of this embryo, and to the corresponding elongation of that part of the auditory region lying between the 1st and 2nd visceral pouches.

The simultaneous growth of the otocyst produces a striking change in its shape and size, its antero-posterior axis now being 0.66 mm. in length, or more than twice as long as that of the embryo last described. The dorso-ventral axis, which has undergone less elongation, now measures 0.50 mm., while in the latero-medial



direction practically no growth has occurred, the length of this axis now being 0.36 mm.

The *otocyst* is approximately ovoid in shape, with a nearly horizontal antero-posterior major axis, its posterior extremity exhibiting a small, somewhat acute peak, while its anterior surface is rather more rounded. Its dorsal half is somewhat latero-medially compressed, and is traversed in an antero-posterior direction by a low dorsal ridge or crest. A shallow groove arises on the antero-ventral surface of the *otocyst*, and passes in a posterior and slightly dorsal direction, traversing the medial lateral and posterior surfaces of the organ. The *otocyst* is thus differentiated externally into a large dorsal *pars superior* and a small ventral, and slightly postero-medial, *pars inferior*, the volume of the latter being equal to only about one-tenth of that of the former.

The *pars superior* ultimately gives rise to the three *membranous canals* and the *utricle*, while the *pars inferior* differentiates into the *sacculus* and *cochlea* (*lagena*). The dorso-lateral extension of the *pars superior* has produced an apparent shifting, in a ventral direction, of the proximal portion of the *ductus endolymphaticus*, which is now a latero-medially flattened tube opening into the cavity of the *pars superior* by a vertically elongated oval aperture situated just dorsal to the centre of the medial wall of the *otocyst*. The ductus runs dorsally and then slightly medially, its distal third being directed anteriorly and swollen into an elliptical, rudimentary *saccus endolymphaticus*. This apparently does not develop from that part of the ductus which, in earlier stages of development, communicated with the exterior by an opening situated on the latero-dorsal surface of the head, but appears to originate as a dorso-medial dilatation situated in the middle third of the ductus. At this stage the length of the ductus (including the developing saccus) is about 9.28 mm., while its antero-posterior diameter is approximately 0.09 mm.

The wall of the *otocyst* is composed of a single layer of epithelium, the cells of which are cubical over the dorsal two-thirds of the lateral and one-third of the medial surface, passing somewhat abruptly into columnar epithelium in the ventral portion of the *otocyst*. The cells of the columnar epithelium are much elongated on the lateral wall immediately above and below the groove, while on the medial wall the thickness is not interrupted by, but is most conspicuous along, the groove. The very tall and narrow columnar cells form a typical neuro-epithelium, exhibiting three or four rows of nuclei. The approximate extent of the neuro-epithelial patch is shown in fig. 25. It does not, however, exhibit a very clearly defined outline, since the columnar cells pass gradually into the surrounding cubical epithelium.

The wall of the *ductus endolymphaticus* and rudimentary *saccus* consists of a single layer of cubical epithelium, the cells of which are somewhat flattened on the medial wall of the structures.

*The Auditory Nerve.*—The somewhat constricted proximal portion of the *acustico*

*facialis neurencytium* is now connected with the wall of the brain just below the middle of its lateral curvature. The developing auditory ganglion is a nearly hemispherical mass, with its convex surface directed antero-ventrally, and separated by a well marked constriction from the developing facial (geniculate) ganglion, which lies ventral to it. The postero-dorsal surface of the auditory neurencytium is hollowed to receive the antero-ventral wall of the otocyst. From the main mass of the neurencytium there grow back two conical processes. The shorter anterior and ventral one embraces the extreme antero-ventral surface of the *pars superior*, the lateral surface of which it slightly invades. The more dorsal and posterior outgrowth is considerably longer, and lies in contact with the medial wall of the otocyst, along which it runs in a posterior and slightly ventral direction to a point just below the opening of the ductus into the cavity of the otocyst. From this level it runs along the groove of the medial wall, terminating near the postero-dorsal extremity of the *pars inferior*. These outgrowths from the *auditory neurencytium* are obviously the earliest representatives of the rami of the auditory nerve of the adult. The anterior outgrowth is the developing ramus anterior, while the posterior portion becomes the ramus posterior, from which ultimately arise the *ramulus saccularis* and *ramulus cochlearis* of the ramus posterior of the auditory nerve. At this stage the neuroblasts of the developing auditory nerve appear still to be of the undifferentiated  $\alpha$ -type.

*Stage O* (Embryo 32, figs. 9, 10, 28).

At this stage a very definite delimitation of the otocyst into *pars superior* and *pars inferior* is observed, the growth of both parts having been very considerable during the interval which has elapsed between Stages N and O. The *pars superior* exhibits a very marked lateral convexity or pocket. An antero-dorsal groove which originates near the anterior extremity of the lateral surface of the *pars superior* runs obliquely in a postero-dorsal direction to a point just in front of, and dorsal to, the centre of its lateral wall. A similar, but less well-defined groove is present on the antero-medial surface, and the pocket situated between these two grooves is obviously the rudiment of the anterior vertical semicircular canal. Just ventral and posterior to the middle of the lateral wall of the *pars superior* is a shallow antero-posterior depression, which, curving backwards and downwards, is continued as a *postero-lateral groove* terminating on the ventral surface of the *pars superior*. The very large lateral pocket lying between the antero-lateral and postero-lateral grooves is the rudiment of the horizontal (lateral) semicircular canal, while posterior to the latter groove is the pocket from which arises the posterior vertical canal. The *pars inferior*, which is less than one-sixth of the size of the *pars superior* and lies ventrally and slightly medially to it, exhibits a small ventro-medial and nearly hemispherical diverticulum, which is the rudiment of the *cochlea*, the main portion of the *pars inferior* being the developing *sacculus*.

The *ductus endolymphaticus* has undergone a marked change in shape, and the present, and, as will be seen, the subsequent, form of this structure suggest that in Stage N the rudimentary *saccus endolymphaticus* was bent forward owing to some distortion of the embryo, and that its real direction should be dorsal instead of antero-dorsal. Be that as it may the *ductus endolymphaticus* now runs dorsally, its distal end swelling gradually into the elliptical *saccus*, the dorsal extremity of which is somewhat more acute than was the corresponding portion in the embryo described in Stage N. The proximal end of the *ductus endolymphaticus* opens into both the cavity of the *pars inferior* immediately below the groove separating it from the *pars superior*, and also into that of the latter as observed in the preceding stage of development. The walls of the otocyst and *ductus endolymphaticus* are similar to those in the embryo last described.

The *auditory nerve* shows little advance on its previous stage of development. Its posterior ramus has extended to pass to the upper part of the developing sacculus, while the anterior ramus is more definitely limited to the antero-ventral surface of the *pars superior*.

The features most characteristic of this embryo are the considerable growth of the otocyst which has taken place almost equally in every direction during the period that has elapsed between Stages N and O, and the incipient differentiation of both the *pars superior* and the *pars inferior* into a number of secondary "pockets."

In the somewhat older embryo next to be described, the process of differentiation has proceeded considerably further, and both the ultimate fate of the different regions of the otocyst and the exact significance of its developing "pockets" and "grooves" are clearly indicated.

*Stage O-P* (Embryo 35a (figs. 29, 30, 31, 32) is referred to either late Stage O or early Stage P).

Little or no growth has occurred during the period intervening between the stage of development represented by this embryo and that last described, but *the conversion of the incompletely bipartite otocyst into a membranous labyrinth is obviously imminent.*

The *pars superior* of the otocyst is an ovoid sac, somewhat compressed latero-medially, with its major axis directed antero-posteriorly and parallel with the mid-ventral axis of the auditory region of the hind-brain. As in the embryos of Stages N and O, the posterior extremity of the *pars superior* is somewhat conical, while its anterior end is more rounded and its dorsal surface is traversed in an antero-posterior direction by a distinct but low and laterally-rounded dorsal crest, the extremities of which pass insensibly into the curvature of the anterior and posterior walls respectively of the *pars superior*. The antero-posterior length of the *pars superior* is 1.08 mm., its dorso-ventral height is 0.70 mm., and its width in a latero-medial direction is 0.60 mm.

Both by the further outgrowth of the *antero-dorsal pocket*, and by the deepening of the *lateral* and *medial antero-dorsal grooves*, the developing *anterior vertical semicircular canal* is more clearly defined. The two grooves have extended inwards almost to meet one another, and, during early Stage P, meeting and fusion occur, their walls thus occluding the central portion of the antero-dorsal region of the lumen of the *pars superior*. The present extent of their ingrowth tends to cut off from the latter a wide tube, nearly circular in cross-section and extending from the anterior to the dorsal extremity of the *pars superior*, its dorsal wall forming the antero-dorsal ridge of the latter structure. Since the formation of the tube is not complete, its lateral walls having as yet failed to grow inwards and fuse ventrally, the lumen of the developing tube is continuous with that of the main portion of the *pars superior* (figs. 30, 31). This incompletely-separated tubular ridge or pocket is the rudiment of the anterior vertical semicircular canal.

In similar fashion, but to a somewhat less extent, the *lateral postero-dorsal* and *medial postero-dorsal grooves* have deepened, while the postero-lateral pocket has enlarged both laterally and in a postero-dorsal direction, thus forming a rudimentary *posterior vertical semicircular canal*. This is now a curved tubular ridge or pocket forming the postero-dorsal crest of the *pars superior*, its lumen being even less completely separated from the general cavity of the otocyst than is that of the developing anterior vertical semicircular canal. The above-mentioned grooves do not traverse either the lateral or the medial surfaces of the mid-dorsal region of the *pars superior*. There appears, therefore, running upwards from just below the centre of the lateral surface of this structure, to the middle point of its dorsal crest, a somewhat convex ridge, the dorsal end of which passes insensibly into the postero-dorsal extremity of the pocket which represents the developing anterior vertical semicircular canal, and the antero-dorsal extremity of that from which is developed the posterior vertical semicircular canal. This ridge, together with its counterpart, which is almost equally conspicuous on the medio-dorsal surface of the *pars superior*, forms an incompletely shut-off rudiment of the vertical, tubular *sinus superior utriculi*.

The ventral third of the lateral surface of the *pars superior* has grown outwards and slightly downwards into a well-developed and strongly convex *lateral (horizontal) pocket*. Its lumen is almost completely shut off from that of the central portion of the *pars superior* by two converging "septa," each of which consists of a double fold of epiblast. These septa grow respectively downwards and inwards from the dorso-lateral groove which lies above the lateral pocket, and upwards and inwards from the *ventro-lateral groove* which forms the boundary of its ventral surface. The lateral pocket included between these two converging septa merges at its anterior end into the general surface of the *pars superior*, just below the ventral extremity of the developing anterior vertical semicircular canal. The posterior extremity of the pocket is much more prominent, forming a strongly convex, almost conical, latero-posterior diverticulum of the posterior region of the lateral surface of the *pars superior*.

The appearance of a horizontally elongated, elliptical depression on the lateral surface of the lateral pocket, just in front of its posterior end, suggests that this region is really the posterior loop of a developing tube, which, having passed horizontally backwards, is now bent sharply upwards and forwards, being doubled upon itself to run in an anterior direction and eventually to sink medially into the general surface of the central region of the lateral wall of the *pars superior* at a point somewhat anterior and dorsal to the posterior convexity of the pocket. The lumen of the lateral pocket, which is obviously the rudiment of a horizontal and lateral tube is only partially cut off from that of the remaining portion of the *otocyst* by the ingrowing septa and depression thus described. The pocket ultimately becomes the *horizontal (lateral) semicircular canal*.

The portion of the *pars superior* not included in the three pockets already described has the form of an inverted T, the long vertical limb only of which is to be distinguished on the lateral surface of the *otocyst*, while all three limbs are clearly to be seen on its medial wall. The long vertical limb, or rudimentary *sinus superior utriculi*, runs dorsally (upwards) from the middle of the *dorso-lateral groove* and, as has already been noted, its upper extremity passes into the posterior extremity of the developing anterior vertical semicircular canal and into the anterior extremity of the posterior vertical semicircular canal. The anterior horizontal limb or sinus passes forward from the central part of the ventral region of the *pars superior* and merges into the ventral extremity of the anterior vertical semicircular canal. This limb or sinus is the rudiment of the *anterior sinus utriculi* or *recessus utriculi* of RETZIUS.

Posteriorly a similar horizontal ridge occupies the ventral portion of the medial surface of the *pars superior*, merging at its anterior end into the junction of the vertical and anterior sinuses above described, and passing at its posterior extremity into the ventral end of the developing posterior vertical semicircular canal. This ridge represents the medial surface of an incompletely shut off horizontal posterior sinus which eventually becomes the *sinus posterior utriculi*.

It may perhaps here be emphasised that at this stage no parts of these developing canals and sinuses are completely walled off from the *pars superior*, their respective lumina being incompletely tubular or pocket-like and each of them constituting a part of the general lumen of the *pars superior*. The extent to which the deepening of the grooves on the walls of the *pars superior* has progressed indicates that the series of occlusions of the lumen of the *pars superior* necessary to complete the "cutting off" of the constituent parts of the membranous labyrinth will not long be delayed. Each groove is formed by the ingrowth of a double fold of the epiblastic wall of the *otocyst* which occurs simultaneously with the outward growth of the "pockets" defined by the grooves. The space between the constituent walls of each epiblastic fold is invaded by mesenchyme, and as the process of ingrowth of the fold progresses a definite "septum" consisting of the epiblastic walls separated by an increasingly thick layer of mesenchyme is formed.

The *pars inferior* is an oval saccular outgrowth from the medio-ventral surface of the otocyst. It opens dorso-laterally into the ventral part of the *pars superior* by a wide antero-posteriorly elongated aperture which occupies rather more than the middle third of the length of the otocyst. In a posterior and ventral direction the *pars inferior* has developed a medial diverticulum which is bluntly conical in shape.

The larger and dorso-lateral portion of the *pars inferior* is the developing *sacculus* while the smaller medio-ventral diverticulum is the *cochlea*, the conical postero-ventral extremity of which is the rudimentary *lagena*.

The antero-posterior length of the developing *sacculus* is 0.60 mm., it is 0.40 mm. in height and its maximum latero-medial width is 0.30 mm., while the diameter of the approximately hemispherical rudiment of the *cochlea* is 0.24 mm. in length.

The *ductus endolymphaticus*, which is a dorsally directed tube, nearly circular in cross-section, appears to spring from the middle of the extreme dorsal surface of the *pars inferior*. The distal (dorsal) half of the ductus endolymphaticus dilates to form an oval *saccus endolymphaticus*, the diameter of the lumen of which is about twice that of the ductus itself. The total length of the ductus and saccus is about 0.90 mm. while the diameter of the ductus is 0.07 mm. and that of the widest portion of the saccus is 0.15 mm. The ventral third of the ductus lies in contact with the lower portion of the medial wall of the *pars superior*; leaving this it bends slightly in a posterior direction but soon resumes its dorsal course and terminates at a point about 0.3 mm. above the level of the dorsal crest of the *pars superior*, and exactly dorsal to the junction of the middle and posterior thirds of this structure.

Examination of transverse sections of this region of the otocyst shows that the ventral third of the ductus opens throughout nearly the whole of its length into the lumina of the *partes superior* and *inferior* by means of a vertically elongated aperture in the medial wall of the otocyst, the ventral boundary of the aperture being situated just below the groove which separates the *pars inferior* from the *pars superior*.

The extreme ventral portion of this aperture places the lumen of the *ductus endolymphaticus* in communication with that of the *pars inferior*, while by the remainder of the aperture the ductus communicates with the *pars superior*. These facts are not revealed, however, by an inspection of the exterior of the otocyst, from which it would on the other hand rather be inferred that during some phase of development subsequent to Stage N the lower extremity of the ductus endolymphaticus has undergone displacement in a ventral direction so that instead of opening, as it formerly had done, into the *pars superior* it now opens into the *pars inferior*. While it appears, therefore, that the junction of the *ductus endolymphaticus* with the *pars inferior* (developing *sacculus*) has assumed a position identical with that which it occupies in the adult structure this is not really the case. The apparently considerable ventral displacement of the terminal aperture of the proximal portion of the *ductus endolymphaticus* is probably mainly to be attributed to extensive growth upwards and outwards of the dorsal region of the *pars superior*. It is possible

that simultaneously with this, a process of converging growth and ultimate lateral fusion of the anterior and posterior walls of the incompletely shut off lower portion of the *ductus endolymphaticus* has occurred. The consequent elongation in a ventral direction of the completely tubular portion of the ductus may thus have caused a slight downward displacement of the upper boundary of the aperture by which its lumen communicates with that of the otocyst. There is, however, no doubt that during this stage of development the *ductus endolymphaticus* still opens by a single aperture into both the *pars superior* and the *pars inferior*.

The walls of the otocyst are now more clearly differentiated into two distinct regions, the one consisting of columnar neuro-epithelial cells, the other of cubical or flattened epithelium. The latter epithelium is certainly composed of a single layer of cells, and the thickened neuro-epithelial wall, although exhibiting two or more rows of nuclei, is probably the same.

The neuro-epithelial region comprises nearly the whole of the ventral half of the medial wall of the *pars superior*, and the whole of the medial wall of the *pars inferior*, together with certain limited areas of the ventral portions of the lateral wall of each of these structures. On the medial wall of the *pars superior* the dorsal border of the neuro-epithelium extends from a point just ventral to the anterior extremity of the otocyst almost horizontally backwards to its posterior end. There are, however, two conspicuous dorsally directed extensions of the neuro-epithelial patch. The more anterior of these is semicircular in shape, the mid-point of its convex border being situated at the centre of the medial wall of the *pars superior*, while the apex of the second, more posterior and triangular, extension reaches to a similar height at the junction of the middle and posterior thirds of the medial wall of this structure.

Posterior to this second dorsal extension the border of the neuro-epithelium retreats almost to the ventral extremity of the *pars superior*, but finally curves in a dorsal direction to reach its posterior end. The neuro-epithelium invades the lateral wall at the extreme antero-ventral and postero-ventral surfaces of the *pars superior*, in the first case forming a large, approximately triangular patch with its apex pointing in a postero-dorsal direction, which occupies about one-eighth of the medial wall of the *pars superior*, and a second much smaller postero-ventral, semi-elliptical patch, the convex border of which is directed antero-dorsally. The second patch occupies the extreme posterior end of the *pars superior* and is a lateral extension of the neuro-epithelium which forms the postero-medial wall of this structure.

The whole of the medial wall of the *pars inferior* is composed of neuro-epithelium, which extends as a small triangular patch on the antero-ventral wall of the developing sacculus and as a smaller elliptical patch on the lateral aspect of the extreme ventral portion of the cochlea (lagena). The approximate shape and extent of the neuro-epithelium of the otocyst of this embryo is shown in fig. 29.

It is evident that there is indicated an approaching division of the neuro-epithelium into the definite isolated sensory patches, or "*maculae*," which are so conspicuous in

the adult condition of the membranous labyrinth. As regards the neuro-epithelium of the *pars superior*, it would appear that the antero-lateral patch is the rudiment of the auditory epithelium of the *ampulla* of the *horizontal semicircular canal*. The antero-medial neuro-epithelium becomes the auditory epithelium of the *ampulla* of the *anterior vertical semicircular canal*, while the anterior dorsal extension becomes that of the *macula recessus utriculi*. It is probable that the posterior dorsal extension of the neuro-epithelium gives rise to the *macula neglecta*,\* while the posterior and postero-medial extremity of the neuro-epithelial patch becomes the auditory epithelium of the *ampulla* of the *posterior vertical semicircular canal*.

Of the neuro-epithelium of the *pars inferior*, it appears probable that the auditory epithelium of the adult *macula sacculi* arises from that which forms the whole of the medial and a small antero-ventral portion of the lateral wall of the developing sacculus, while of the neuro-epithelium of the medial wall of the rudimentary cochlea the dorsal portion gives rise to the macula of the *pars basilaris*, while the ventral portion forms the *macula lagenæ*.

*The Auditory Nerve*.—The auditory neurencytium now shows an increased complexity of anatomical and histological structure, which renders possible a preliminary suggestion as to the nature and distribution of the various parts into which it is now undergoing differentiation. The main mass of the *acustico facialis neurencytium* is attached to the medial wall of the hind-brain by a thick but very short trunk, which is elliptical in cross-section, and the major axis of which runs in a postero-dorsal direction. This massive nervous connection shows signs of division into an anterior and a posterior portion, from the former of which it is probable that the root of the facial nerve and the anterior ramus of the auditory nerve are ultimately developed, while the posterior portion gives rise to the posterior ramus of the auditory nerve. The main mass of the developing auditory ganglion is oval in shape with its major axis running antero-posteriorly and three times as long as the dorso-ventral axis. The anterior end of the ganglion is bluntly convex, while its lateral surface is concave, being hollowed out to receive the convex medial wall of the otocyst. The posterior extremity of the ganglion bifurcates into a longer dorsal and a slightly shorter ventral conical process. The anterior extremity of the lateral surface of the ganglion is in contact with the neuro-epithelium of the antero-ventral portion of the medial wall of the *pars superior* and corresponds topographically with, and doubtless gives rise to, the ramulus which is distributed to the ampulla of the anterior vertical semicircular canal.

Ventrally and slightly posterior to this region the auditory ganglion extends laterally to form a cupular investment of that portion of the neuro-epithelium from

\* VILLY (1890) erroneously includes the *macula neglecta* in his list of cochlear sense-organs. AYERS (1892) concludes (*op. cit.*, p. 213) that it is developed from the sense-organ of the posterior semicircular canal of an ancestral type, from the remaining portion of which sense-organ the *crista acustica posterioris* is produced.



which it was suggested the *macula* of the *ampulla* of the *horizontal semicircular canal* is ultimately formed. This portion of the auditory ganglion probably gives rise to that branch of the ramus anterior which is distributed to this macula. Immediately above this region the dorsal border of the lateral surface of the auditory ganglion shows a slight dorsal outgrowth, this portion of the ganglion probably forming the branch of the anterior ramus of the auditory nerve that is distributed to the *macula recessus utriculi*. Of the two posterior outgrowths of the auditory ganglion, the more dorsal passes to the neuro-epithelium of the posterior region of the *pars superior* and to that of the dorso-medial wall of the developing sacculus. It is probably a common rudiment from which develop both the *posterior ampullary* and the *saccular branches* of the *ramus posterior*. The slightly shorter and ventral process traverses the medial wall of the developing sacculus, and extends almost to the lagenar prominence, and may therefore be presumed ultimately to give rise to the *ramulus lagenæ* of the *ramus posterior acustici*.

Although the indifferent state of preservation of the available material renders a definite statement impossible, there appears to be evidence that histological differentiation of the neurencygium has now commenced. The main portion of the auditory ganglion certainly contains both  $\alpha$ - and  $\gamma$ -neuroblasts, while definite nerve fibres appear to be developing within that portion of the neurencygium which unites the auditory ganglion with the brain.

#### *Stages P and Q.*

The later phase of *Stage P* is represented by Embryo 45*a* (figs. 11, 12, 14, 33, and text-fig. 6), and, although this embryo is probably separated by only a short interval from that last described, the external appearance of its developing membranous labyrinth is strikingly different from that of the otocyst of the latter. This is chiefly due to the increased differentiation of its constituent parts—more particularly the conversion of the anterior horizontal and posterior pockets into definite canals—and to the very considerable growth of every part of the membranous labyrinth.

Embryo 51*a*, Stage P-Q (text-figs. 13, 14), and Embryo 52*a*, Stage Q (fig. 42), differ so little in their main features from Embryo 45*a* (late Stage P) now to be described that their separate treatment appears to be unnecessary. The consideration of any important modifications of structure exhibited by the membranous labyrinth and auditory nerve of these embryos will therefore be included in the present subsection.

In the preceding descriptions of the different embryos examined, it has been customary to speak only of the antero-posterior, dorso-ventral, and latero-medial axes of the otocyst.

These were taken respectively to signify the imaginary lines joining the anterior and posterior, the dorsal and ventral, and the lateral and medial extremities of the otocyst, and they retain this significance. Owing, however, to the increasing

differentiation of the parts of the membranous labyrinth, it is now essential that the orientation of these be defined relative to the horizontal and sagittal planes, of which the mid-ventral longitudinal axis of the auditory region of the hind-brain is the intersection, and to a transverse plane at right angles to each of these.

In Embryo 45a (late Stage P) the *pars superior* has developed into a labyrinth of communicating canals and sinuses, the ventral portion of the lumen of which is continuous with that of the *pars inferior*, which is now more clearly differentiated into a dorso-lateral *sacculus* and a ventro-medial *cochlea*.

The dorsal portion of the membranous labyrinth consists peripherally of an anterior vertical, a horizontal, and a posterior vertical semicircular canal, together with a central triradiate *utricle*, while the ventral portion consists of a dorso-lateral *sacculus*, which communicates both with the more ventro-medially situated *cochlea* and with the *utricle*, and from the medial wall of which arises dorsally the *ductus endolymphaticus* with its distal *sacculus endolymphaticus*.

The antero-posterior axis of the membranous labyrinth (otocyst) is approximately horizontal and is 1.50 mm. in length, but the upper end of the dorso-ventral axis has been displaced in an anterior direction, so that the axis, the length of which, from the ventral surface of the *sacculus* to the dorsal crest of the anterior vertical semicircular canal, is 1.60 mm., is deflected about 30° from the vertical (transverse) plane, while the horizontal latero-medial axis, which lies in the same plane as does the horizontal semicircular canal, is 1.0 mm. in length.

The *utricle* consists of a wide *sinus superior utriculi* inclined in an antero-dorsal direction at an angle of 15° from the vertical, its ventral junction with the *anterior* and *posterior sinuses* of the *utricle* being situated almost exactly in the centre of the labyrinth. It is oval in cross-section, and opens dorsally into the expanded dorsal ends of the anterior and posterior vertical semicircular canals. Its length is about 0.56 mm., its antero-posterior axis being somewhat less than this, while latero-medially it measures about half as much. The *anterior sinus (recessus) utriculi* and *posterior sinus utriculi* are wide tubes, each about 0.2 mm. in length, the junction of the three sinuses forming a central oval cavity (*fundus utriculi*). Distally the *recessus utriculi* dilates into a large oval bilobed sinus, which represents the imperfectly separated ampullæ of the anterior vertical and horizontal semicircular canals. The distal end of the *posterior sinus utriculi* receives the posterior extremity of the horizontal and the ventral extremity of the posterior semicircular canals. Ventro-laterally the *utricle* opens into the *sacculus* by a wide, nearly circular aperture, situated just anterior to the centre of the dorso-medial wall of the latter.

The anterior vertical semicircular canal is inclined at an angle of about 50° to the sagittal plane, and in shape is that of a somewhat flattened semicircle. Its dorsal end is dilated, and terminates in a nearly hemispherical "*ama*," the base of which opens into the dorsal extremity of the *sinus superior utriculi*, while the ventral extremity of the canal is greatly dilated to form the rudimentary ampulla. This is

the more anterior and medial lobe of a large bilobed sinus, the postero-lateral portion of which represents the ampulla of the horizontal semicircular canal, and which opens into the anterior end of the *recessus utriculi*. The length of the canal is approximately 1.36 mm., while the diameter of its circular cross-section is 0.14 mm., the maximum diameter of the "ama" being about twice, and that of the ampulla three times, as great as this.

The anterior extremity of the horizontal semicircular canal is dilated to form the nearly hemispherical but somewhat elongated rudiment of its ampulla, the vertical diameter of which is approximately 0.4 mm., while its length is 0.44 mm. The canal is circular in cross-section, its diameter being approximately equal to that of the anterior vertical semicircular canal. It passes laterally, posteriorly, and finally antero-medially, in a somewhat postero-laterally elongated semicircular curve to enter the lateral surface of the *recessus posterior utriculi*. The length of the canal is 1.80 mm., and its posterior extremity, although slightly dilated, is much less so than is the dorsal extremity of the anterior canal.

The ventral extremity of the posterior ventral canal passes backwards parallel to the sagittal plane and slightly downwards, almost immediately dilating into an oval ampulla, the vertical diameter of which is 0.34 mm. in length and slightly shorter than its antero-posterior axis. The canal then bends rather sharply in a dorsal direction, passes antero-dorsally and finally dilates into a funnel-shaped "ama" opening into the posterior region of the dorsal extremity of the *sinus superior utriculi*. The length of the canal is approximately 1.80 mm., and the diameter of its circular cross-section 0.14 mm., although this shows some increase towards either end of the canal, as is also the case in those previously described.

The *sacculus* is an oval sac somewhat compressed latero-medially, and with a slightly acute postero-ventral extremity. Its (antero-posterior) length is 0.66 mm., its (dorso-ventral) height 0.7 mm., and its (latero-medial) width 0.35 mm. Its lumen communicates with that of the utriculus by a wide, nearly horizontal, antero-posteriorly elongated aperture, which occupies the central portion of its dorsal surface. The antero-posterior axis of the sacculo-utricular aperture is 0.38 mm. in length, and its width is 0.24 mm. The extreme dorsal crest of the sacculus is visible as a slight antero-posterior ridge rising just above the lower border of the lateral wall of the central portion of the utriculus.

The *ductus endolymphaticus* is a dorsally-directed tube, with a circular cross-section 0.1 mm. in diameter, its proximal (ventral) end being somewhat dilated and opening into the middle portion of the dorsal extremity of the medial wall of the sacculus just on the groove which marks the utriculo-saccular junction. The oval opening by which the *ductus endolymphaticus* opens into the sacculo-utricular junction appears to lie partly above and partly below the groove, and the length of its vertical axis is 0.2 mm., while its antero-posterior axis is 0.14 mm. in length.

The length of the *ductus endolymphaticus*, including the distal saccus, is 0.96 mm.,

the dorso-ventral height of the saccus being 0.39 mm., and the diameter of its nearly circular cross-section 0.21 mm. The *saccus endolymphaticus* is irregularly oval in shape, its anterior, medial, and lateral surfaces being convex, and the lower part of its posterior surface strongly convex, while the upper portion is concave. This irregularity of shape may be due to distortion of the sections employed in the reconstruction model of this embryo. A comparison of this *saccus endolymphaticus* with those of embryos of Stages P, P-Q, Q, and R, suggests that the true shape is pyriform, the more rounded surface of the sac being dorsally directed while its proximal ventral apex tapers gradually into the *ductus endolymphaticus*.

The sacculus communicates with the cochlea by a vertically elongated elliptical aperture, the axes of which are respectively 0.2 mm. and 0.16 mm. in length. This sacculo-cochlear aperture is situated in the postero-ventral third of the medial wall of the sacculus. The cochlea is an irregularly oval sac lying medio-ventrally to the sacculus. It is 0.25 mm. long, 0.45 mm. in height, and 0.21 mm. in width. Its lateral surface is somewhat flattened, but the postero-ventral region of its medial wall bears a small conical and somewhat dorsally curving prominence—the distal *pars lagenæ*.

It is evident that the differentiation of the *pars inferior* into sacculus and cochlea has proceeded considerably further than during the immediately preceding stage of development, while the long vertical aperture by which the *ductus endolymphaticus* during that period communicated with the utriculus and sacculus is now considerably shortened, the position of its ventral extremity remaining unchanged. This shortening of the aperture, and the consequent elongation of the tube, can be explained only by adopting the suggestion previously made, viz., that there is a ventral extension of the completely closed lateral surface of the ductus produced by convergence and lateral fusion of the dorsal region of the infolded junctions of the anterior and posterior walls of the ductus with the wall of the utriculus. The effect of this obviously would be completely to shut off the ductus from the utriculus, while leaving open the extreme ventral portion of the original aperture whereby the ductus would communicate with the lumen of the sacculus. This latter condition appears to obtain in all embryos older than those referred to Stage Q.

#### *The Intra-capsular Mesenchyme.*

During Stages P and P-Q the conversion of the pro-cartilaginous auditory capsule into hyaline cartilage is not complete, and the inner surface of the dense pro-cartilaginous tissue of the ventral region of the capsule becomes, in many places, a rather less dense mesenchyme closely investing the walls of the membranous labyrinth. In Stage Q, the auditory capsule has been converted into hyaline cartilage, and the existence of a layer of mesenchyme between it and the

membranous canal is evident, more especially in the extreme ventral region. Examination of later embryos (Stages R and S) discloses the ultimate fate of this mesenchyme. It forms the very delicate connective tissue investment of the membranous canals, the layer of so-called "*nerve-cartilage*" (HAASE, RETZIUS, HOFFMANN) or "*spindle-cartilage*"; (OSAWA), the connective tissue walls of the *ductus perilymphaticus*, and external to these the delicate connective tissue lining the cavity of the auditory capsule.

*The Auditory Neuro-epithelium* (fig. 33).

The neuro-epithelium of the membranous labyrinth now shows signs of approaching division into definite areas, or "*maculae*." Raised patches, or *crista acustica*, have already made their appearance in the neuro-epithelium of the ampullæ of the three semicircular canals. For the sake of brevity, during the present description of the distribution of the neuro-epithelium, the names of these canals will be shortened to "anterior," "horizontal," or "posterior" canal respectively.

(a) *The Neuro-epithelium of the Ampulla of the Anterior Canal*.—The whole of the floor and the lower third of the lateral and medial walls of this ampulla are occupied by an oval patch of neuro-epithelium. The lateral and medial boundaries of this patch are somewhat thickened and are approximately semicircular in outline, each apparently representing a rudimentary *planum semilunatum*. The centre of the patch is elevated into a nearly hemispherical crest or *crista acustica* which is set somewhat obliquely along the floor of the ampulla, the extremities of its long axis being respectively antero-medially and postero-laterally situated. The crista is approximately 0.2 mm. in length, 0.15 mm. in height, and 0.16 mm. in width. The crista consists of much elongated columnar epithelial cells among which no auditory hair-cells can as yet be distinguished.

Posterior to the crista the neuro-epithelial area is continuous in the lateral direction with that of the antero-medial wall of the imperfectly differentiated ampulla of the horizontal canal, while postero-medially it passes into that of the medial and medio-ventral walls of the *recessus utriculi*.

(b) *The Neuro-epithelium of the Ampulla of the Horizontal Canal*.—This forms a somewhat less clearly defined but generally similar oval patch on the medial and ventral walls, and, more posteriorly, on the latero-ventral wall of this ampulla. The *crista acustica* is lower, less convex and less clearly defined than that previously described, its approximate dimensions being:—antero-posterior length 0.16 mm., height 0.10 mm. and width 0.15 mm. It is situated on the ventro-lateral wall of the ampulla. Of the lateral extensions of the neuro-epithelium (*plana semilunata*) neither is well marked, the lateral being perhaps rather the more conspicuous.

(c) *The Neuro-epithelium of the Ampulla of the Posterior Vertical Semicircular Canal*.—This is generally similar in appearance and distribution to that of the ampulla of the anterior vertical semicircular canal. The crista is well developed and strongly

convex, 0.15 mm. in length, 0.12 mm. in width, and 0.10 mm. in height, and is situated in the floor of the ampulla, the ventro-medial region of which it occupies. Two well marked *plana semilunata* are present. In an anterior direction the sensory epithelium of the crista passes insensibly into a tract of low columnar epithelium which here occupies the floor of the ampulla, and which appears to be continuous with that of the floor of the *sinus posterior utriculi*.

(d) *The Neuro-epithelium of the Utriculus*.—This is not well defined, nor does it exhibit any *crista acustica*. It consists of a large patch of comparatively low columnar epithelium which appears to occupy nearly the whole of the medial wall of the *recessus utriculi*. It shows a slight dorsal extension into the lower part of the *sinus superior utriculi* while it is confined to the extreme ventro-medial angle of the *sinus posterior utriculi*, in the posterior region of which it becomes very indistinct although it apparently passes backwards into the floor of the ampulla of the posterior canal. The cells of the extreme ventro-medial region of the *recessus utriculi* appear to be somewhat taller than those of the remaining portions of the utricular neuro-epithelial area. This probably foreshadows the ultimate formation of the *macula recessus utriculi* in this region.

(e) *The Neuro-epithelium of the Sacculus*.—The whole of the medial wall of the sacculus is composed of low columnar epithelium continuous with that just described. Near the anterior extremity of the sacculus the cells are somewhat taller, and two low diverging ridges formed by these elongated cells run backwards, one just below the utriculo-saccular groove, and a second, more ventrally, in the direction of the sacculo-cochlear aperture. Both ridges disappear just before reaching the posterior border of the sacculus. The columnar epithelium invades the extreme anterior border of the lateral wall of the sacculus, where it soon disappears.

(f) *The Neuro-epithelium of the Cochlea*.—The whole of the medial wall and the middle third of the anterior extremity of the lateral wall of the cochlea are composed of low columnar epithelium continuous with that of the sacculus. In the lagenar prominence the cells are more elongated. It is probable that from the dorsal portion of the cochlear neuro-epithelial tract is formed the *macula basilaris* while the ventral region represents the developing *macula lagenæ*.

Those regions of the wall of the membranous labyrinth not included in the foregoing neuro-epithelial tracts consist of a single layer of cubical epithelial cells. In the dorsal and lateral regions of the membranous labyrinth and also in the *saccus endolymphaticus*—but not in the *ductus endolymphaticus*—these cells tend to become considerably flattened, while at the periphery of the neuro-epithelial areas just described they pass somewhat abruptly into the columnar epithelium.

*The Auditory Nerve*.—The auditory neurencytium has now undergone differentiation into a very short and stout proximal portion or root, which passes laterally and ventrally from the medial wall of the hind-brain to a horizontally elongated oval ganglionic mass which is now beginning to show signs of division into an anterior and a posterior

lobe or ramis (*anterior* and *posterior rami acustici*). This nerve mass is prolonged distally into a number of outgrowths or developing ramuli. The main nerve mass—or auditory ganglion—is convex on its anterior and medial surfaces and concave dorso-laterally where it comes in contact with the ventro-medial walls of the component parts of the membranous labyrinth. The developing *anterior ramus acusticus* is in contact near its dorsal extremity with the ventro-medial wall of the *recessus utriculi* and more anteriorly it gives off a long narrow antero-lateral branch which passes to the ventral surface of the ampulla of the anterior vertical semicircular canal, along which it runs, finally tapering and terminating at the extreme antero-ventral border of the ampulla. This branch is evidently the *ramulus ampullaris anterior*. The posterior portion of the ramus anterior gives off a stouter branch which passes outwards and upwards to the ventral surface of the ampulla of the horizontal semicircular canal where it terminates just below the posterior extremity of the developing *crista acustica*. This branch is evidently the *ramulus ampullaris horizontalis* (or *lateralis*). The developing *ramus (posterior) acusticus* forms a stout cup-like outgrowth embracing the medial wall of the sacculus and which is probably the developing *ramus sacculi*. The posterior portion of the *ramus posterior acusticus* is elongated and bifurcated into a more dorsal branch which passes to the ventral surface of the ampulla of the posterior semicircular canal (*ramus ampullaris posterior*) and a more ventral and anterior branch, the *ramus lagenæ*, which passes along the medial wall of the cochlea, to terminate just in front of the lagenar prominence. In addition to the  $\alpha$ -neuroblasts characteristic of the earlier auditory neurencytium, there are now present, especially in the central ganglionic mass, a number of the larger oval ganglion cells or  $\nu$ -neuroblasts, while in the proximal roots, and also in the nerve branches passing to the developing “maculæ,” there are a number of the elongated  $\beta$ -neuroblasts, together with fine nerve fibres.

*Stage Q* (Embryo 52a).

The developing membranous labyrinth of this embryo differs so little from that of the embryo just described that a separate account of its main features is unnecessary.

The differentiation of the component parts of the membranous labyrinth has progressed little beyond the condition obtaining in Stage P. The chief external differences are a more constricted periphery of junction of utriculus with sacculus and of sacculus with cochlea, and a clearer definition of the ampullæ of the semicircular canals. The *saccus endolymphaticus* is more dilated, and the extension and increasing convexity of its postero-dorsal surface have given the structure a more definitely pyriform shape.

Whereas during Stage P the external surface of the otocyst was in contact over the greater part of its area with the internal surface of the developing auditory capsule, there is, in the embryo now under consideration, a considerable intracapsular space between the hyaline cartilage wall of the auditory capsule and the epithelium of that of the developing membranous labyrinth. This space is almost completely

filled with dense mesenchymatous tissue, consisting of a well-defined fibrous network containing numerous spindle-shaped cells. From this tissue is developed, first, the looser connective tissue investment of the membranous labyrinth of Stage R, and, ultimately, the masses and sheets of *spindle connective tissue* ("spindle cartilage," OSAWA) which invest and support the epithelial walls of the membranous labyrinth in embryos of Stage S, and which also persist in the adult organ (OSAWA).

The *cristæ acusticæ ampullarum* are more clearly defined and approximate more nearly in appearance and structure to those described below in embryos of Stages R and S, although their *lateral crests* and the *plana semilunata* are somewhat less conspicuous than those of these later embryos. The epithelium of the *cristæ acusticæ ampullarum* is differentiated into tall and somewhat tapering hair-cells, each of which bears a single fine auditory hair, now distinguishable for the first time, and into narrow interstitial cells, both types of cells being fully described below (*sub-Stage R*). A number of hair-cells are present in the *maculæ* of the utriculus, sacculus, and cochlea. Their presence in every part of these *maculæ* could not be demonstrated since, unfortunately, longitudinal sections only of this embryo were available for examination, and identification of the presence of hair-cells in these situations was difficult and uncertain.

*Stages R and S* (figs. 16 to 22 and 34, 41, text-figs. 7, 8, 9, 10, 15, 16).

The gross structure of the membranous labyrinth undergoes so little variation subsequent to Stage R that it is unnecessary to give a separate complete account of that of an embryo of Stage S. The histological differences are somewhat more obvious. The following description is mainly that of Stage R (Embryo 141), but when necessary reference is made to Stage S (Embryos 11 and 9a).

*Stage R* (Embryo 141).

*The Utriculus.*—The junction of the three rays or sinuses of the utriculus results in the formation of a large oval central utricular sinus (*fundus utriculi*), which is situated at about the middle level of the immediate wall of the labyrinth, at the junction of its middle and posterior thirds. The apparent backward shifting of the central portion of the utriculus (and of the *sinus superior utriculi*) appears to be due to a considerable anterior extension of the *pars superior* of the labyrinth, which has taken place during the interval which separates Stages Q and R. This growth chiefly involves the *recessus utriculi* and the ventral half of the anterior ventral semicircular canal (including its ampulla), and also the anterior extremity and ampulla of the horizontal semicircular canal.

The *recessus utriculi* is now a stout, cylindrical and nearly horizontal sinus, which is inclined forward and laterally at an angle of about 15° with the sagittal plane. It is 1.2 mm. long and 0.36 mm. wide and exhibits a small conical anterior extremity, just lateral to which there is a wide aperture by which it communicates with the junction of the ampullæ of the anterior and horizontal semicircular canals.



The *sinus superior utriculi* rises to a height of about 0.99 mm. above the level of the dorsal crest of the horizontal sinuses of the utriculus and opens into the contiguous "ama" of the two vertical semicircular canals. At its dorsal extremity it is nearly circular in cross-section (diameter 0.33 mm.) and dilates somewhat at its junction with the *fundus utriculi*, although it is somewhat flattened antero-medially in this region. Its posterior border exhibits a marked "pocket" at the level of the medial boundary of the horizontal semicircular canal which lies immediately lateral to it, and it almost suggests that the latter has just been "pinched off" from this region of the utriculus, which is not improbably the case. The *sinus superior utriculi* is not directed forwards as in Stage P, but it now rises in a postero-dorsal direction at an angle of about 75° to the horizontal plane.

The semicircular curve of the anterior vertical canal is considerably elongated in an antero-ventral direction, the total length of the canal and its ampulla being 3.24 mm. The lumen of the canal, possibly owing to partial collapse, is not quite circular, but somewhat laterally compressed. It is approximately 0.24 mm. in diameter and its dorsal extremity is gradually dilated to form an approximately hemispherical "ama," the base of which has a diameter of 0.50 mm. and opens into the anterior surface of the dorsal extremity of the *sinus superior utriculi*. The ampulla, which occupies about three-quarters of the anterior ventral and horizontal limb of the canal, is oval in shape. Its length is 0.66 mm., its height 0.63 mm., and its width 0.45 mm. It opens by a horizontally elongated elliptical aperture, common to itself and to the ampulla of the horizontal canal, into the anterior extremity of the *recessus utriculi*.

The *horizontal semicircular canal* forms rather more than three-quarters of a horizontal and lateral circle. In the present embryo the canal is somewhat distorted, owing to a slight forward and upward displacement of its posterior curvature and a consequent slight ventral dip of its extreme lateral region. At its antero-lateral end the canal is dilated into a pyriform ampulla opening at its blunt anterior extremity into the *recessus utriculi*, and its acute postero-lateral extremity tapering gradually into the canal. This, for the greater part of its course, is circular in cross-section and uniform in diameter (0.24 mm.). It runs laterally and slightly ventrally, then slightly dorsally, and turns medially, passing immediately across the dorsal surface of the ampulla of the posterior semicircular canal and immediately in front of the latter. Here it bends sharply in an anterior direction, dilates slightly, and runs forward finally to enter the medio-dorsal region of the *fundus utriculi*. This is the longest of the three semicircular canals, its length—including that of its ampulla—being 4.75 mm. The ampulla is nearly circular in cross-section, 0.75 mm. in length and 0.45 mm. in diameter.

The *posterior vertical semicircular canal* extends horizontally in a posterior direction from the *posterior sinus utriculi*, dilating almost immediately to form an oval, laterally compressed ampulla 0.66 mm. in length, 0.54 mm. in height, and 0.48 mm. in width. It then bends sharply in a lateral direction, narrows

considerably, and then becomes an antero-dorsally curved nearly semicircular canal, circular in cross-section, with its dorsal third gradually dilating, and bending medially to terminate in a pyriform "*ama*," the maximum width of which is about 0.42 mm.—or rather more than twice that of the narrowed central portion of the canal. The "*ama*" opens into the posterior region of the dorsal extremity of the *sinus superior utriculi*.

The *sacculus* is a large oval sac, with an antero-posterior and horizontal major axis. Its rather more convex lateral surface shows several ridges, but these—like those of the *saccus endolymphaticus* described below—are possibly the result of distortion of the sections used in reconstructing the model of this embryo. The length of the *sacculus* is 1.41 mm., its height 1.0 mm., and its width 0.6 mm. It opens into the ventral part of the lateral wall of the *fundus utriculi* by a very short and narrow circular canal, 0.12 mm. in diameter, the utriculo-saccular canal. The smaller, short, elliptical sacculo-cochlear canal (*canalis reuniens*, OSAWA) is situated almost exactly in the centre of the medial wall of the *sacculus*. The ventral extremity of the *ductus endolymphaticus* opens into the *sacculus* by a nearly equal and similarly vertically elongated foramen (0.12 mm. vertical and 0.06 mm. horizontal diameter), situated on the medial wall of the *sacculus* immediately anterior and ventral to the *utriculo-saccular foramen*.

The *ductus endolymphaticus* is a narrow circular tube 0.15 mm. in diameter, and, including the distal *sacculus*, 2.34 mm. in length. It emerges from the auditory capsule by a vertically elongated foramen (*foramen ducti endolymphatici*) slightly anterior to the centre of its medial wall and passes in a dorsal direction, lying medial and approximately parallel to the anterior margin of the *sinus superior utriculi*. Near the dorsal extremity of the latter it dilates into the large pyriform *saccus endolymphaticus*, 0.87 mm. in height, and the approximately equal antero-posterior and latero-medial axes of which are 0.78 mm. in length. The ventral half of the antero-medial surface of the *saccus* is somewhat hollowed out where it lies closely in contact with the convex dorso-lateral surface of the roof of the 4th ventricle. Near the middle of its dorso-lateral surface the sac exhibits a conical, dorsally and laterally directed diverticulum about 0.2 mm. in height, which lies in a foramen in the intercapsular cranial roof (*foramen sacci endolymphatici*). This diverticulum, which, together with its foramen, is also present in Embryos 11 and 9a of Stage S, is probably a vestige of the narrow distal duct by which the *ductus endolymphaticus* and developing *saccus endolymphaticus* opened to the exterior on the dorso-lateral surface of the head—during earlier stages of development. Its presence appears to confirm the suggestion, made earlier in this paper, that the *saccus endolymphaticus* of adult *Sphenodon* is developed, not from the distal extremity, but from the medial side of the central region of the rudimentary duct which connects the otocyst with the surface of the head in the early embryo.

The *cochlea* is a latero-medially flattened and vertically elongated sac, which lies

medial and ventral to the sacculus, to the medial wall of which it is laterally attached by the short, narrow *canalis reuniens*. The lower half of the cochlea is considerably dilated and its conical ventral extremity curves inwards and upwards, forming the incomplete first turn of a cochlear spiral. The flattened, tall, and narrow dorsal portion of the cochlea extends about half-way up the medial wall of the sacculus, and is known as the *pars basilaris*, while the swollen incurved ventral region is the *pars lagenæ*. The vertical axis of the cochlea is 1.2 mm. in length and about twice as long as its horizontal axis.

*The Anatomy and Histology of the Maculae and Cristae Acusticae and the Histology of the Component Parts of the Membranous Labyrinth.*

The position, shape and microscopic structure of the individual *maculae* and *cristae acusticae* will next be described. In each case the description of the macula or crista will immediately be followed by a brief account of the chief histological features of that part of the membranous labyrinth in which it is situated.

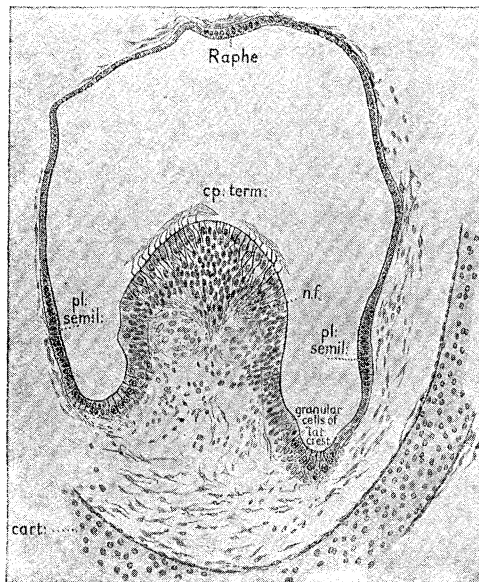
(A) *The Maculae and Cristae Acusticae of the Ampullae of the Semicircular Canals.*

The maculae and cristae of the ampullae of the three semicircular canals are identical in anatomical and histological structure. They vary only in details of dimension and orientation. A detailed description of a selected example—the *macula* and *crista acustica* of the ampulla of the posterior semicircular canal—will be given, and a brief account of the variation exhibited by those of the other canals will then be given. The maculae of the utriculus, sacculus and cochlea will be separately considered.

(i) *The Macula and Crista Acustica of the Ampulla of the Posterior Semicircular Canal* (text-figs. 7 and 8).

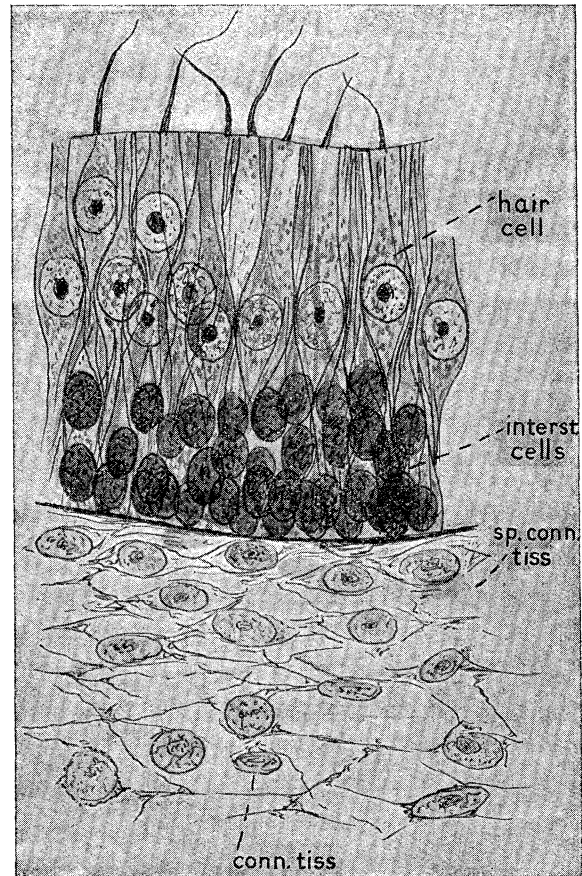
The macula is situated on the floor of the ampulla. It is elliptical in shape, its antero-posterior length being 0.55 mm. and its width 0.31 mm. Its centre is occupied by the antero-posteriorly elongated crista, the dorsal surface of which is strongly convex, 0.45 mm. in length, 0.21 mm. in width, and 0.22 mm. in height. On either side of the crista the border of the macula is thickened, forming a slight convex ridge or crest, 0.02 mm. high and 0.05 mm. wide, which will be called the *lateral crest*. In both the anterior and the posterior direction the columnar epithelium of the border of the macula passes somewhat abruptly into the cubical epithelium of the floor of the ampulla. From the lateral crest of either side there extends laterally and dorsally on the wall of the ampulla a large semicircular and slightly raised area, the *planum semilunatum*, 0.4 mm. in length and 0.35 mm. in height. The crista is divided into a nearly hemispherical central or *apical crest*, 0.24 mm. in length, 0.22 mm. in height, and 0.21 mm. in width, and two similar but

smaller crests—the *anterior* and *posterior axial crests*, which lie against and are partly fused with its anterior and posterior surfaces respectively. These axial crests are approximately equal in size, each being 0.12 mm. high, 0.12 mm. long, 0.15 mm. wide. The whole crista may therefore be regarded as a single, elongated oval mass incompletely divided into three serially arranged nearly hemispherical lobes, of which the central one is considerably the largest.



TEXT-FIG. 7.

TEXT-FIG. 7.—Stage R. Embryo 141. Diagrammatic transverse section through the *Crista acustica* of the ampulla of the left posterior vertical semicircular canal.



TEXT-FIG. 8.

TEXT-FIG. 8.—Stage S. Embryo 9a. Diagram of sensory epithelium and supporting tissue ("spindle cartilage") of the wall of the Sacculus. (Zeiss D, Oc. 2.)

(For explanation of lettering see pp. 367–368).

The ventral surface of the wall of the ampulla shows a longitudinal *sulcus* most clearly marked below the raised centre of the crista. Along this "sulcus" runs, in a posterior direction, the terminal portion of the *ramulus ampullaris posterior* which is a branch of the posterior ramus of the auditory nerve. In Stage R (Embryo 141) the nerve-fibres are embedded in a mass of loose connective tissue continuous with that which invests the exterior of the ampulla. In Stage S

(Embryos 9a and 11) this is found to be largely converted into a more dense mass of closely-packed fusiform, or oval connective tissue cells, which form the so-called "spindle-cartilage" (OSAWA), or "nerve-cartilage" (HASSE, RETZIUS). The wall of the crista, which lies immediately dorsal and lateral to the longitudinally arranged bundle of nerve fibres, consists of a mass of elongated and much tapered interstitial or supporting cells, each of which contains finely granular cytoplasm and a single oval deeply-staining nucleus. Between the interstitial cells are situated the numerous auditory cells proper—the "hair-cells"—which constitute the sensory epithelium. These are tall, tapering cells with very clear finely granular cytoplasm, each cell containing a single nucleus larger, more nearly spherical, and less deeply staining, than that of a supporting cell, and frequently exhibiting a small nucleolus. From the distal surface of each hair-cell is given off a rather stout conical filament, or auditory hair, which projects into the lumen of the ampulla, and the average length of which appears to be about one-third of that of the cell from which it originates. Many of the hairs are shorter than this, and a number of cells are devoid of hairs, possibly owing to mechanical injury sustained during the preparations of the sections. Distally, many of the auditory hairs are in contact with, and perhaps slightly penetrate, the lower surface of the *cupula terminalis*, which is a flattened mass apparently containing very fine fibres and a number of small polygonal, or nearly spherical, granules and which overlies the crista.

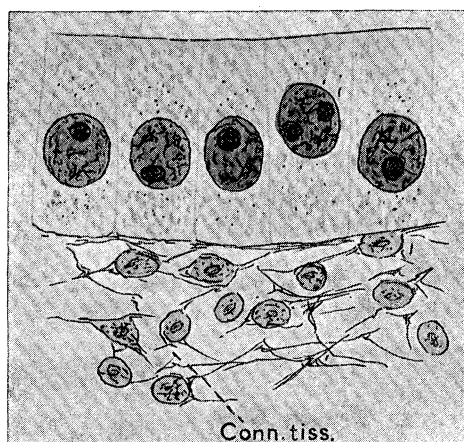
Although the presence of the crowded nuclei of the closely-packed filamentous supporting cells, and the several rows of nuclei of the hair-cells, suggest a multi-layered condition of the epithelial wall, it is by no means certain that this is really the case, although HOFFMANN speaks of the auditory epithelium of *Lacerta* as "multi-layered." It is possible that this appearance is due to the arrangement at different levels of the nuclei of the tapering and closely-packed cells, and it appears impossible definitely to assert that the epithelium, either here or in any other of the cristæ or maculæ, is other than single-layered.

The wall of each lateral crest is composed of a single layer of columnar cells rather wider, and possessing more coarsely granular cytoplasm, than those of the wall of the crista proper. These cells are not tapered, each possesses a very large, nearly spherical, and coarsely granular nucleus, with a small, dense, spherical nucleolus, situated near, and usually just below, the centre of the cell. The wall of the lateral crest, therefore, exhibits a more obviously unilayered appearance. These cells are very conspicuous in embryos of Stage S (text-fig. 9).

The *planum semilunatum* consists of a single layer of low columnar epithelial cells with large oval and somewhat deeply-staining central nuclei. These cells are tallest near the centre of the planum, and at its border pass gradually into the cubical epithelium which forms the wall of the ampulla in this region.

The roof and dorsal half of the walls of the ampulla are composed of a single layer

of flattened epithelium of which, more particularly in Stage S, the cells are frequently so flattened and contain so little cytoplasm that the presence of the oval nucleus in each cell causes a protrusion of its inner wall into the lumen of the ampulla.



TEXT-FIG. 9.—Diagram of epithelium from the lateral crest of the *Crista acustica* of the ampulla of the left posterior vertical semicircular canal. (Zeiss D, Oc. 2.)  
(For explanation of lettering see pp. 367-368.)

Traversing in an antero-posterior direction the whole of the roof of the ampulla, and extending for some distance along the wall of the semi-circular canal, is a narrow low convex ridge. A cross-section shows this to consist of a band of seven or eight elongated cells, of which the lateral are rather longer than the central, arranged radially so that their wider distal extremities form a convex ridge projecting from the roof of the ampulla. This is the *raphe*, and since it is present in each ampulla and throughout a considerable part of each of the three semicircular canals, its situation and appearance seem to suggest that it represents the line of coalescence of the walls of the structures in which it occurs when these were cut off by the fusion of the walls of the pockets from which they respectively were formed.

(ii) *The Structure of the Wall of the Posterior Semicircular Canal and Ampulla, excluding the Region of the Macula Acustica.*

During Stage R the wall of the posterior canal and ampulla consists of a single layer of cubical epithelium which becomes somewhat more flattened on the roof of the ampulla and on the dorso-lateral surface of the canal. Externally both structures are invested by a thin layer of connective-tissue consisting of a network of fine fibres in which are embedded numerous oval connective-tissue cells. This layer is thickest and most dense in the region of the floor of the ampulla, but everywhere it blends with the much looser connective tissue which is composed of a very open mesh-work of fine fibres and somewhat sparsely scattered fusiform and elongated cells which extends almost completely throughout the intra-capsular spaces. There appears to be

between this connective tissue investment and the epithelial wall of the semicircular canal and ampulla a very fine "basement membrane," in which it is possible to distinguish a few widely separated and extremely flattened cells, consisting of little more than a much flattened nucleus. This is more conspicuous in embryos of Stage S, in which also the connective tissue investment appears to be extensively converted into a layer of so-called *spindle-cartilage*, consisting of closely packed, oval or short, thick, fusiform connective-tissue cells. In certain situations, more particularly on the medial wall of the sacculus, the outlines of these cells become so indistinct as almost to suggest the approaching formation of a cartilaginous matrix, and this is probably responsible for the name commonly given to this tissue.

(iii) *The Macula and Crista Acustica of the Ampulla of the Anterior Semicircular Canal.*

This macula is 0.51 mm. in length and 0.36 mm. in width and is similar in shape to that previously described. Its *crista acustica*, which closely resembles that of the posterior canal, is 0.24 mm. in height and 0.45 mm. in length. Its long axis is slightly oblique, the anterior end of the crista lying somewhat medial to the mid-ventral line of the ampulla. Its sulcus contains the anterior extremity of the *ramulus ampullaris anterior*, a small branch from which runs forwards and dorso-laterally along the side of the ampulla. The *planum semilunatum* of the medial side is 0.44 mm. in height and 0.36 mm. in length and is somewhat taller and slightly more anterior than that of the lateral wall. From the posterior margin of the macula there runs backwards and laterally across the floor of the ampulla a somewhat narrower tract of low columnar cells which connects the former with the antero-medial border of the macula of the horizontal canal.

(iv) *The Macula and Crista Acustica of the Ampulla of the Horizontal Semicircular Canal.*

This macula is elliptical in shape, 0.54 mm. in length, 0.24 mm. in width. It is situated in the ventral third of the lateral wall of the ampulla. Its crista, which is much lower than those previously described, is only 0.15 mm. in height, its length is 0.48 mm., its width 0.21 mm., and its differentiation into apical and axial crests is not well marked, although it possesses well developed lateral crests similar in size and shape to those already described. The *plana semilunata* are approximately equal in size and similar in shape, each being 0.33 mm. in height and 0.48 mm. in length. The lateral *planum semilunatum* occupies the anterior half of the middle and ventral thirds of the lateral wall of the ampulla, while the medial planum occupies the greater part of the ventral region or floor and of the lower third of the medial wall of the ampulla. The wide and shallow sulcus, which runs in an antero-posterior direction along the middle of the ventral third of the lateral wall of the ampulla, contains the terminal fibres of the stout *ramulus ampullaris horizontalis*.

(B) *The Maculae of the Utriculus.*

(i) *The macula recessus utriculi* is situated in the floor of the anterior third of the *recessus utriculi*, extending laterally about one-quarter of the distance up the side of the recessus, and to a rather less extent on its medial wall. Laterally it appears to be united by a narrow tract of columnar cells with the posterior border of the macula of the ampulla of the anterior semicircular canal. It is elliptical in shape, 0.63 mm. in length and 0.30 mm. in width, and consists of columnar epithelial cells forming a very slightly raised area on the floor of the recessus and gradually merging into the cubical cells of the lower part of its walls.

The cells of this macula are either typical hair-cells, or supporting cells, some of which are tapering while others are dilated at each end and narrow in the middle. The epithelium has the typical multi-layered appearance owing to the presence of two or three rows of oval, deeply stained nuclei of the supporting cells. There is no conspicuous sulcus on the floor of the utriculus but the macula receives nerve fibres from the stout *ramus utriculi* of the anterior ramus of the auditory nerve. In embryos of Stage S the earlier connection existing between this macula and that of the anterior semicircular canal seems to have disappeared.

(ii) *The macula neglecta* is a small, circular, not very clearly defined patch of columnar epithelium lying on the floor and extending to the extreme ventral region of the medial wall of the *fundus utriculi*, immediately dorsal and posterior to the utriculo-saccular canal. It receives nerve fibres from a very thin, dorsally directed *ramulus maculae neglectae*, derived from the dorsal surface of the ramus posterior of the auditory nerve. In Stage R no auditory hairs could be detected on the surface of this macula, but in Stage S numerous typical hair-cells were found, more especially in the postero-ventral region of the macula.

(iii) *The wall of the utriculus* consists of a single layer of cubical epithelium, which passes into flattened epithelium in the dorsal and lateral regions. The flattening of the epithelium is more marked in embryos of Stage S, the cubical epithelium then being almost entirely confined to the neighbourhood of the maculae and to the wall of the utriculo-saccular canal. There is in some parts of the roof of the *sinus posterior utriculi* a not very clearly defined raphe of cubical cells. During Stage R the epithelial wall of the utriculus is invested with a thin layer of loose connective tissue, which at Stage S is converted into a thin layer of "spindle-cartilage," which in many parts of the lateral and dorsal wall is reduced to a layer of two or three rows of spindle-cells.

(C) *The Macula Acustica, and Wall, of the Sacculus.*

(i) *The macula acustica sacculi* is a large horseshoe-shaped patch of sensory epithelium, its anterior convex border being situated at the centre of the anterior wall of the sacculus, on the lateral wall of which its apex slightly encroaches. The



two diverging *crura* of the macula extend along the medial wall of the sacculus, the upper limb running postero-dorsally towards the utriculo-saccular aperture, just anterior to which it terminates. The *ventral crus* passes obliquely in a medial direction across the anterior curvature of the sacculus and runs in a postero-ventral direction to terminate on the medial wall just above the centre of the floor of the sacculus. The *macula sacculi* receives, at nearly all parts of its course, fibres from the saccular branch of the ramus posterior, the detailed distribution of which is described below (*vide* auditory nerve).

The macula consists of tall hair-cells with copious granular cytoplasm. Each cell contains a single, large, nearly spherical and finely granular nucleus, and bears a stout, conical and apparently rather short, auditory hair. The tapering bases of the hair-cells are prolonged as fine filaments passing between the supporting cells. The latter are tall and filamentous, each containing a small, oval, densely granular and deeply stained nucleus.

The length of the *dorsal crus* of the macula is approximately 0.60 mm., while the ventral limb measures 0.87 mm. and the average width of the tract is 0.16 mm. It is, however, not very well defined, since, owing to imperfect preservation of the available specimens, many of the hair-cells have lost their hairs, and the cells at the periphery of the macula are only distinguishable with difficulty from the surrounding columnar epithelium.

(ii) *The Wall of the Sacculus.*—In embryos of Stage R the medial wall of the sacculus in the neighbourhood of the macula consists of columnar epithelium, which exhibits two rows of basal nuclei. This gradually shades off into cubical epithelium, which in its turn is continuous with the flattened epithelium of the lateral and dorsal walls. It is everywhere supported by a thin layer of loose connective-tissue, which becomes very scanty on the lateral surface of the sacculus. During Stage S this connective-tissue has been converted into spindle connective-tissue (“spindle-cartilage”), which is thickest on the ventral third of the medial wall, where two different varieties of the tissue can be distinguished. It consists of an external zone, which is composed of a fairly open network of fine fibres with numerous “spindle-cells,” and of a more dense inner zone, in which the “spindle-cells” are very closely packed and the fibrous elements are inconspicuous. On the dorsal and ventral walls the layer of “spindle tissue” is much thinner, while on the lateral wall it is reduced to one or two rows of “spindle-cells,” united by a fine fibrous membrane closely investing the single layer of extremely flattened epithelial cells.

#### (D) *The Macula, and Wall, of the Cochlea.*

(i) *The macula acustica basilaris* is a nearly rectangular, clearly defined raised area of sensory epithelium, situated in the ventral third of the medial wall of the *pars basilaris*. Its antero-posterior axis runs obliquely at 45° in a postero-ventral

direction and is 0·48 mm. in length, the dorso-ventral axis of the macula being 0·18 mm. in length. The epithelium consists of large hair-cells, the swollen and rounded base of each of which contains a single large, spherical nucleus, while the cell exhibits a long, clear, and somewhat tapering zone at its distal end, which bears a single short stout, conical auditory hair. OSAWA states that in the adult each of these hair-cells bears a bunch of short cilia, but these were not observed in embryos of Stages R or S. Between the hair cells are the tall, narrow supporting cells, the nuclei of which are very characteristically arranged, forming two conspicuous basal rows. The supporting cells are most numerous near the periphery of the macula.

(ii) The *Macula Acustica Lagena*.—This macula is a large, crescent-shaped epithelial patch, one cornu of which occupies rather more than half of the medial wall of the lagena, across which it extends. The lateral horn of the macula occupies the antero-dorsal third of the lateral wall of the lagena. The medial portion of the macula is 0·75 mm. in length and measures 0·39 mm. in a dorso-ventral direction, while on the lateral wall of the *pars lagena* it forms a nearly equilaterally triangular patch, the convex walls of which are approximately 0·30 mm. in length. It consists of hair-cells and supporting cells, similar in appearance and arrangement to those of the *macula acustica basilaris*.

In the lumen of the cochlea, and overlying the maculae, there is found a flattened, nearly homogeneous mass, apparently containing fine fibres and small granules (“otolith crystals”—OSAWA).

(iii) *The Wall of the Cochlea*.—This consists of a single layer of low, cylindrical or nearly cubical epithelial cells, which are slightly more flattened on the lateral wall than in other regions. In embryos of Stage R the epithelial wall is supported by a connective-tissue layer, rather more abundant and dense than that which is present around the other parts of the membranous labyrinth. It is thickest on the medial side of the *pars basilaris* and *pars lagena*, but along the groove which marks the junction of these two parts of the cochlea it is much thinner. In Stage S a very conspicuous spindle connective-tissue (“spindle-cartilage”) layer has taken its place, and is thickest in the neighbourhood of the maculae, and more especially near their anterior borders, while it is thinner along the groove between the *pars basilaris* and the *pars lagena*, and is very scanty on the lateral surface of the cochlea.

The *macula acustica basilaris* receives nerve fibres from the *ramus basilaris*, and the *macula lagena* from the *ramus lagena*, of the ramus posterior of the auditory nerve. In all cases the nerve fibres are seen to penetrate the connective tissue or “spindle-cartilage,” to come in contact with the bases of the hair-cells of the maculae, to which they are respectively distributed. OSAWA states that in the adult he has observed nerve fibrils entering and traversing the basal portions of the hair-cells of some of the maculae, and AYERS (1892) describes and figures similar penetration in the case of nerve fibres distributed to auditory epithelium in *Petromyzon*, *Salmo*,

*Lepus* and *Felis*, but in none of the specimens now examined could this intracellular penetration be demonstrated.

*The Auditory Nerve.*

The *acustico facialis nerve complex* is an oval, antero-posteriorly elongated mass, which projects from the lateral wall of the hind-brain. At its anterior extremity it gives off the stout facial nerve, which at once enters the *canalis facialis*. Immediately posterior to the origin of the facial nerve the auditory nerve root divides into two very stout rami.

(A) The *ramus acusticus anterior* passes through the *foramen acusticum anterior*, enters the *sinus anterior* of the *recessus ellipticus*, and divides into three stout branches :—

(i) The *ramulus ampullaris anterior* is the most anterior of these branches. It passes immediately forward and in a dorsal direction, to reach the posterior region of the floor of the ampulla of the anterior vertical semicircular canal, along the sulcus of which it runs, its radiating terminal fibres being distributed to the *crista acustica* of this ampulla. The fibres penetrate the “ spindle connective-tissue ” of the floor of the ampulla, and reach the bases of, and presumably terminate within, the hair-cells of the crista.

(ii) The *ramulus ampullaris horizontalis* (or *lateralis*) is a stout nerve given off from the postero-ventral surface of the *ramus acusticus anterior*, and passes outwards and upwards, posterior and slightly lateral to the *ramulus ampullaris anterior*, eventually entering, almost at right angles, the middle region of the sulcus of the ampulla of the horizontal semicircular canal. Its terminal fibres spread fanwise along the sulcus, and are distributed to the sensory cells (hair-cells) of the *crista acustica*, while a few groups of fibres pass in a dorsal direction, some traversing the medial and others the lateral wall of the ampulla, and terminates in the region of the *plana semilunata*.

(iii) The *ramulus recessi utriculi* is a somewhat latero-medially flattened nerve, which leaves the dorsal surface of the *ramus acusticus anterior*, and passes to the floor of the *recessus utriculi*, to the sensory epithelium of the macula, of which its fibres are distributed.

(B) The *ramus acusticus posterior* is a very stout, short nerve-trunk, which runs laterally and in a slightly posterior direction, and, passing through the *foramen acusticum posterior*, enters the *recessus sphaericus*, and at once divides into two stout and two much more delicate ramuli :—

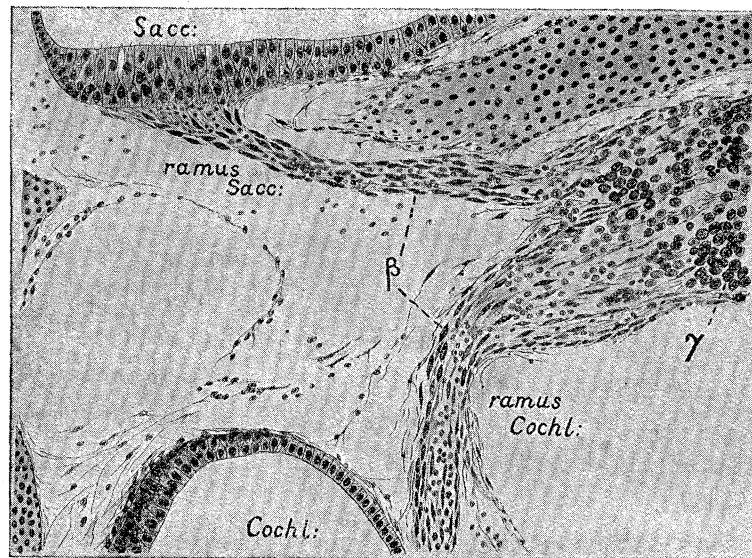
(i) The first ramulus to be given off is the very delicate *ramulus ducti endolymphatici*. This leaves the dorsal surface of the *ramus posterior* just as the latter emerges from the foramen into the recessus. It runs in a dorsal direction, being distributed

to, and terminating in, the ventral third of the medial wall of the *ductus endolymphaticus*.

(ii) Immediately posterior to this nerve is a second and very delicate ramulus, the *ramulus maculae neglectae*, which runs dorsally and in a slightly posterior direction, entering the junction of the medial wall and the floor of the *fundus utriculi* in the region of the *macula neglecta*, to the hair-cells, of which the terminal fibres of the nerve are distributed.

(iii) From the postero-dorsal surface of the *ramus posterior*, the stout, cylindrical *ramulus ampullaris posterior* enters and runs horizontally in a posterior direction within its special canal (*canalis ramuli ampullae posterior*) in the medial wall of the auditory capsule.

The nerve emerges into the *posterior sinus* of the *recessus ellipticus* just anterior and ventral to the ampulla of the posterior vertical semicircular canal, along the sulcus of which it passes, and terminates in the ventro-medial region of the posterior wall of the ampulla.



TEXT-FIG. 10.—Stage R. Embryo 141. Diagram of the distal extremities of the saccular and cochlear (Lagenar) rami of the auditory nerve showing  $\beta$  and  $\gamma$  neuroblasts, and sensory epithelium.

(For explanation of lettering see pp. 367–368.)

(iv) Laterally and slightly anterior to the *ramulus ampullaris posterior* the stout *ramus saccularis* is given off laterally and ventrally, immediately dividing into :—

(a) A stout *ramulus saccularis proprius*, passing to the medial wall of the sacculus, on which its fibres extend fanwise, one anterior group of these being distributed to the anterior border of the sacculus and ending on its anterior ventral surface.

(b) The *ramulus basilaris*, which runs laterally and nearly parallel to the *ramulus*

*ampullaris posterior*, is distributed to the medial wall of the *pars basilaris*, and terminating in the sensory epithelium of the *macula basilaris*.

(c) The *ramulus lagenæ (r. cochlearis)*, which bifurcates immediately on leaving the ventro-posterior surface of the *ramus saccularis*. The anterior branch, or *ramulus lagenæ anterior*, passes in an antero-ventral direction, and is distributed to the extreme anterior lateral and medial parts of the *macula lagenæ*. The second, more posterior and latero-medially flattened, wide band of nerve fibres, the *ramulus lagenæ posterior*, curves laterally and then eventually to meet the antero-medial wall surface of the *pars lagenæ*, across which it runs in a posterior direction to terminate at the ventral tip of the *lagenæ*, its fibres being distributed to the medial half of the *macula lagenæ*.

#### *The Ductus Perilymphaticus.*

This structure first appears during Stage R. Its intra-capsular extremity appears to be continuous with a not very clearly defined "perilymphatic space" situated on the medial side of the *foramen ovale*, and extending ventrally between the ventro-lateral wall of the sacculus and the wall of the auditory capsule. It swells up somewhat between the ventro-medial wall of the sacculus and the lateral wall of the cochlea, in which region its wall becomes more clearly defined. It passes ventrally to the cochlea as a narrowed, somewhat elliptical canal, and again dilates and runs medially as a fairly wide, tubular *ductus perilymphaticus* proper, occupying nearly the whole of the lumen of the *foramen rotundum* (which also contains the *vena cochlearis*). On emerging from this foramen into the *canalis jugularis (foramen jugularis interna)*, it swells up into the irregularly oval *saccus perilymphaticus*. One portion of the saccus extends forwards on the medial side of the cranial wall and becomes continuous with the connective tissue of the subarachnoid space. In a posterior direction the saccus extends ventrally to end blindly at the exterior opening of the *foramen jugulare*, from the orifice of which its convex surface slightly protrudes. The fibres of the wall of the saccus become continuous with those of the loose connective tissue here lying outside the lateral and ventral surfaces of the cranial wall (exoccipital cartilage). It appears, therefore, that proximally the *ductus perilymphaticus* is continuous with an extensive intra-capsular system of "perilymphatic spaces," while distally the lumen of the *saccus perilymphaticus* communicates in an anterior direction with the intra-cranial lymph spaces and in a posterior direction with those of the extra-cranial connective tissue. The walls, both of the saccus and of the *ductus perilymphaticus*, consist of a fairly stout, fibrous connective-tissue, containing numerous flattened cells, and blending externally with the mesh-work of the surrounding loose connective-tissue,

CONSIDERATION OF THE RESULTS OBTAINED IN THE PRESENT STUDY OF THE  
DEVELOPMENT OF THE INNER EAR AND AUDITORY NERVE.

It is evident that the foregoing account of the development of the inner ear and auditory nerve of *Sphenodon* is, as regards its general features, entirely in accord with current views respecting the development of these structures in the Vertebrata, more particularly with the observations of KASTSCHENKO, HOFFMANN, HIS, VILLY, AYERS, LILLIE, and CAMERON and MILLIGAN; while the observations now recorded concerning these structures on late embryos (*e.g.* those of Stages R and S) confirm and supplement those given by OSAWA for the adult auditory organ and nerve of this reptile.

As regards the earlier phases of development there is evident a remarkable uniformity in all the types hitherto examined. The auditory organ of either side first appears as a nearly circular, and slightly hollowed, patch of single-layered epiblast situated on the dorso-lateral surface of the head just in front of the 2nd mesoblastic somite. The patch rapidly develops into a deep pit, overgrowth of the anterior and ventral borders of which immediately occurs, the originally circular opening of the pit assuming the form of a vertically elongated ellipse. Rapid upward growth of the ventro-lateral border of the pit ensues, the auditory pit being converted into an otocyst (auditory sac), the lumen of which communicates with the exterior by a narrow primitive *ductus endolymphaticus*.

The distal portion of the primitive *acustico facialis neurencygium*, by which the sensory end organ was connected with the hind-brain, undergoes a simultaneous progressive differentiation into a dorsal or auditory and a ventral or facial ganglionic rudiment, still united proximally to the hind-brain by a common root.

The superficial area of the otocyst undergoes rapid expansion and soon becomes constricted into a *pars superior* and a smaller *pars inferior*. The constriction passes through the large patch of neuro-epithelium (primitive auditory epithelium)—which now occupies nearly the whole of the medial and a portion of the ventral wall of the otocyst—and divides it into two parts, each of which is connected with a portion of the auditory neurencygium. The subsequent further division of these primitive sensory epithelial patches into the various *maculae acusticae* is accompanied by a corresponding division of the distal portion of the auditory neurencygium, which thus ultimately gives rise to the various ramuli of the auditory nerve. This process has already been observed and briefly recorded in a number of vertebrate embryos by CAMERON and MILLIGAN (1910). These investigators consider that they have clearly established the fact that "the breaking-up of the primitive auditory ganglion is a necessary accompaniment of the process of resolution of the sense-epithelium patch into its various macular areas" (*op. cit.*, p. 118). With their observations it is obvious that the results recorded in the present paper are in complete agreement.

The final closure of the otocyst takes place just dorsal to the middle of the lateral

surface of the developing *ductus endolymphaticus*, and a protrusion of the medial surface of the same region now occurs, thus producing the rudiment of the *saccus endolymphaticus*. It is noteworthy that a vestige of the distal portion of the *ductus endolymphaticus*, now separated from the superficial epiblast of the head, persists in the oldest *Sphenodon* embryos examined (Stages R and S) in which it occurs as a conical prolongation of the dorsal region of the *saccus endolymphaticus*, and is situated in a foramen (*foramen sacci endolymphatici*) piercing the cranial roof of either side, not far from the mid-dorsal line. This is obviously a persistent primitive feature, and has not been recorded in any of the higher vertebrata. The aperture by which the lumen of the *ductus endolymphaticus* communicates with that of the otocyst now undergoes displacement in a medio-ventral direction, owing chiefly to the expansion of the surface of the latter in a dorso-lateral direction, but, as I have already suggested, the process appears to be due in part to ventral elongation of the closed portion of the ductus which results from a progressive lateral fusion of its anterior and posterior walls, thus shutting off more and more of the length of its lumen from that of the otocyst.

Simultaneously with this process there occurs a differentiation of the *pars superior* into a system of communicating canals and sinuses. These are formed by the outgrowth of a number of pockets and the ingrowth of the walls of a number of deepening grooves. The septa formed by these double-walled epiblastic folds, and by the mesoblast included between them, result in the formation of a central tri-radiate utriculus, the extremities of which are united by an anterior vertical, a posterior vertical and a horizontal semicircular canal, each of which possesses a dilated "ampulla" on the floor of which arises a sensory crest or *crista acustica*. To each of these is distributed a ramus of the auditory nerve. On the medial wall of the utriculus occurs a number of sensory epithelial patches derived, like the epithelium of the *crista acustica*, from the neuro-epithelium of the *pars superior*. These macular areas are at first united with one another and with the neuro-epithelium of the *pars inferior* by tracts of neuro-epithelium, but in the adult organ they are entirely separated.

The appearance of the grooves and pockets of the *pars superior* suggest that the anterior, vertical and horizontal, semicircular canals are formed somewhat earlier than the posterior vertical canal, but, on the other hand, the *crista acustica* of the horizontal semicircular canal appears to develop somewhat later than do those of the other canals. The question of the order of development of the canals and of their phylogeny is discussed by VILLY (1890) and by AYERS (1892), and the results of the present research appear to lend some support to the view advanced by the latter (*op. cit.*, pp. 210 *ff.*).

In the present section the development of the canals, macular areas, and branches of the auditory nerve has been fully discussed, and it remains only to draw attention to the existence of a well-developed *macula neglecta*—a primitive feature—and a nerve ramulus supplied to it, and also to the presence of a similar nerve-branch to the

*ductus endolymphaticus*. No sensory epithelium was, however, discovered in the *saccus endolymphaticus*.

The *pars inferior* meanwhile undergoes differentiation into sacculus and cochlea, the latter exhibiting a curved distal *pars lagenæ* and a proximal *pars basilaris*—each with its own macular area and nerve supply.

A complete account of the histology of the inner ear was not attempted but sufficient data have been obtained to confirm and supplement the histological details recorded by OSAWA (1898). The maculæ and cristæ contain hair-cells (auditory sense epithelium cells) and interstitial (supporting) cells, while the non-sensory areas of the walls of the inner ear consist of flattened or cubical epithelium supported by an external investment of “spindle connective-tissue.”

#### V. THE AUDITORY CAPSULE, COLUMELLA AURIS, AND ASSOCIATED BONES.

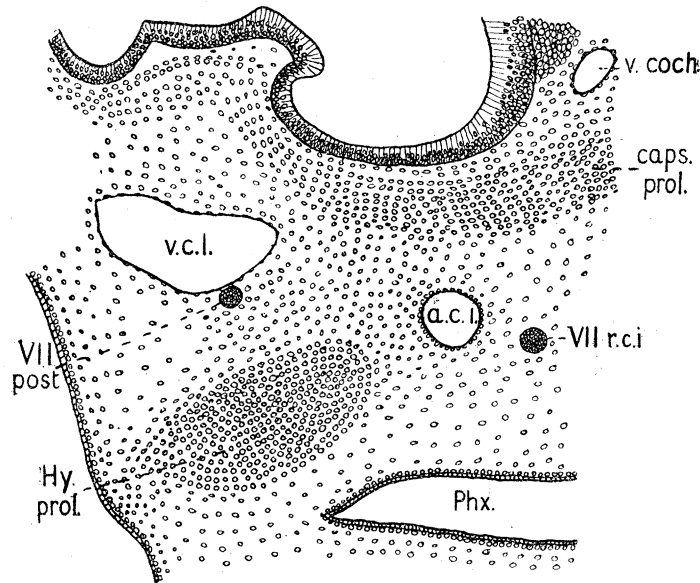
As GEOFFREY SMITH (1904) justly observes, a true conception of the origin and relationships of the auditory capsule, columella, and hyoid can result only from an examination of embryos in which chondrification of the rudiments of these structures has not yet occurred—in specimens, therefore, younger than those described by previous writers on this subject. The conditions obtaining in such early embryos are now recorded for, it is believed, the first time, together with the inferences drawn therefrom.

In a consideration of the much-discussed question of the origin and affinities of the columella-hyoid complex a repetition of some of the work of earlier investigators—more especially of that of HOWES and SWINNERTON (1901)—is inevitable, but where the results now obtained agree with those already recorded, a bare statement to that effect is, if possible, substituted for detailed description.

*Stage O-P. The Auditory Capsule.*—The first sign of a capsular investment of the membranous otocyst occurs in embryos of late Stage O or early Stage P (Stage O-P, Embryo 35 $\alpha$ , text-figs. 5, 11), simultaneously with the appearance of the epiblastic folds from which are ultimately developed the septa which delimit the membranous canals of the inner ear. At this stage no chondrification has taken place within the auditory region, but the otocyst is closely invested by a *blastema* composed of rapidly proliferating mesenchyme cells. A particularly dense mass of these cells occurs in the parachordal region, from which results the formation of a horizontal and approximately rectangular sheet of tissue with well-developed dorsal and ventral axial ridges, which indicate the position of the enclosed notochord. This *parachordal proliferation* is the rudiment of the parachordal plate. Its width is approximately three-quarters of that of the head of the embryo, but it narrows considerably in both the pre-otic and post-otic regions. The widening of the parachordal proliferation in the region of the otocyst is due to its extension in a latero-



dorsal direction. Its lateral margin, which closely envelops the ventro-lateral surface of the otocyst, merges in the less dense mesenchyme layer which invests the lateral surface of this structure.



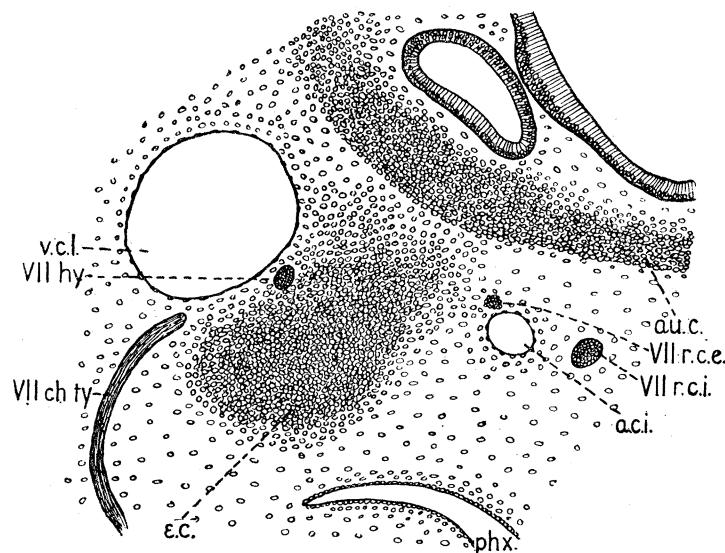
TEXT-FIG. 11.—Stage O-P. Embryo 35a. Diagram of the hyoidean and capsular proliferations. First stage in the development of the hyoid-columella complex.

(For explanation of lettering see pp. 367-368.)

A similar but less prominent extension of the parachordal proliferation passes between the medio-ventral surface of the otocyst and the brain, but undergoes rapid attenuation and finally passes into the mesenchymatous investment of the *pars superior* of the otocyst. On the postero-medial surface of this capsular proliferation there occurs a small, nearly circular area of less dense tissue, which in subsequent stages of development remains unchondrified. This marks the position of the future *foramen rotundum*.

Immediately postero-dorsal to the still open first visceral cleft is a second proliferation, which appears in transverse section as an oval patch of very dense mesenchyme, with its long axis directed in a dorso-medial direction between the *vena capitis lateralis* and the *arteria carotis interna*. Its anterior surface is convex, but posteriorly it is prolonged into a boomerang-shaped tract of cells similar to, but somewhat more densely arranged than, those of the *capsular proliferation*. It curves first in a ventral and then in an anterior direction, is circular in cross-section and gradually tapering, and terminates ventrally to the lateral margin of the pharynx at a level just posterior to that of its dorsal extremity. This tract of mesenchyme may be called the *hyoidean proliferation*. At no point is there any continuity between the capsular and hyoidean proliferations, the space included between these, the *vena capitis lateralis*, the pharynx, and the *arteria carotis*

*interna* being occupied by mesenchyme, the cells of which are slightly larger and more oval than those of the above-mentioned tracts.



TEXT-FIG. 12.—Stage P. Embryo 45*a*. Diagram showing the developing hyoid and capsular procartilagenous tracts. The extra-stapedial rudiment is seen to originate from the hyoidean tract. (For explanation of lettering see pp. 367–368.)

*Stage P*.—During Stage P (Embryo 45*a*, figs. 39, 40, text-figs. 6, 12) the formation of a more clearly defined procartilagenous auditory capsule becomes evident. In shape it is approximately ovoid with nearly equal dorso-ventral and medio-lateral axes, these being slightly shorter than the antero-posterior axis. The curved anterior surface of the auditory capsule is somewhat flattened, the dorsal surface is traversed in an antero-posterior direction by a strong dorsal ridge, and the convexity of the lateral surface is interrupted by a broad, shallow depression, which traverses it longitudinally and occupies the middle third of its surface (figs. 39, 40). The *parotic process* is present as a horizontal and laterally-directed, bluntly conical process, situated on the extreme postero-lateral convexity of the capsule.

The conversion of the original investing connective-tissue into procartilage is less complete in the medial and dorso-medial regions than in other parts of the capsule. A large lacuna in the middle third of the medial surface serves to transmit in a dorsal direction the *ductus endolymphaticus* (text-fig. 6), while ventral to this emerges the massive roots of the auditory nerve, together with the blood-vessels of the membranous labyrinth, with the exception of the *vena cochlearis*, the space between them being filled with mesenchyme. The *foramen rotundum* (fig. 40) is a small, circular foramen in the postero-medial surface of the auditory capsule. The loose mesenchyme with which it is filled is penetrated by the *vena cochlearis*.

Immediately behind the posterior surface of the otic capsule the lateral margin of the stout chondrified parachordal plate bears a well-developed latero-dorsal lobe (the

*exoccipital lobe*), between which and the capsule is a large interspace traversed by the *vena cephalica posterior* and the proximal portions of Nerves IX, X, and XI. In the exoccipital region the parachordal plate is perforated by a series of four small foramina, through which pass the five roots of Nerve XII. These foramina are situated nearly midway between the axial ridge and the lateral margin of the parachordal plate.

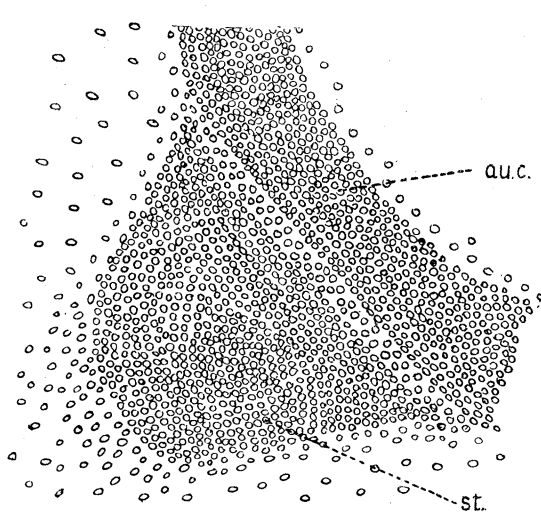
During the immediately preceding phase of development, the ingrowth of the septa, which delimit the various parts of the membranous labyrinth, has been followed by proliferation of the invading mesoblast cells, which have migrated inwards to occupy the space between the epiblastic folds of the septa, and chondrification is now proceeding. As a result of this the membranous inner ear is closely invested by these tissues (text-fig. 12). The cavity of the auditory capsule consists, therefore, of a system of communicating canals and saccular recesses, whose walls are lined with epithelial tissue, and whose shape is similar to that of the membranous labyrinth, which it contains. It communicates with the exterior by the two foramina already described.

While these changes are in progress chondrification has been taking place within the hyoidean proliferation, the antero-dorsal extremity of which is now connected with the auditory capsule by a cylindrical rod of tissue. This rod is in process of chondrification at its lateral extremity, but consists, at its somewhat expanded capsular end, of a mass of proliferating mesenchyme cells. There is no sign of a corresponding extension outwards of the procartilage of the auditory capsule. It is obvious that this medially chondrifying rod of tissue is the developing columella, the expanded and already chondrified lateral extremity of which represents the *extra-stapedial cartilage (extra-columella)*. It is situated just anterior and ventral to the parotic process and between the 1st and 2nd visceral pouches (fig. 39 and text-fig. 12).

A well-developed *anterior cornu* of the *hyoid cartilage* (fig. 39) has now been formed by the extension of the process of chondrification throughout the curved connective-tissue mass present in the preceding stage of development, and it is evident that the whole tract is continuous, from its dorso-medial margin lying against the auditory capsule to its ventro-medial pharyngeal extremity. Immediately posterior to the extra-stapedial region there is a slight constriction, which suggests "jointing," between the latter and the more posterior cornu proper, which, on a superficial examination, might be suspected of indicating the existence of a joint between two separate procartilaginous tracts. Microscopical examination of serial sections conclusively proves that no such discontinuity exists. HOWES and SWINNERTON (1901) also note the existence of apparent "jointing," but their conclusion—with which I am in entire agreement—is that this "cannot be regarded as evidence of original discontinuity between the columella and the hyoid cornu. It is seen to be but a passing phase, indicative of either a probable ancestral

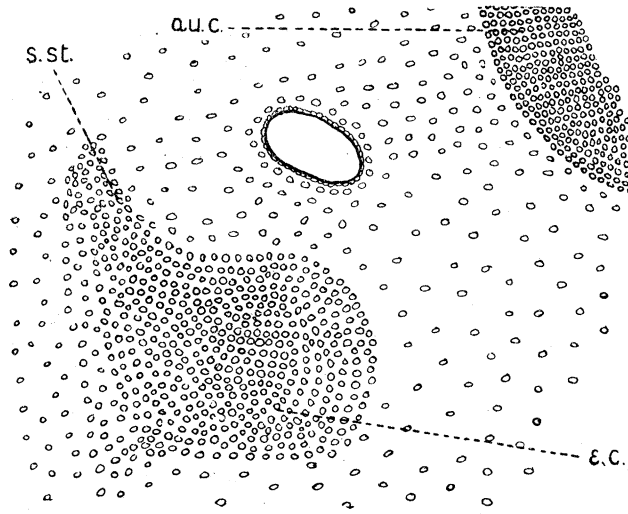
or an incipient 'jointing,' such as takes place elsewhere along the cornu . . ." (*op. cit.*, p. 48).

The procartilagenous mass which now appears, replacing the connective tissue proliferation in the mandibular arch in Stage O-P, requires no detailed description, as an examination of fig. 39, representing the condition obtaining in Stage P, Embryo 45*a*, sufficiently indicates its form and topographical relationships, which are in agreement with those described by HOWES and SWINNERTON (*op. cit.*, p. 44).



TEXT-FIG. 13.

TEXT-FIG. 13.—Stage P-Q. Embryo 51*a*. Diagram showing the lack of continuity of the developing proximal extremity (foot-plate) of the columella auris and the auditory capsule. These structures are separated by a narrow zone of less dense tissue.



TEXT-FIG. 14.

TEXT-FIG. 14.—Stage P-Q. Embryo 51*a*. Diagram showing the continuity of the developing supra-stapedial process with the extra-stapedial cartilage.

(For explanation of lettering see pp. 367-368.)

*Stage P-Q.*—The period of transition from Stage P to Stage Q (Embryo 51*a*, text-figs. 13 and 14) presents two additional developmental features.

A conical, dorsally directed process, the *supra-stapedial process*, is now apparent at the distal end of the extra-stapedial cartilage, no line of demarcation being distinguishable between this process and the original extra-stapedial chondrification. More medially, the region of proliferating mesenchyme cells, extending from the chondrified zone of the columella inwards to the lateral surface of the auditory capsule, is also undergoing conversion into cartilage. A faint line of demarcation is evident between this newly chondrifying tract and the cartilage of the auditory capsule. This suggests that the formation of the stapes, or medial region of the columella, including a slightly expanded base, or rudimentary *foot-plate*, is resulting from a medially directed extension and chondrification of the original hyoid proliferation.

*Stage Q* (Embryo 52*a*, figs. 42A, 42B).—During this stage a considerably increased

complexity of the skull in general is accompanied by somewhat extensive development in the auditory region.

The procartilage of the auditory capsule has been almost completely converted into hyaline cartilage, and, although the capsule does not exhibit very marked increase in size, two outstanding new features are distinguishable.

From the medio-dorsal surface of the posterior part of the auditory capsule a domed sheet of tissue—mainly procartilaginous—unites the capsule with its fellow on the opposite side of the head. From the anterior border of this inter-capsular tract there extends forward in the mid-dorsal line, and just below the dorsal surface of the head, a narrow band of dense tissue, which runs forward as far as the point immediately dorsal to the anterior border of the auditory capsule. This tract is undergoing conversion into procartilage, and it is evidently the anterior process of the developing supra-occipital cartilage. Meanwhile the exoccipital cartilage of either side has undergone considerable extension dorsally, laterally, and in an anterior direction, and is united with the postero-medial surface of the hinder part of the auditory capsule. This cartilaginous union forms a dorsal bridge across the previously existing interspace, thereby converting it into the *foramen jugulare*, which persists in adult *Sphenodon*.

Minor features characteristic of this stage of development are the first appearance of the *squamosal* and *parietal bones*, both of which are paired structures. Each squamosal bone is a small, semi-lunar ossification with its long axis directed antero-dorsally, its ventral and posterior cornu being in close proximity to the postero-dorsal process of the quadrate. Each of the parietal bones is situated postero-dorsally to the epipterygoid cartilage, and between it and the antero-lateral surface of the auditory capsule. It is similar in shape to an inverted letter L, one limb of which is directed in a ventral and one in an anterior direction.

The *parotic process* is somewhat more conspicuous than during the preceding stage of development and is more definitely lateral in position, the posterior portion of the auditory capsule having become larger by extension in a posterior and postero-dorsal direction.

*The Columella-hyoid Complex.*—Like the auditory capsule, the procartilaginous structures which become the columella-hyoid complex have undergone conversion into hyaline cartilage. The *supra-stapedial process* has developed into a stout, conical rod, which springs from the antero-dorsal surface of the distal extremity of the extra-stapedial cartilage. It extends in a dorsal direction, its distal extremity being situated postero-ventral to, and near the surface of, the postero-dorsal angle of the quadrate, and immediately ventral to the lower cornu of the squamosal.

The cartilaginous rod which represents the developing *columella* shows a constriction at the middle of its length which foreshadows its division into a lateral *extra-stapedial cartilage* and a medial *stapes*. The capsular extremity of the columella is expanded

to form a foot-plate which lies in contact, and may be continuous, with the cartilaginous lateral wall of the auditory capsule. The foot-plate is certainly continuous with the stapes, the cells of both being densely packed, while there is, as already noted in Embryo 51*a*, Stage P-Q, a distinct zone of demarcation, in which the cells are much more sparsely scattered, between the foot-plate and the auditory capsule. This suggests that the foot-plate is hyoidean and not capsular in origin.

The "jointing" between the extra-stapedial cartilage and the dorsal extremity of the hyoid cornu—a purely transitory feature apparently characteristic of embryos of Stage P, since it has been separately noted in different embryos of this stage of development by HOWES and SWINNERTON (1901), and by myself—has now disappeared. There is, however, a marked development of the "scroll"-like curvature of this proximal (dorsal) extremity of the hyoid cornu, first noted by HUXLEY (1869) in adult *Sphenodon*. At the point of transition from the "scroll" to the main portion of the hyoid cornu, which curves away from it in a ventral direction there is produced a conspicuous postero-dorsal "elbow" which is present in all subsequent stages of development and persists in the adult.

*Stage R* (Embryo 141, figs. 17, 18, 43 and text-fig. 15).

*Auditory Capsule*.—This stage is characterised by a further considerable growth of the auditory capsule, the greatest increases taking place in the antero-posterior and dorso-ventral directions. The capsule therefore appears to have become somewhat flattened latero-medially. In the stapedial region the thinning of the capsular wall, already noted in Stage Q, has resulted in the formation of a nearly circular *foramen ovale*, in which is set the foot-plate of the stapes, attached to its periphery, as described below.

The inter-capsular (supra-occipital) roof is now a dome of massive cartilage extending forward from the *foramen magnum*, on either side of which it comes in contact with the ex-occipital cartilage, to the level of a transverse plane which would pass through the long axis of the stapes. In the mid-dorsal line the anterior margin of the supra-occipital roof is prolonged forward as the spatulate anterior limb of the supra-occipital cartilage, the anterior extremity of which extends as far forward as the anterior border of the auditory capsule. This cartilage and the domed sheet from which it arises are convex in both the postero-anterior and dorso-ventral directions, following the cephalic curvature. The inter-capsular cranial roof bears on its postero-dorsal aspect a sharp medial ridge, which terminates in a somewhat flattened pyramidal projection immediately dorsal to the *foramen magnum*. Behind, below, and on the medial side of each auditory capsule, the *pleurooccipitalia*, which arise from the ex-occipital region of the parachordal plate, by coming into contact with the posterior tragus of the auditory capsule, have completed dorsally the periphery of the elongated *foramen jugulare*. The basal portion of each pleurooccipital cartilage, immediately ventral to the posterior boundary of the *foramen jugulare*, is perforated

by three foramina, serially arranged in an antero-posterior direction, through which emerge the roots of Nerve XII. The fact that at Stage P there are four foramina, transmitting five nerve roots, has already been noted. In Stage S the condition observed is the same as in Stage R, but in adult *Sphenodon* two foramina only have been found by HOWES and SWINNERTON (1901).

On the ventral surface of the parachordal cartilage there is, in this region, a decided thickening and incipient ossification, which extends outwards from a single centre and is evidently the developing medio-ventral *basioccipital bone*. Opening into the antero-lateral region of the *foramen jugulare* is a conspicuous circular foramen which penetrates the postero-medial wall of the auditory capsule. This is the *foramen rotundum*, which transmits the *saccus perilymphaticus* and the *vena cochlearis*. Both the *foramen jugulare* and the *foramen rotundum* are conspicuous in embryos of Stage S and are present in adult *Sphenodon*, although the former foramen has then become somewhat reduced. VERSLUYS (1898) appears to exaggerate the amount of retrogression undergone by the lateral portion of this foramen, which, as I have already shown, transmits Nerves IX, X and XI, the *vena cephalica posterior*, and contains the distal portion of the *saccus perilymphaticus*.

In Stages R and S there is no trace of the *supra-occipital foramen* found by DENDY (1910) in the adult skull, but almost immediately posterior to the point of origin of the anterior process of the supra-occipital cartilage from the main cartilage of the cranial roof, and one-third of the distance outwards from the mid-dorsal line towards the dorsal crest of the auditory capsule, there is on either side of the skull a small round foramen, apparently unnoted by early investigators (figs. 17, 18). These two foramina I propose to call the *foramina endolymphatici* since each contains a conical diverticulum of the dorso-lateral wall of the corresponding *saccus endolymphaticus*. Each diverticulum is long enough just to penetrate the thickness of the cranial roof but not to emerge into the supra-occipital connective tissue. It is evidently a vestige of the epithelial canal by which the *saccus endolymphaticus* of either side communicated with the exterior during the early stages of development. I have not found these foramina in the adult skull.

The medial wall of the auditory capsule is penetrated at the junction of its anterior and middle thirds by the large, oval *foramen acusticum anterior*, which transmits the anterior ramus of the auditory nerve. It occupies a position in the middle third of the capsular wall and immediately posterior to it is a slightly longer and more horizontally elongated foramen—the *foramen acusticum posterior*, which transmits the posterior ramus of the auditory nerve. In the medial wall of the capsule is a narrow, circular canal running horizontally backwards from the posterior boundary of this foramen and opening into the *recessus sphericus* (OSAWA, 1897) of the capsule at a point nearly midway between the *foramen acusticum posterior* and the posterior boundary of the capsule. This canal contains the posterior ampullary branch of the posterior ramus of the auditory nerve. The capsular wall immediately dorsal to the

*foramen acusticum posterior* is penetrated by a smaller vertically elongated foramen, through which emerges the *ductus endolymphaticus*. From the antero-ventral boundary of the *foramen acusticum anterior* arises the *foramen facialis*, which transmits Nerve VII. This foramen traverses the medial wall of the capsule in an antero-lateral direction finally opening on the latero-ventral wall of the anterior tragus (pro-otic region) of the auditory capsule.

The cavity of the auditory capsule is divided by a small horizontal ridge (*cricoid ledge*, OSAWA) into a dorsal and a ventral division. The dorsal portion of the cavity or *recessus ellipticus* approximates in shape to a horizontally elongated ellipse extending throughout nearly the whole antero-posterior length of the auditory capsule. Its anterior portion (anterior sinus) contains the ampulla of the anterior vertical semicircular canal and the anterior sinus utriculi (*recessus utriculi*, RETZIUS), while the posterior sinus contains the ampulla of the posterior vertical semicircular canal. The horizontal semicircular canal extends in a lateral direction and passes from the anterior to the posterior sinuses of the *recessus ellipticus* as a tubular channel hollowed out in the cartilaginous lateral wall of the auditory capsule. From near the centre of the medial half of the dorsal region of the *recessus ellipticus* there extends a nearly vertical (dorsal) sinus superior, which contains the sinus superior utriculi of the membranous labyrinth and which at its dorsal extremity is united both to the anterior and to the posterior sinuses of the *recessus ellipticus* by the anterior and the posterior vertical semicircular canals respectively.

The ventral portion of the cavity of the auditory capsule is the *recessus sphericus*, which contains the sacculus, while a postero-medially directed conical diverticulum of this recessus, the so-called *recessus cochlearis* (OSAWA), receives the cochlea.

During Stages Q and R the capsule consists of hyaline cartilage, which even in Stage S shows (except in the basi-occipital region) no signs of ossification. The whole of the cavity of the auditory capsule is lined with a delicate connective-tissue, consisting of a single epithelial layer of fusiform or much flattened cells, together with a loose network of fine fibres, which appear to be continuous with those of the loose connective-tissue which at this stage occupies much of the space between the walls of the component parts of the membranous labyrinth and the walls of the corresponding parts of the cavity of the auditory capsule.

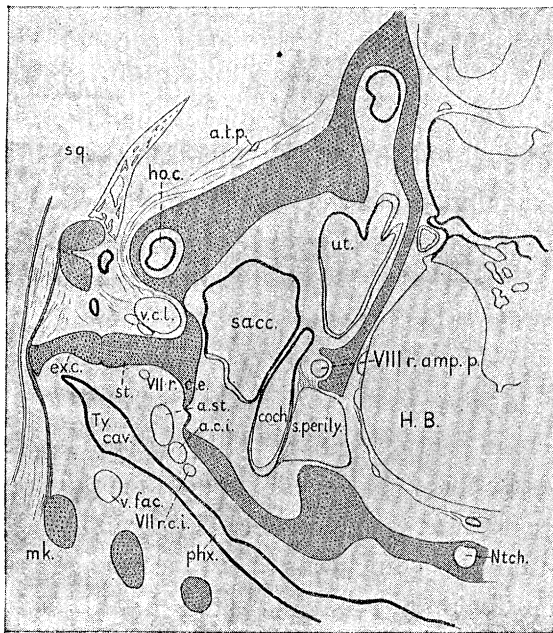
It was thought unnecessary to pursue a detailed investigation of the development of the auditory capsule beyond Stages R and S, as it has by this time practically reached the adult condition so exhaustively and accurately described by OSAWA (1898).

The further modifications observed in the skull during Stage T by HOWES and SWINNERTON (1901) are mainly due to the appearance and expansion of bones overlying or associated with the *chondrocranium* and which, when necessary, are referred to below.

It may be permissible here to point out that in addition to embryos specially

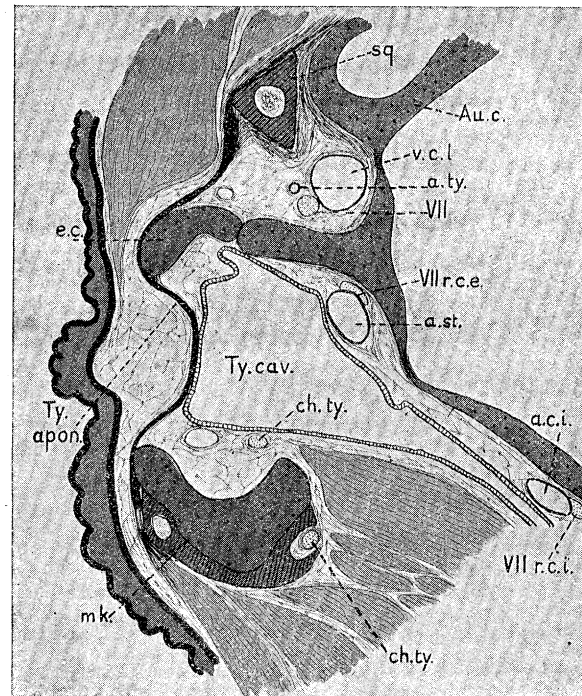


selected and prepared for the purpose of this research I have examined the following embryos previously described by these observers, viz., Stage Q, Embryo 52*a*, Stage R, Embryos 142 and 162, Stage R-S, Embryos 1 and Stage S, Embryos 11. I am in entire agreement with HOWES and SWINNERTON as regards the anatomical details of embryos of these later stages, and my drawings and the models from which they were made afford singularly complete confirmation of theirs, although it should be noted that their embryo of Stage P is somewhat younger than my Embryo 45*a* referred by DENDY to the same stage of development.



TEXT-FIG. 15.

TEXT-FIG. 15.—Stage R. Embryo 141. Diagrammatic transverse section through the left auditory capsule and associated structures, showing the stapes and extra-stapedial cartilage, together with the developing tympanic diverticula.



TEXT-FIG. 16.

TEXT-FIG. 16.—Stage S. Embryo 9*a*. Diagrammatic transverse section of the left tympanic region showing the stapes, the extra-stapedial cartilage, the tympanic cavity and the tympanic aponeurosis.

(For explanation of lettering see pp. 367-368.)

*The Columella.*—The dorsal and posterior portions of the anterior cornu of the hyoid undergo considerable increase of size during Stages R and S, but they present no structural changes such as would necessitate detailed description, this having already been given for an embryo of Stage Q. The same cannot be said of the *columella auris*, which shows a considerably increased complexity (figs. 17, 43, 44, 45 and text-fig. 16).

The *extra-stapedial cartilage* is approximately ovoid in shape, its apex being

united with the scroll-like dorsal extremity of the hyoid cornu and its long axis directed antero-posteriorly. It is somewhat flattened laterally, becoming almost discoid (VERSLUYS, 1898) in the adult, and bears an antero-ventral *inferior process*, which in Embryo 141 is much more strongly developed than in HOWES and SWINNERTON'S embryo of the same stage (*op. cit.*, fig. 11, p. 48).

The *supra-stapedial cartilage* now extends to the ventral surface of the posterior extremity of the quadrate, to which it is attached by a thin sheet of fibrous connective-tissue. The head or dorsal extremity of the supra-stapedial cartilage is expanded in a postero-medial direction, this expansion being the rudiment of the *intercalare* of the adult (VERSLUYS, 1898, 1903). A conspicuous *recurrent process* is borne on the medial surface of the supra-stapedial cartilage just ventral to the *intercalare*, and extends in a ventro-medial direction almost to the dorsal surface of the medial (stapedial) extremity of the extra-stapedial cartilage, to which it is firmly attached by a band of ligamentous fibres (fig. 43). These run parallel to the long axis of the recurrent process, and are set obliquely into the dorsal surface of the extra-stapedial cartilage. The triangular space included between the supra-stapedial, its recurrent process, and the extra-stapedial cartilage, is *Huxley's foramen*. The columellar rod is divided into a distal extra-stapedial cartilage, and a proximal segment or stapes by a secondary "joint," now apparent for the first time, the interval between the two cartilages being filled by a thin layer of connective-tissue. The joint is not well marked externally, owing to the presence of an investing layer of perichondrial tissue, but it is very conspicuous in sections cut parallel to the long axis of the stapes. The distal end of the stapes is somewhat swollen and rounded at this point of junction with the extra-stapedial cartilage. The proximal extremity is expanded into a well-developed foot-plate, while the connecting rod of cartilage is somewhat constricted. The periphery of the foot-plate is connected by fibrous tissue with the cartilaginous border of the *foramen ovale*, which, like that of the majority of the *Reptilia* (and *Monotremata*), is nearly circular in shape. The lateral surface of the foot-plate is flush with that of the capsular wall, the *foramen ovale* possessing no "pelvis." The medial surface of the foot-plate is slightly concave, and is invested with a lining (*endosteum* in the adult) continuous with that of the cavity of the auditory capsule.

In *Stage S* (figs. 44, 45, and text-fig. 16) the only additional changes to be recorded are the further development of the *intercalare*, which is in contact at its anterior and medial surfaces with the quadrate, while its postero-medial extremity is in contact with the posterior process of the squamosal, to which it is attached by a thin sheet of fibrous tissue. The quadrate, which is partly overlain by the squamosal, is unossified dorsally, and the statement of HOWES and SWINNERTON (*op. cit.*, p. 47), that the union between the quadrate and the *intercalare* is secondary, is confirmed by a study of the above-described conditions obtaining in embryos of Stages Q, R and S. I agree with these observers and with GADOW (1889), as against HUXLEY

(1869), that a cartilaginous connection between the supra-stapedial cartilage and the cranium is absent.

The ventral extremity of the recurrent process of the supra-stapedial cartilage has now extended to and fused with the dorsal surface of the extra-stapedial cartilage (figs. 44, 45).

VERSLUYS (1898, p. 108 *ff.*) has given an account of the columella-hyoid complex of adult *Sphenodon*. It agrees in all essentials with that given above, as do also the accounts of OSAWA (1897) and GRAY (1913). He notes, however, that in his specimen a gap occurs between the recurrent process of the supra-stapedial cartilage and the dorsal surface of the extra-stapedial cartilage. He suggests that this may be due to damage received by the specimen during dissection, and this is probably the case, since the gap appears to be bridged by ligamentous fibres in embryos of Stage R (Embryos 141, 142), and in both embryos of Stage S (11 and 9a) examined by me there is continuity of the recurrent process with the extra-stapedial cartilage. It is possible, on the other hand, that a development of the recurrent process sufficient to produce this distal fusion with the extra-stapedial cartilage may not invariably occur (*cf.* GADOW, 1889, p. 468 ; also HOWES and SWINNERTON'S comment (1901, p. 47) on GADOW, p. 467).

GAUPP (1891, 1898) appears to doubt the existence in Lacertilian embryos of a cartilaginous connection between the epipterygoid rudiment and the quadrate. BROOM (1903) agrees that such a connection is absent in *Lacerta* embryos, but he demonstrates its presence in those of *Zonurus*, *Eremias* and *Mabuia*. It is undoubtedly present in *Sphenodon*, in which, during the earlier phases of Stage P, the epipterygoid and quadrate are pre-formed, as stated by HOWES and SWINNERTON (*op. cit.*, p. 45), in a single continuous tract of cartilage, which also I have found to be the case, and have shown in fig. 39 (Stage P, Embryo 45a).

During Stages R and S, first the pterygoid and quadrate, and, finally, the cartilaginous connection between them all, undergo ossification. It would appear probable that this is the primitive condition, and that, like *Sphenodon*, the ancestors of existing *Lacertilia* possessed a fixed quadrate.

A careful examination of embryos of Stages P to S inclusive, fails to yield any confirmation of the assumption of OSAWA (1897), noted and rejected by HOWES and SWINNERTON (*loc. cit.*, Footnote 2), that the "pterygoid arises from two ossific centres, of which the hinder has in *Sphenodon* become co-ossified with the quadrate." I agree with the latter observers that "there is no trace of any such posterior pterygoid bone, actual or potential" (*loc. cit.*).

#### *The Relationship between the Columella Auris and the Anterior Cornu of the Hyoid.*

Some discussion of this question appears to be a necessary adjunct to an account of the developmental changes occurring within the auditory region of *Sphenodon*, but since the observations of earlier investigators have been restated at considerable

length by VERSLUYS (1898), and HOWES and SWINNERTON (1901), it is not proposed to recapitulate these, but rather to refer to them as briefly as possible.

HUXLEY (1869), VERSLUYS (1898), and HOWES and SWINNERTON (1901) regard the extra-stapedial cartilage of *Sphenodon* as hyoidean in origin, and KINGSLEY (1900) comes to the same conclusion respecting the columella of the Lacertilia, as does also GEOFFREY SMITH (1904) in the case of the Chick. PETERS (1870 and 1874), BAUR (1887), GADOW (1889), and OSAWA (1897), conclude, on the other hand, that the union between the extra-stapedial and hyoid cartilages of *Sphenodon* is secondary.

PETERS (*op. cit.*) considers that the supra-stapedial originates as a separate cartilage, while KINGSLEY (*op. cit.*, p. 215) states that the extra-columella (extra-stapedial) is at first “. . . a discrete part. It appears first as a slender rod of procartilage just in front of the hyoid and ventral to the tympanic cavity. Its upper end is closely related to the dorsal end of the hyoid and the distal end of the stapes.” This is not the case in embryos of *Gecko*, or of *Lacerta* (VERSLUYS, 1903), nor in *Sphenodon*, as is shown in the present research. The above-quoted passage, and also the figure given by KINGSLEY, appear to indicate that he is really referring *not* to the extra-stapedial but to the supra-stapedial cartilage. He may therefore be considered to conclude that the supra-stapedial cartilage does not originate from the extra-stapedial but is, from the first, an entirely separate cartilage.

In a discussion of the whole question of the origin and relationship of the *auditory capsule*, *columella*, and *anterior cornu* of the *hyoid*, three separate issues appear to be involved. These are :—

- (i) Whether the union between the extra-stapedial cartilage and the hyoid cornu be primary or secondary ?
- (ii) Whether the supra-stapedial cartilage be developed as an outgrowth of the extra-stapedial or as a separate cartilage ?
- (iii) What part, if any, is contributed by the auditory capsule to the formation of the stapes ?

It is preferred, however, to consider and discuss the available data without attempting always to keep separate the three questions now proposed.

By the examination of embryos younger than those described by SCHAUINSLAND (1900), or HOWES and SWINNERTON (1901), an attempt has now been made to determine the conditions obtaining in the auditory region previous to the onset of chondrification.

The cartilaginous auditory capsule and the anterior cornu of the hyoid are evidently products of the two connective-tissue proliferations described above in Stage O-P, Embryo 35*a*. That two centres of chondrification—one hyoidean and one capsular—originally separated by an intervening tract of mesenchyme, are subsequently found is indisputable. During Stage P a procartilaginous hyoid tract exists in the region eventually occupied by the extra-stapedial cartilage and the anterior

cornu of the hyoid. In spite of the apparent jointing noted therein, no reason exists for regarding the dorsal and ventral parts of the cornu as being other than parts of a continuous procartilagenous structure originating from what has now been termed the "hyoid proliferation." In this stage it was observed that while the dense procartilage of the extra-stapedial region of the hyoid proliferation appears to be extending inwards to form the stapes, there is no corresponding lateral extension of that of the auditory capsule, although a narrow neck of less dense tissue is now bridging the gap between the two tracts of procartilage. This narrow neck of tissue is evidently equivalent to the "constriction" noted by GEOFFREY SMITH (1904), in 5th- and 6th-day Chick embryos, and which he states corresponds topographically with the junction of the extra-stapedial cartilage and the stapes. The similarity between the conditions obtaining in *Sphenodon*, Stage O-P, Embryo 35*a*, and those in a 5th-day Chick embryo, and also between Stage P, Embryo 45*a*, and a 6th-day Chick embryo, is made evident by a comparison of text-figs. 11, 12, 13 and 14 of this paper with GEOFFREY SMITH'S, figs. 4, 5, and 6 (*op. cit.*, pp. 17, 18, 19).

In Stage P-Q there is obvious continuity between the stapes and the extra-stapedial cartilage, but there is to be discerned a line of demarcation between the foot-plate region of the former and that part of the auditory capsule with which it is in contact.

The available evidence may be insufficient to justify a denial to the procartilage of the auditory capsule of any share in the formation of the proximal portion of the stapes. If, however, there be any outgrowth of the auditory capsule to meet the ingrowing stapes it is comparatively insignificant, and the capsular contribution to the formation of the basal portion of the stapes must necessarily be small.

The description of the development of the columella previously given (sub: Stages O-P to Q inclusive) is conclusive in favour of a common origin of the extra-stapedial cartilage and the stapes. An approaching separation of the two may possibly be foreshadowed by the constriction of the columella noted in Stage Q, but, since they first appear as separate cartilages in Stage R, this separation must be regarded as secondary.

Proceeding next to a consideration of the origin and relationship of the supra-stapedial cartilage, it may first be noted that HUXLEY (1869, p. 397) believed that in adult *Sphenodon* this cartilage was connected with the parotic process; but, as HOWES and SWINNERTON (1901, p. 46) suggest, it is probable that what he was really describing was a union of the supra-stapedial cartilage with the quadrate. GADOW (1889, p. 468), appears to have found the supra-stapedial to be variable as to the degree of its postero-dorsal development and its relationship to the quadrate and to the parotic process. KINGSLEY (1900, p. 215), if, as appears probable, he was describing the supra-stapedial cartilage as "extra-columella," thinks that it arises as a "discrete part" in some Lacertilian embryos, but an examination of the models

reconstructed from serial sections of embryos referred to in Stages P, Q, R and S (figs. 32, 42, 43*a*, 43*b*, 48, 56, 57, 58), does not support this conclusion as regards *Sphenodon*.

In Stages O–P and P there is no sign of a supra-stapedial cartilage, which first appears as a dorsally-directed, conical rod, growing from the antero-dorsal surface of the extra-stapedial cartilage in Stage Q (Embryo 52*a*, figs. 42*a*, 42*b*), but which has not yet reached the ventral surface of the quadrate. In Stage R (Embryo 141, figs. 17, 43) it is attached to the latter by a ligamentous connection. In this embryo the recurrent process of the supra-stapedial cartilage appears for the first time, and it possesses a fibrous connection with the extra-stapedial cartilage, as previously described, thus closing HUXLEY'S foramen, but, in and after Stage S, a cartilaginous connexion of the recurrent process and the extra-stapedial cartilage is established (figs. 44, 45).

It is evident, therefore, that the supra-stapedial is not originally a separate cartilage, but arises as a comparatively late outgrowth from the antero-dorsal surface of the extra-stapedial cartilage, and eventually undergoes a partial secondary fusion with the ventral surface of the postero-dorsal limb of the quadrate and with the posterior process of the squamosal. If the suggestion of HOWES and SWINNERTON (*op. cit.*, p. 47) regarding HUXLEY'S statement be adopted, his description of the relationship of these cartilages is brought into agreement with that observed in Stage 8 (Embryo 11 and 9*a*).

#### *Conclusions.*

It must be concluded that :—

- (i) The *columella auris* is derived from the *hyoid arch*, with which it is continuous throughout all stages of development. The *extra-stapedial cartilage* is therefore *primarily* united with the *anterior cornu of the hyoid*.
- (ii) The *supra-stapedial cartilage* (including the *recurrent process*) is developed, and persists, as an outgrowth from the extra-stapedial cartilage, and is therefore a *hyoidean* derivative.
- (iii) The auditory capsule contributes at most a portion of the *foot-plate* of the *stapes*, which is probably *partly capsular and partly hyoidean in origin*. The *distal portion of the stapes is exclusively hyoidean*.

In addition it may be noted that :—

- (iv) At no period of its life-history does *Sphenodon* possess any cartilaginous attachment between the supra-stapedial process and the cranium.
- (v) During the later stages of the embryonic period and in adult life there is a *secondary attachment* between, and partial fusion of, the *supra-stapedial process* and the *quadrate*.

The foregoing observations and conclusions concerning the origin and relationships of the *columella auris* and *anterior cornu* of the *hyoid* of *Sphenodon* are in

agreement with, and supplementary to, those of HOWES and SWINNERTON (*op. cit.*). GEOFFREY SMITH (1904) finds, as I have already indicated, the existence of a similar series of conditions in the embryo Chick.

While a consideration of the homologies of the structures above described is entirely outside the scope of the present research, it is evident that the results now recorded lend considerable support to the suggestion of GAUPP (1889) that the stapes of Sauropsida is morphologically equivalent to that of Mammalia and to the hyomandibular cartilage of Fishes. Evidently, as GEOFFREY SMITH (*op. cit.*, p. 21) points out, both Sauropsid and Mammal alike "have converted the dorsal or hyomandibular region of the hyoid cartilage into the stapes, but subsequently they have gone on different lines in evolution."

Whereas the remaining auditory ossicles of the Mammalia are derived from the 1st (mandibular) instead of from the 2nd (hyoid) arch, the quadrate and the articulare giving rise respectively to the incus and malleus, the Sauropsidan analogue of these (*viz.*, the extra-stapedial, including the supra-stapedial cartilage) is derived from a region of the hyoid arch immediately ventral to that from which the stapes is developed.

#### VI. THE MIDDLE EAR AND CHORDA TYMPANI.

Subsequent to the closure of the 1st visceral cleft, there persists for some time, notably during *late Stage P* (Embryo 45*a*, figs. 38, 39, 40), a nearly cylindrical, cicatricial cord of thickened tissue connecting the superficial epiblast in the neighbourhood of the closed cleft with the distal extremity of the persistent portion of the 1st visceral pouch. Immediately medial and posterior to the distal extremity of the pouch its wall exhibits a patch of thickened epithelium and from this region there now grows in a dorsal direction a conical diverticulum, the *anterior tympanic diverticulum*. In Stage Q (Embryo 52*a*, figs. 42*a*, 42*b*) this anterior tympanic diverticulum, which thus originates from the postero-dorsal region of the 1st visceral pouch, extends between the dorsal boundary of the quadrate and the anterior surface of the supra-stapedial process reaching the level of the middle of the latter cartilage.

It has already been mentioned that a considerable antero-dorsal extension of the lateral region of that portion of the pharynx included between the 1st and 2nd visceral pouches, and also of the anterior portion of the 2nd visceral pouch, has taken place during late Stage P. The pharynx in this region now develops a rather wide, conical diverticulum, which extends upwards, forwards and slightly outwards and begins to grow in an anterior direction above the postero-dorsal surface of the stapes. This diverticulum will here be referred to as the *posterior tympanic diverticulum* and is to be regarded as a product, partly of the 2nd visceral pouch, and partly of the pharyngeal region immediately anterior to it. There also develops, between these two diverticula, a laterally-directed pharyngeal pocket, situated below the distal extremity of the extra-stapedial cartilage. This will be referred to as the *lateral tympanic*

*diverticulum* and is obviously derived from the posterior region of the 1st visceral pouch and from the lateral region of the pharynx immediately posterior to it. Viewed from the side it exhibits an approximately wide semi-lunar form with the concave dorsal border situated immediately below the under-surface of the extra-stapedial cartilage.

In *Stage R* (Embryo 141, figs. 17, 43, and text-fig. 15) the *anterior tympanic diverticulum* has grown upwards immediately in front of the stapes and extends as a narrow, conical pharyngeal pocket to a point immediately between the antero-lateral wall of the ascending *arteria stapediales* and the medio-ventral border of the posterior process of the quadrate.

The *lateral tympanic diverticulum* has now developed into a large, latero-medially flattened, oval pocket, with a well-marked antero-lateral border, but gradually merging in a posterior direction with the general surface of the pharynx in the neighbourhood of the 2nd visceral pouch, where its lateral wall is indistinguishable from that of the proximal portion of the *posterior tympanic diverticulum*. The latter diverticulum has extended in a dorsal and anterior direction above the stapes and passes immediately medial to the recurrent process of the supra-stapedial. It terminates at a point just anterior to this and medial to the ventral border of the posterior process of the quadrate. Its anterior extremity lies almost in contact with the dorsal tip of the *anterior tympanic diverticulum*, with which it just fails laterally to unite.

Since it is known that in adult *Sphenodon* the stapes is surrounded on its dorsal surface by a double fold of tympanic (pharyngeal) mucous membrane (VERSLUYS, GRAY), between which is included a nearly obliterated dorsal extension of the tympanic cavity, it might reasonably be expected that this *circum-stapedial tympanic diverticulum* would be found to result from a fusion of the adjacent extremities of the anterior and posterior tympanic diverticula. This, however, is not the case.

In *Stage S* (Embryos 11 and 9a) it is found that the proximal (ventral) portion of the *anterior tympanic diverticulum* is obliterated, and that the distal (dorsal) portion persists as an isolated, ventro-dorsally elongated and rather broad fusiform cavity, situated between the posterior dorsal border of the quadrate and the *arteria stapediales*. Apparently, therefore, subsequent to Stage S (Embryo 9a, figs. 44, 45), the *posterior tympanic diverticulum* grows forwards and downwards to unite with the persistent proximal portion of the anterior tympanic diverticulum.

The *lateral tympanic diverticulum* has now greatly expanded both in a lateral and a posterior direction, to form the persistent tympanic diverticulum whose cavity becomes the *tympanic cavity* of the adult. Its anterior border has become much flattened, and does not extend so far forward as it did during Stage R, while the cavity of the lateral portion of the pharynx immediately in front of it has undergone considerable obliteration from its dorso-lateral border inwards. This process has considerably reduced the antero-posterior diameter of that portion of the pharyngeal



cavity by which the developing tympanic cavity communicates with the lumen of the flattened, main pharyngeal tube. The tympanic cavity has now reached a stage of development approximating to that of the tympanic cavity of the adult, as described by VERSLUYS (1899) and GRAY (1913). It is evident that Stages P, Q, R and S exhibit a process of gradual reduction of the anterior portion of the primitive tympanic diverticulum and a corresponding increase of its posterior region, and that only the most anterior portion of the tympanic cavity of the adult can be regarded as originating from the 1st visceral pouch, the tympanic cavity being mainly derived from the pharynx immediately posterior to this pouch, and also to some extent from the anterior portion of the 2nd visceral pouch. It does not appear that this view of the origin of the tympanic diverticulum in any way conflicts with the evidence adduced by investigators of the anatomy and topographical relationships of this structure in the adult.

It may here be noted that the separation of the distal portion of the anterior tympanic diverticulum in Stage S, where it occurs on both sides in Embryos 11 and 9a, is not unique, as LILLIE (1908) records a similar phenomenon in an eight-day Chick embryo, adding, however, that he does not know the ultimate fate of the isolated portion of the diverticulum. GOODRICH (1915) describes the occurrence in *Lacerta* embryos of anterior, lateral, and posterior tympanic diverticula somewhat similar to those now found in embryo *Sphenodon*, but in the former reptile the encirclement of the columella is due to an upward and backward growth of the anterior and lateral diverticula, the latter of these ultimately meeting and fusing with the posterior diverticulum, the cavity of the tympanum thus surrounding the extra-columella.

*The Tympanic Membrane and the Extra-Columellar Sinew.*

GÜNTHER (1867) in his description of the anatomy of adult *Sphenodon*, states (p. 620) that both tympanum and tympanic cavity are "entirely absent," but HUXLEY (1869), while admitting the absence of an externally-visible tympanic membrane, refers to the presence of "a strong aponeurotic expansion which takes its place," the fibres of which "are seen to pass from the posterior edge of the quadrate bone and from the angle of the mandible to the anterior margin of the anterior cornu of the hyoid." GADOW (1889, p. 451) also recognises the aponeurosis as "an imperfect tympanum." It is briefly commented upon by IWANZOFF (1894) and OSAWA (1898), while VERSLUYS (1898) gives a detailed description of its anatomy and discusses its homology, and it has also been more briefly described by GRAY (1913). It is, therefore, unnecessary here to give more than a brief account of the development of this structure.

As late as *Stage Q* the space included between the quadrate, the columella, the primary tympanic diverticulum (vestige of 1st visceral pouch), MECKEL'S cartilage, and the lateral wall of the head contains, in addition to the nerves and blood-vessels

of this region, only a tract of somewhat loose mesenchyme. During late Stage Q the mesenchyme immediately surrounding the above-mentioned cartilages increases in density, its fibrous mesh-work becomes more pronounced and arranged as a definitely-investing fibrous layer, in which the elongated cells are closely arranged with their long axes parallel to the surface of the underlying cartilage.

The first appearance of the *aponeurotic expansion*, and of the developing posterior portion of the facial musculature, takes place, however, during the period between Stages Q and R. In the latter stage (Embryo 141) rudiments of the *musculus depressor mandibulae*, *musculus sphincter colli*, and other muscles are clearly distinguishable as mesoblastic tracts of greater density than that of the surrounding tissue, and composed of a fibrous reticulum containing very numerous, regularly arranged, fusiform mesoblast cells, the long axis of which conform to the contours of the developing muscle-tracts, which occupy the same relative positions as do the respective muscles of the adult.

The developing aponeurosis (*functional tympanic membrane*) is present as a well-defined tract of similarly elongated and densely arranged cells, the long axes of which are arranged in approximately a dorso-ventral direction, following the contour of the developing membrane. The antero-dorsal border of the tract passes insensibly into the dense mesoblastic investment of the posterior margin of the quadrate, while its central portion is continuous with that investing the distal surface of the extra-stapedial cartilage, and its posterior and postero-dorsal border with that of the antero-dorsal portion of the 1st cornu of the hyoid. On both sides of the developing membrane lies the loose mesenchyme referred to above, and in the regions of the latter situated immediately lateral to the quadrate, MECKEL'S cartilage and the ventro-lateral surface of the pharynx, are seen the developing muscle-masses. The central area of the developing *tympanic membrane* is bulged outwards by the distal extremity of the extra-stapedial cartilage and lies close below the surface of the head, being separated from the exterior in this region by only the superficial epiblast and a thin layer of circularly disposed fibres lying immediately below the latter, but elsewhere there is a considerable thickness of intervening mesenchyme. The medial surface of the developing tympanic membrane is similarly somewhat widely separated from the *lateral diverticulum* (*primitive tympanic cavity*) of the 1st visceral pouch.

The *extra-columellar sinew* arises in the position it ultimately occupies in the adult, extending from the ventral border of the posterior process of the squamosal to the dorsal and dorso-lateral border of the extra-stapedial cartilage just posterior to the supra-stapedial process. The sinew appears as a thickened band or tract on, continuous with, and similar in structure to the dorsal region of the medial wall of the developing aponeurosis. Dorsally and ventrally its fibres are continuous with the similar investment of the squamosal (and quadrate) and the extra-stapedial cartilage.

In *Stage S* (text-fig. 16) the *tympanic membrane* appears as a somewhat lax sheet of fibrous connective tissue, the medial surface of which is closely adherent to the

lateral wall of the considerably expanded and outwardly extended lateral tympanic diverticulum. Its postero-ventral border is attached chiefly on its lateral surface to the fibrous connective tissue investment of the antero-ventral region of the *musculus depressor mandibulæ*. In the latter structure, and also in the adjacent muscles, definite bundles of typical muscle-fibres can now be distinguished.

Between this region and the posterior margin of the quadrate is a roughly triangular area within which the tympanic membrane is separated from the sub-epithelial fibrous layer by only a loose connective-tissue consisting of an open mesh-work of fine fibres and containing scattered flattened cells. This area evidently represents the vertically wedge-shaped subcutaneous area of the fascia described by GRAY, who finds, in the adult, that the posterior region of the aponeurosis is overlain by muscle just as is the case in the embryo now described.

Below the rugose epidermal layer of the auditory region there occurs a thin sheet of circularly disposed fibres, which apparently encircles the head, and is separated from the epidermis by a thin layer of dense connective-tissue.

The general relationships of the *membrana tympani* at this stage of development are thus found to be similar in every respect with those obtaining in the adult condition, as described by VERSLUYS and GRAY. The *extra-columellar sinew* has also assumed its adult condition—consisting of a thick bundle of dense fibrous tissue, some of the ventro-lateral components of which appear to blend with the similar fibrous tissue of the tympanic membrane. The attachments of the sinew are as already stated above, and were correctly described by SCHAUNSLAND (1900) and by VERSLUYS (1903), who corrects (p. 165) his previous error (1898, p. 109) in this respect. SCHAUNSLAND finds no muscle-fibres in this sinew in adult *Sphenodon*, and GRAY also remarks that no intra-tympanic muscles are present. VERSLUYS (1903) finds no trace of muscle-fibres in the sinew of *Platydictylus* embryos. There are, in the *Sphenodon* embryos now examined, no traces of muscular tissue in this structure, and VERSLUYS' statement that there is no indication that this sinew represents an earlier muscle appears to be correct, nor does the present investigation appear to necessitate any modification of his observations concerning this structure in particular or of the middle ear in Reptilia in general.

It may be concluded, as GRAY remarks, that while the inner ear of *Sphenodon* differs little from that of other Reptilia, with the exception of Crocodilia, the middle ear really represents a transition stage in the evolution of the middle ear of living reptiles.

#### *The Chorda Tympani.*

It has already been stated that this nerve arises as a post-trematic branch of the *nervus facialis*, and is first distinguishable during Stage N. Subsequent to the closure of the 1st visceral cleft, during Stage P, the development of the lateral tympanic diverticulum gradually forces the nerve into a nearly pre-tympanic

position. During Stage Q (figs. 43*a*, 43*b*), as in Stages O-P and P, the nerve, after leaving the *ramus hyomandibularis*, pursues a course parallel to and just above the dorsal surface of the columella. It then passes across the lower region of the posterior surface of the developing supra-stapedial process, and, running in a postero-ventral and slightly medial direction, lateral and ventral to the developing lateral tympanic diverticulum, is distributed to the medial surface of Meckel's cartilage, along which it runs in an anterior direction. It pursues a similar course during Stage R (figs. 48, 56).

When passing posterior to the recurrent process of the supra-stapedial and crossing the middle region of the posterior surface of the supra-stapedial cartilage, it turns ventrally, traverses the antero-lateral surface of the extra-stapedial cartilage, and, running in a postero-ventral direction, leaves the inferior process of the latter. The very marked immediately subsequent development of the lateral diverticulum of the tympanic cavity brings the antero-lateral surface of this structure into contact with the nerve, which crosses it obliquely in an antero-dorsal to postero-ventral direction, finally entering a canal on the medio-dorsal surface of the posterior region of the ossifying lower jaw. This condition obtains during Stage S, and is shown in figs. 44, 45.

The developmental changes now recorded are entirely in accord with the observations of GOODRICH (1915), who discusses the distribution of this nerve in embryos of Reptiles, Birds, and Mammals, and with the accounts of the nerve in adult *Sphenodon* given by OSAWA (1898) and VERSLUYS (1898), the latter of whom also describes its relationships in Lacertilian Embryos (1903).

## APPENDIX I.

### REFERENCE LIST OF LITERATURE ON *Sphenodon punctatus*.

1899. DENDY, A., "Summary of the Principal Results obtained in a Study of the Development of the Tuatara (*Sphenodon punctatus*)," 'Roy. Soc. Proc.,' vol. 63, pp. 440-448.
1899. *Id.*, "Outlines of the Development of the Tuatara (*Sphenodon punctatus*)," 'Q. J. M. S.,' vol. 42, pp. 1-87.
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## REFERENCE LIST OF LITERATURE ON THE AUDITORY REGION AND ADJACENT STRUCTURES.

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## DESCRIPTION OF PLATES.

(Unless otherwise stated the organs of the left side are figured.)

## PLATE 11.

*Stage H.*

Fig. 1.—Embryo 78, anterior half, seen from above as a transparent object. ( $\times 25$ .)

*Stage J.*

Fig. 2.—(Early Stage J), Embryo 44. Reconstruction drawing. Lateral view of auditory region ( $\times 100$ ).

Fig. 3.—(Late Stage J), Embryo 79. Reconstruction drawing. Lateral view of auditory region ( $\times 100$ ).

*Stage K.*

Fig. 4.—Embryo 39. Model of auditory region ( $\times 100$ ). Frontal view.

Fig. 5.—Embryo 39. Model of auditory region ( $\times 100$ ). Lateral view.

*Stage L.*

Fig. 6.—Embryo 50. Model of auditory region ( $\times 70$ ). Lateral view. (This model was constructed from longitudinal sections. The hind-brain and veins are not shown.)

## PLATE 12.

*Stage M.*

Fig. 7.—Embryo 51. Model of auditory region ( $\times 100$ ). Lateral view.

*Stage N.*

Fig. 8.—Embryo 14*a*. Model of auditory region ( $\times 50$ ). Lateral view.

*Stage O.*

Fig. 9.—Embryo 32*a*. Model of auditory region. Medial view. (This model was made from longitudinal sections. Part of hind-brain and its veins omitted.)

Fig. 10.—Embryo 32*a*. Model of auditory region ( $\times 50$ ). Lateral view.

*Stage P.*

Fig. 11.—Embryo 45*a*. Model of auditory region, showing nerves and blood-vessels ( $\times 35$ ). Seen from below.

Fig. 12.—Embryo 45*a*. Model of auditory region, showing auditory capsule, blood-vessels and nerves ( $\times 35$ ). Seen from above. (The Sinus longitudinalis posterior has been removed.)

## PLATE 13.

*Stage N.*

Fig. 13.—Schematic representation of the principal blood-vessels of the auditory region ( $\times 50$ ).

*Stage P.*

Fig. 14.—Embryo 45*a*. Model of auditory region ( $\times 50$ ). Lateral view. (Pharynx and aortic arches omitted.)

*Stages O-Q.*

Fig. 15.—Schematic representation of principal blood-vessels of the auditory region.

*Stages R and S.*

Fig. 16.—Schematic representation of principal blood-vessels of the auditory region. Lateral view.

*Stage R.*

Fig. 17.—Embryo 141. Model of auditory region ( $\times 25$ ). Lateral view.

## PLATE 14.

*Stage R.*

Fig. 18.—Embryo 141. Model of posterior portion of auditory region seen from in front. The section passes through the left foramen saccus endolymphaticus ( $\times 33$ ). (Bones and cartilages overlying the auditory capsule omitted.)

Fig. 19.—Embryo 141. Model of left membranous labyrinth and auditory nerve ( $\times 33$ ). Lateral view.

Fig. 20.—Embryo 141. Medial view of same.

Fig. 21.—Embryo 141. Posterior view of same.

Fig. 22.—Embryo 141. Model of the crista acustica and ventral half of the ampulla of the posterior vertical semicircular canal ( $\times 100$ ). (Crista, green; planum semilunatum, red.)

PLATE 15.

*Stage M.*

Fig. 23.—Embryo 51. Diagram of auditory sac, showing the approximate distribution of the neuro-epithelium, red ( $\times 100$ ).

Fig. 24.—Embryo 51. Diagram of auditory sac and acustico facialis neurencygium ( $\times 100$ ).

*Stage N.*

Fig. 25.—Embryo 14*a*. Diagram of auditory sac, showing approximate distribution of neuro-epithelium, red ( $\times 50$ ).

Fig. 26.—Embryo 14*a*. Diagram of auditory sac and acustico facialis neurencygium, with developing branches of Nerve VII ( $\times 50$ ).

*Stage O.*

Fig. 27.—Embryo 32*a*. Auditory sac ( $\times 50$ ). Lateral view.

Fig. 28.—Embryo 32*a*. Diagram of auditory sac with developing facial and auditory ganglia and nerves ( $\times 50$ ).

*Stage O-P.*

Fig. 29.—Embryo 35*a*. Diagram of auditory sac, showing approximate distribution of neuro-epithelium, red ( $\times 50$ ).

Fig. 30.—Embryo 35*a*. Auditory sac ( $\times 50$ ). Lateral view.

Fig. 31.—Embryo 35*a*. Auditory sac ( $\times 50$ ). Medial view.

Fig. 32.—Embryo 35*a*. Diagram of auditory sac and auditory and facial nerves ( $\times 50$ ).

*Stage P.*

Fig. 33.—Embryo 45*a*. Diagram of membranous labyrinth with developing sensory patches (Neuro-epithelium, red) ( $\times 50$ ).

*Stage R.*

Fig. 34.—Embryo 141. Diagram of left membranous labyrinth, showing cristæ and maculæ acusticæ ( $\times 50$ ).

PLATE 16.

Fig. 35.—Diagram to illustrate the relationship of the visceral arches and clefts during Stage N—(A) Lateral view, (B) Seen from above.

Fig. 36.—Diagram to illustrate the early stages of the “overgrowth” (formation of operculum) by which the ultimate closure of the 2nd and 3rd visceral clefts is effected. These clefts are first converted during Stage O into tubes with a common ventral opening—(A) Lateral view, (B) Seen from above. (Thickening visceral arches are coloured: 1st arch, yellow; 2nd arch, green; 3rd arch, red.)

*Stage O-P.*

Fig. 37.—Embryo 35*a*.—Model of the pharynx in the auditory region, showing visceral pouches and clefts ( $\times 50$ ). Lateral view.

*Stage P.*

Fig. 38.—Embryo 45*a*. Model of pharynx in the auditory region, showing visceral pouches and clefts and part of developing trachea ( $\times 50$ ). Lateral view. (The lumen of the ventro-medial portion of the 1st visceral pouch forms the rudimentary tympanic cavity. The dorso-lateral portion (*x*) is a solid neck of tissue, expanded distally.)

Fig. 39.—Embryo 45*a*. Model of developing cartilaginous auditory capsule, hyoid and mandibular cartilages, pharynx, and thyroid gland ( $\times 25$ ). Lateral view.

Fig. 40.—Embryo 45*a*. Model of posterior half of cartilaginous auditory capsule ( $\times 50$ ). Frontal view.

Fig. 41.—Embryo 45*a*.—Schematic representation of the principal nerves of the auditory region, Stages R and S. Lateral view.

PLATE 17.

*Stage Q.*

Fig. 42.—Embryo 52*a*. Model of the developing tympanic diverticula, auditory cartilages (extra-stapedial, supra-stapedial, etc.), chorda tympani, and their relationship to the quadrate and hyoid ( $\times 50$ ). (A) Lateral view. (B) Posterior view.

*Stage R.*

Fig. 43.—Embryo 141. Model of left tympanic region, including the stapedial cartilages, and chorda tympani (blood-vessels omitted) ( $\times 33$ ). Lateral view.

*Stage S.*

Fig. 44.—Embryo 9*a*. Model of left tympanic region (blood-vessels omitted) ( $\times 33$ ). Lateral view.

Fig. 45.—Embryo 9*a*. The same seen from a position slightly posterior to that of Fig. 57. Principal blood-vessels and nerves shown ( $\times 33$ ).

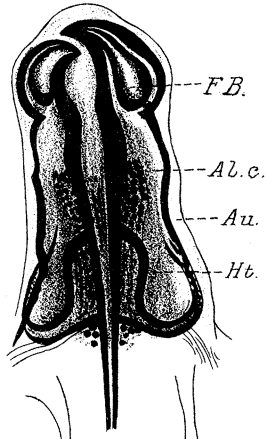


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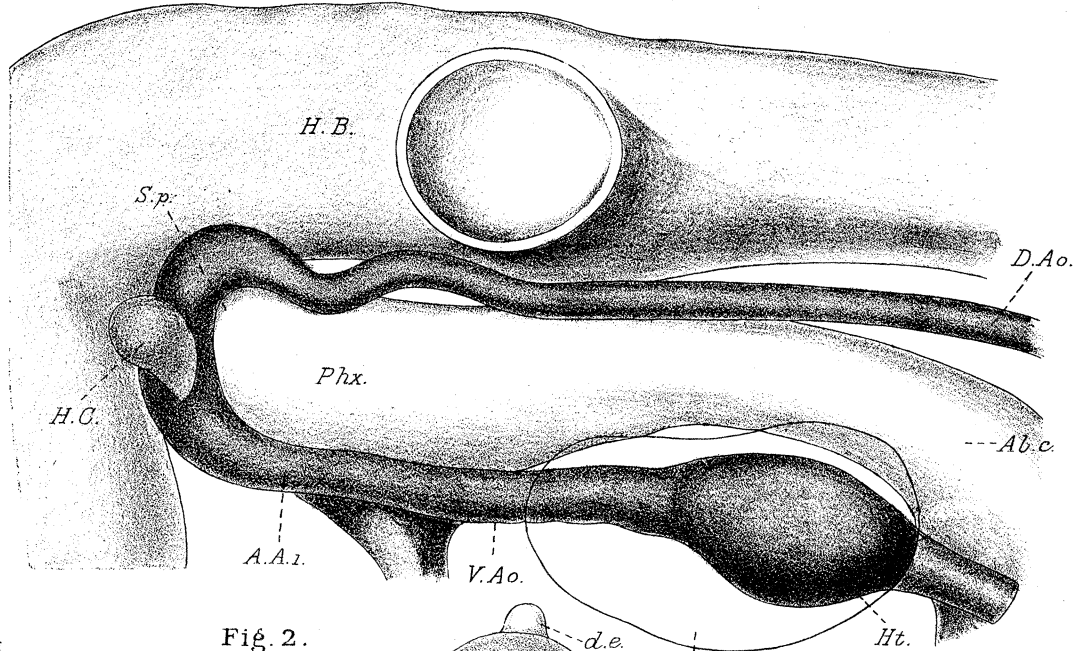


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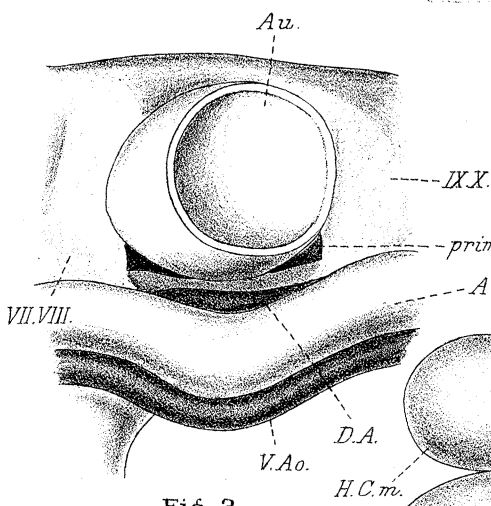


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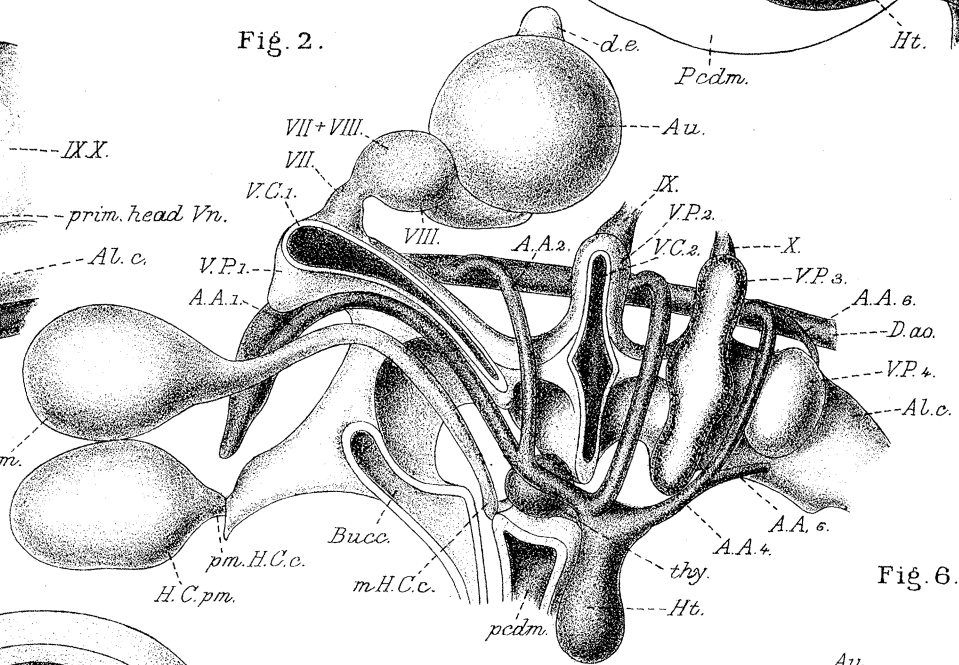


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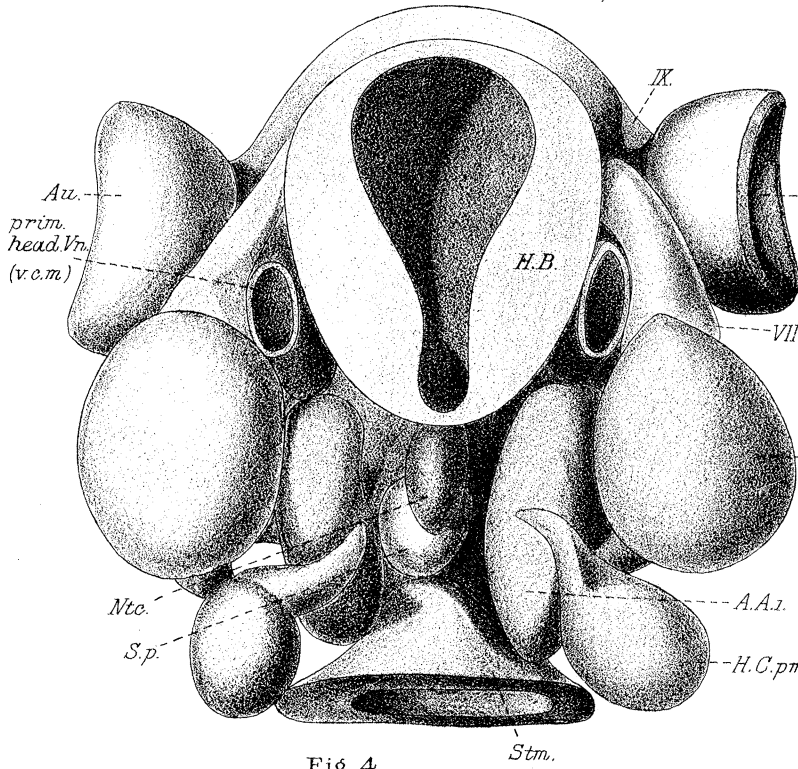


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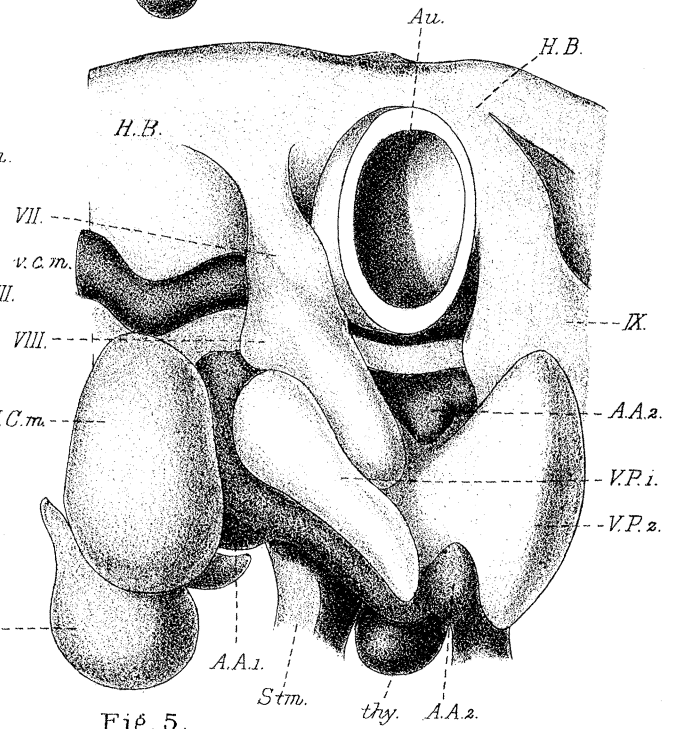


Fig. 5.

Fig. 7.

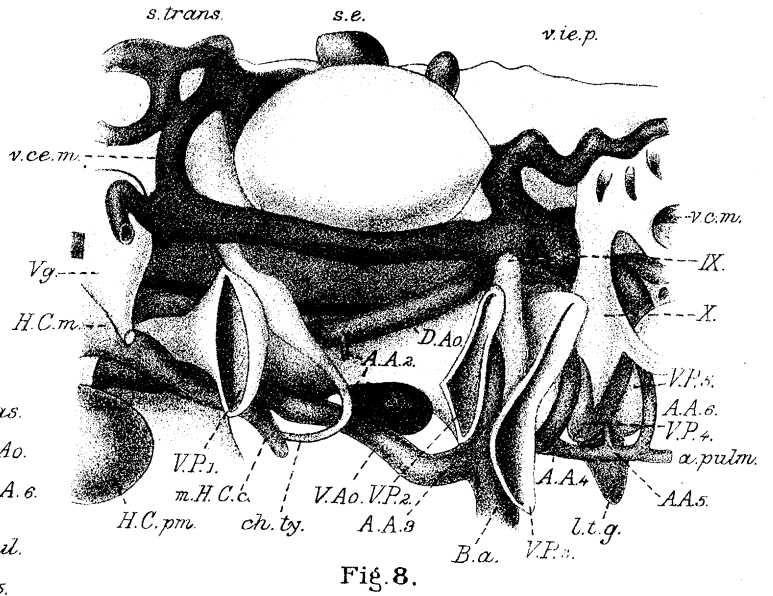
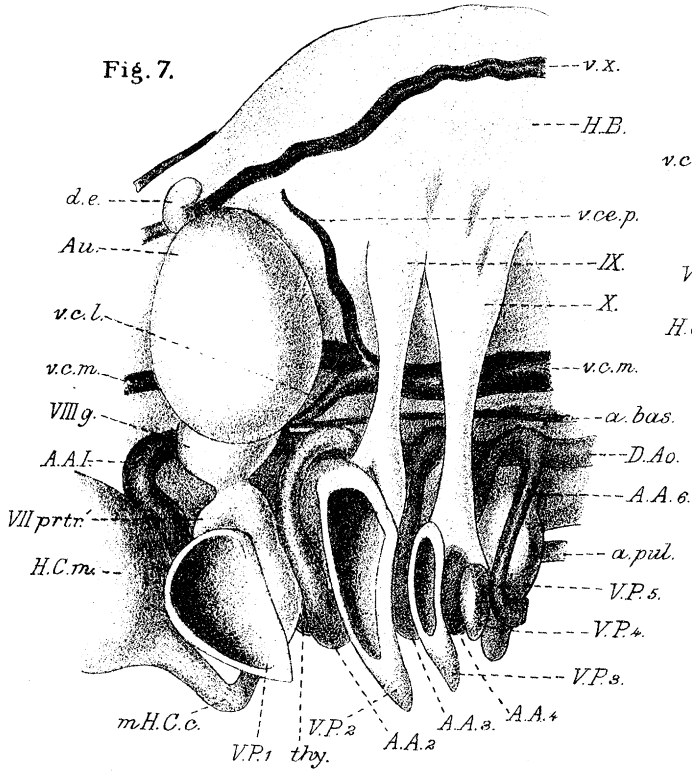


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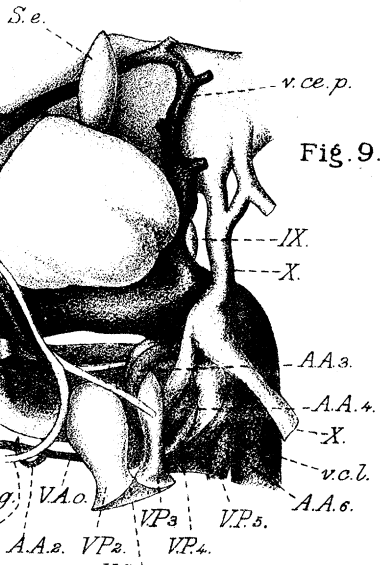


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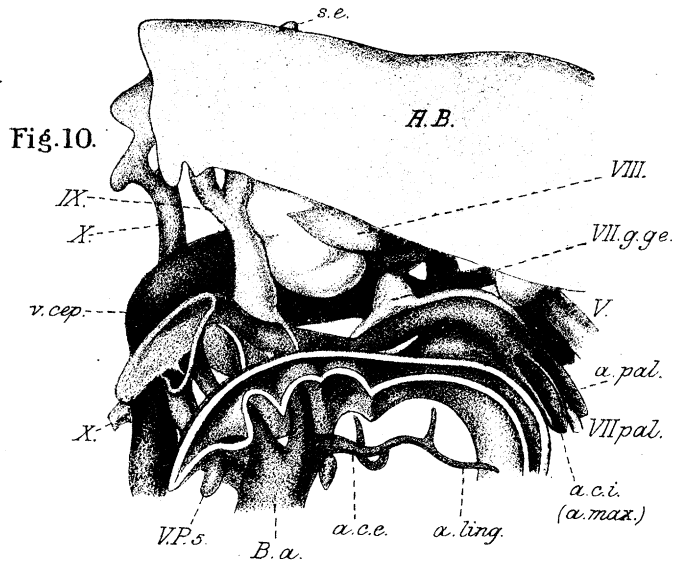


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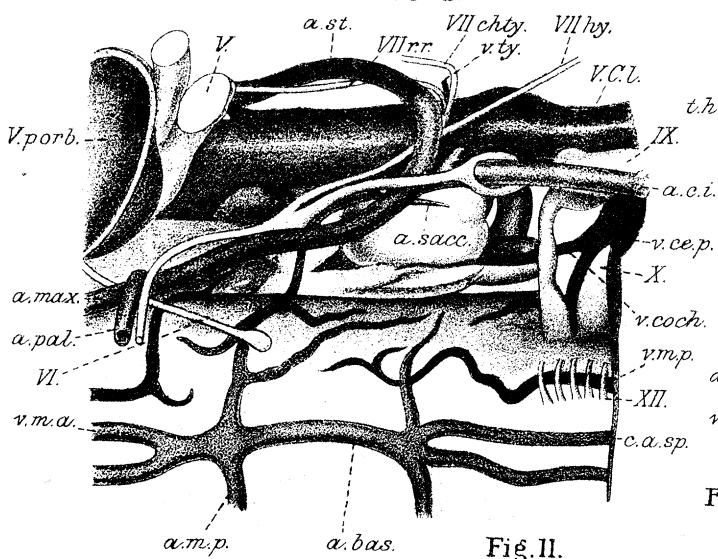


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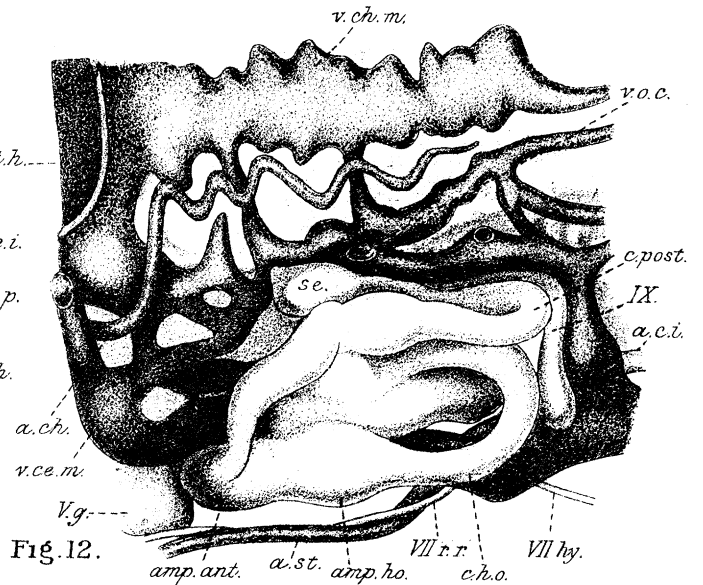
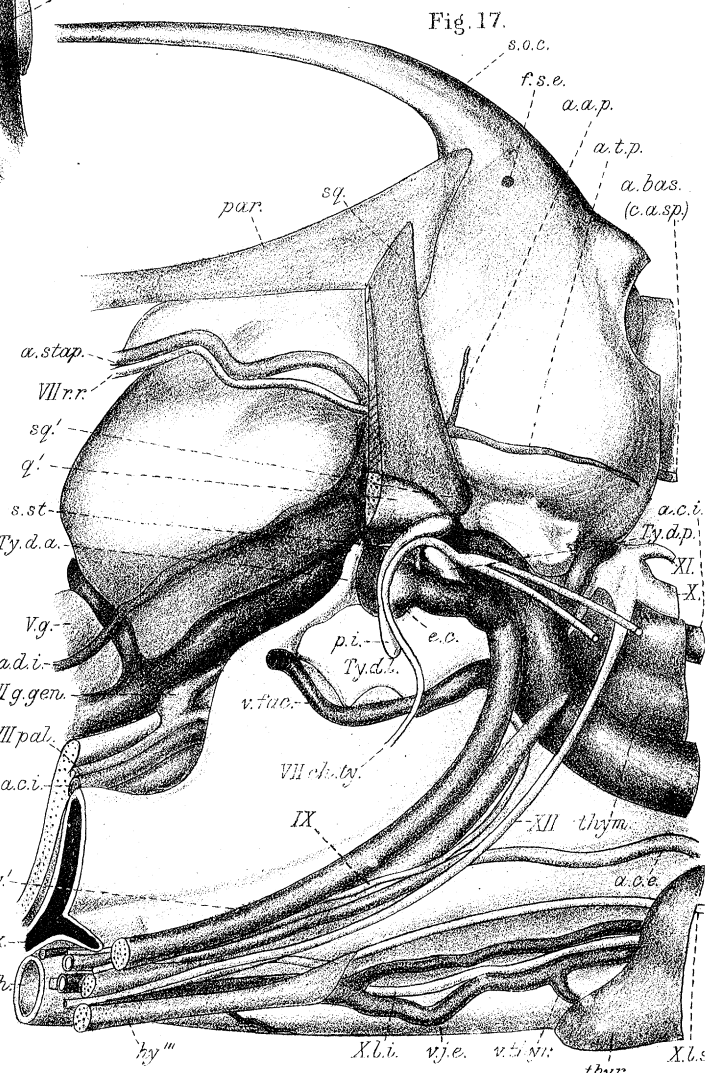
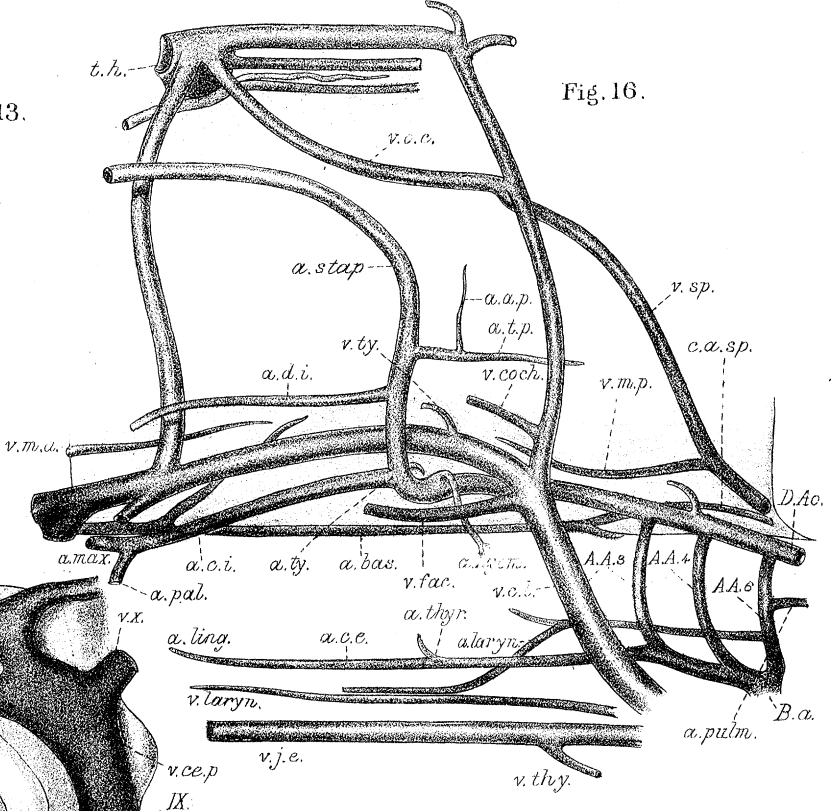
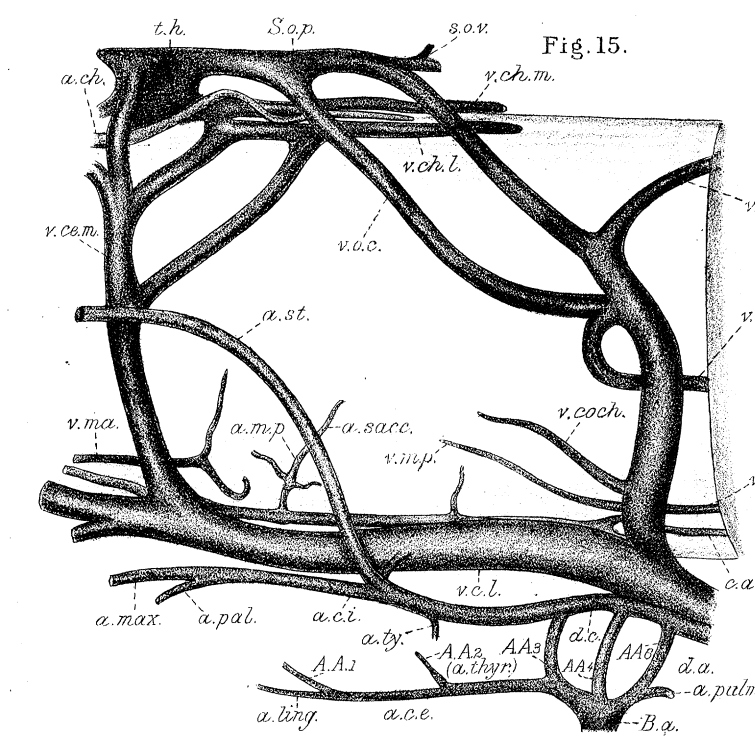
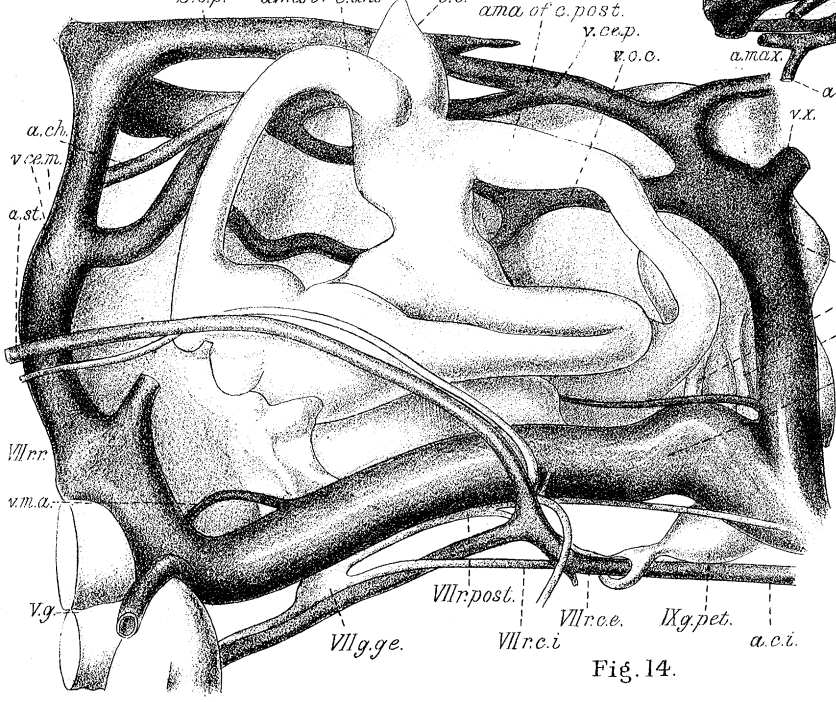
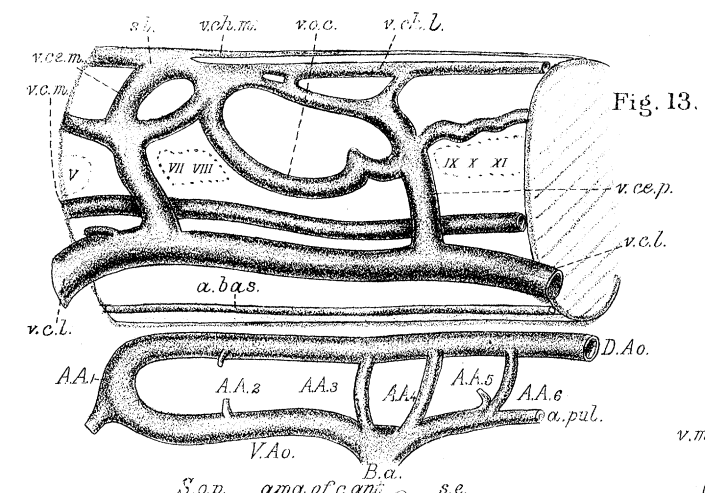


Fig. 12.







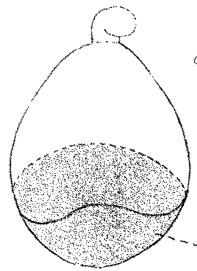


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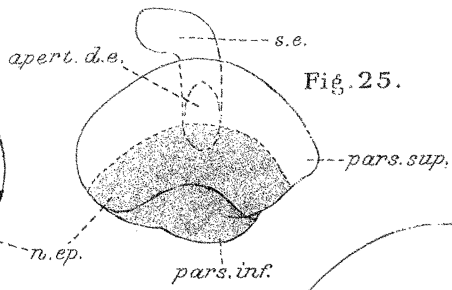


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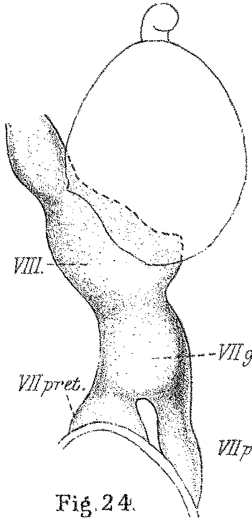


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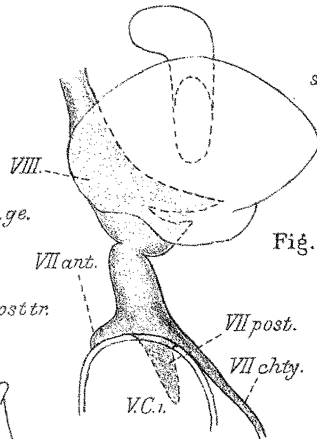


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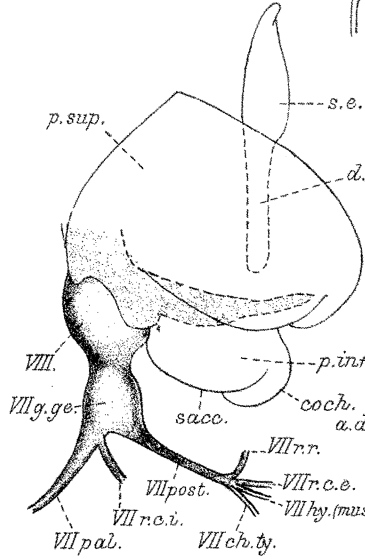


Fig. 28.

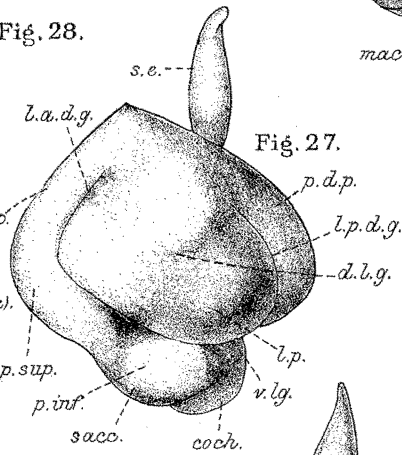


Fig. 27.

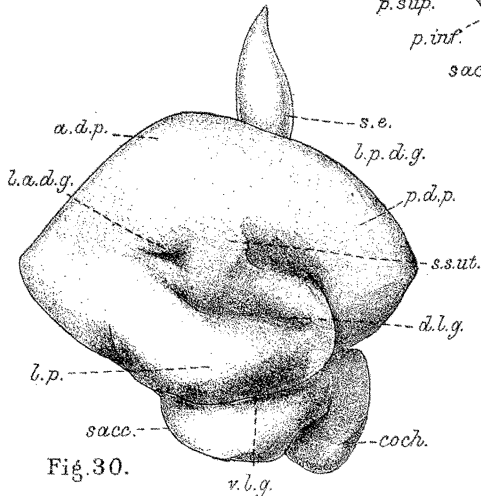


Fig. 30.

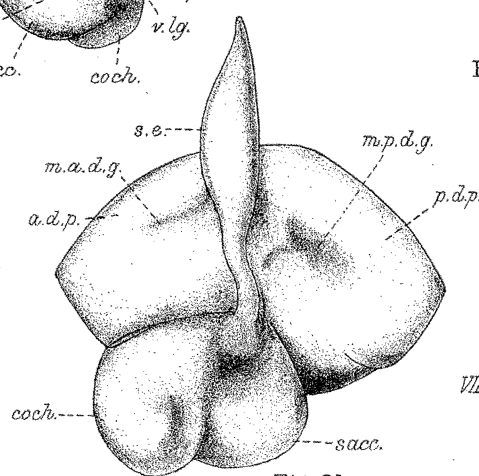


Fig. 31.

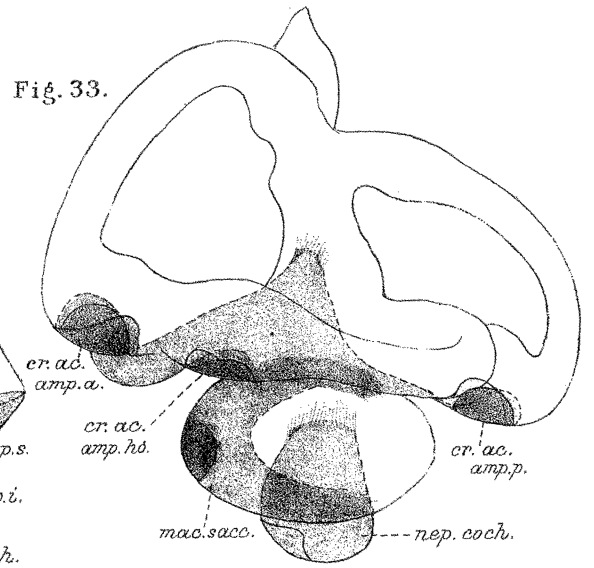


Fig. 33.

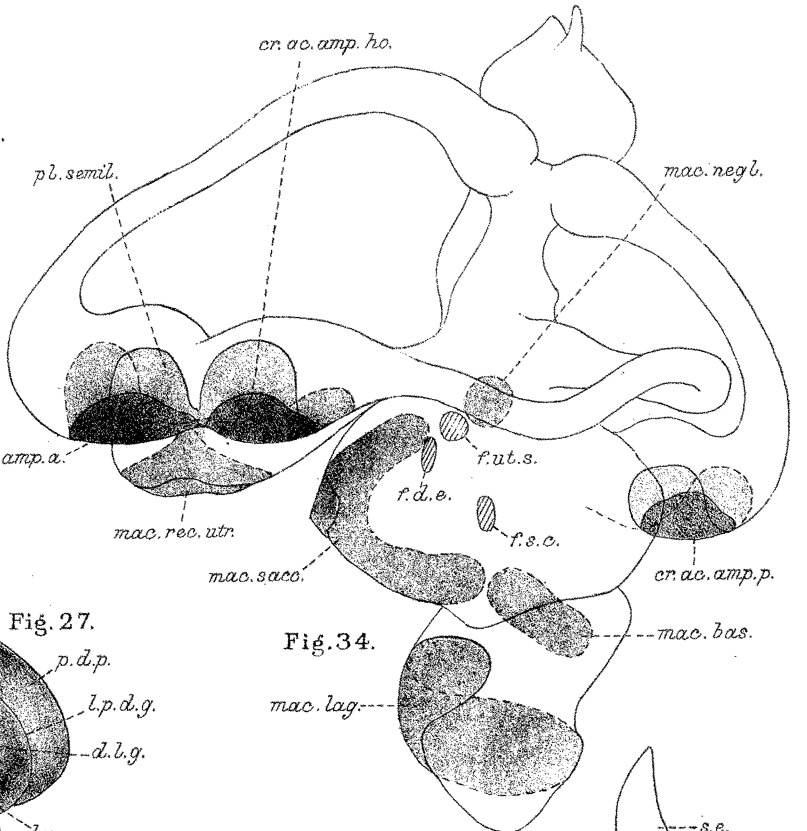


Fig. 34.

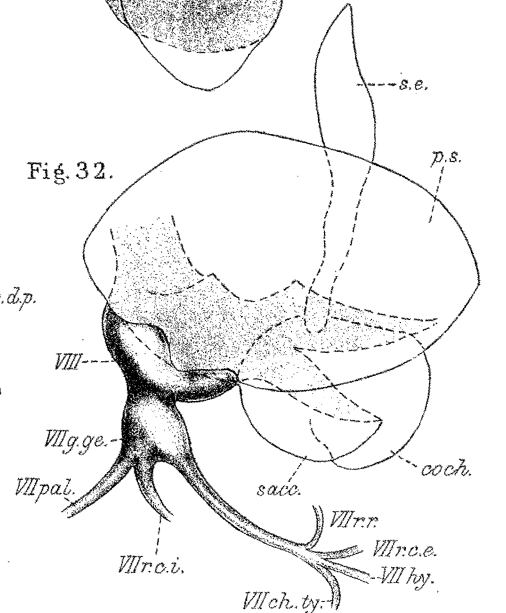


Fig. 32.

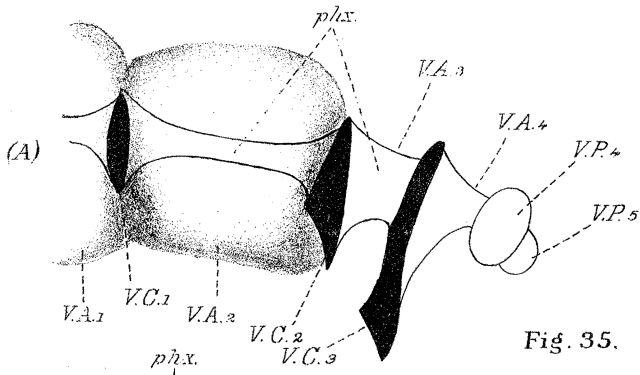


Fig. 35.

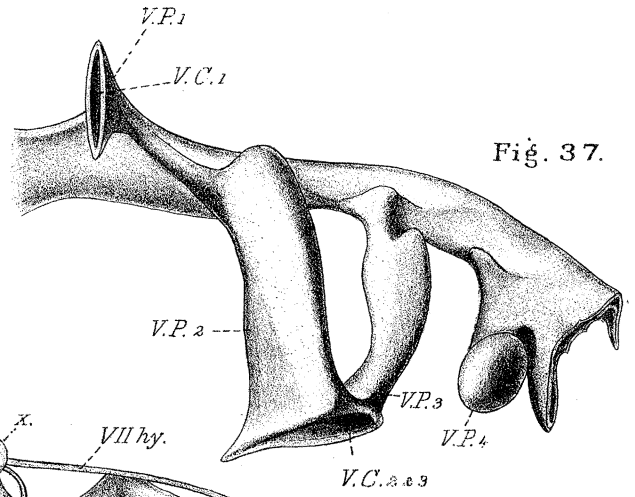


Fig. 37.

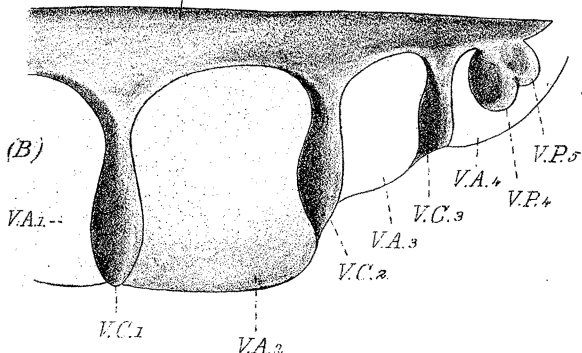


Fig. 36.

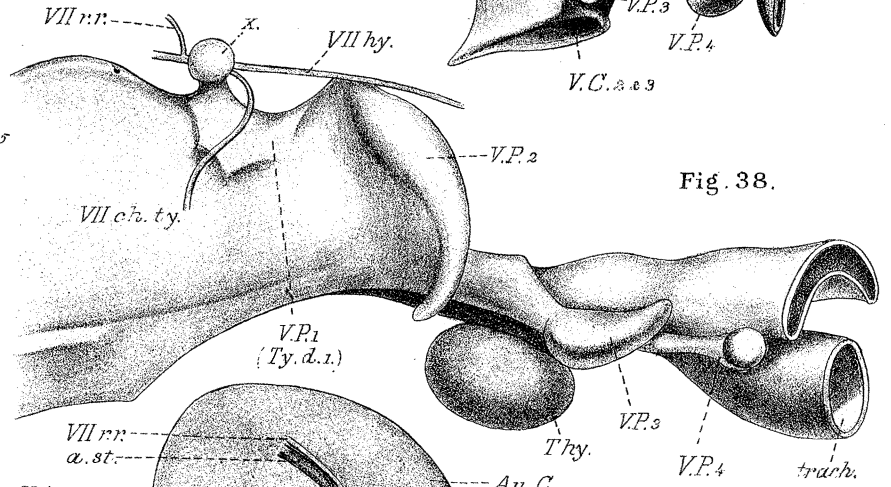


Fig. 38.

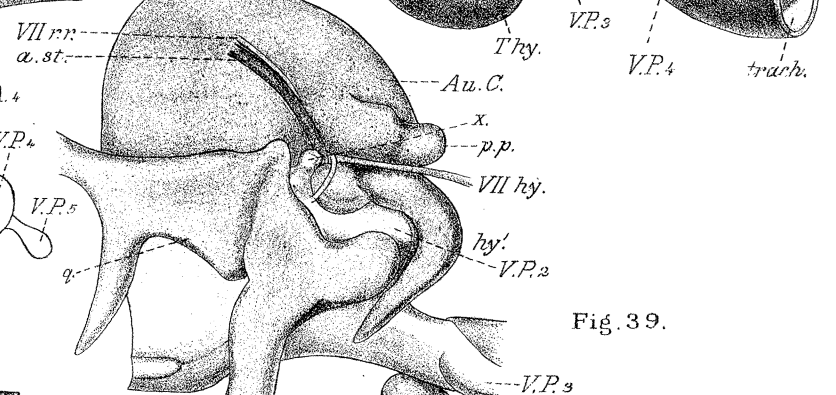
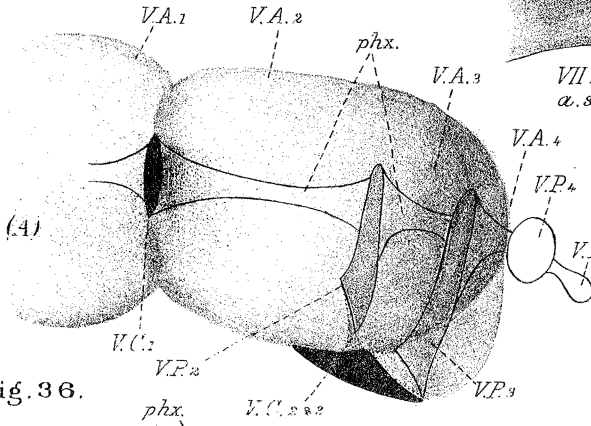


Fig. 39.

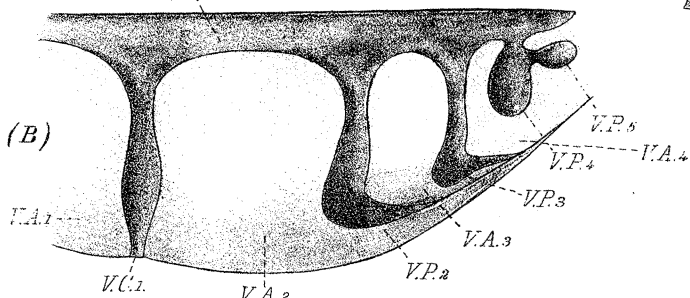


Fig. 40.

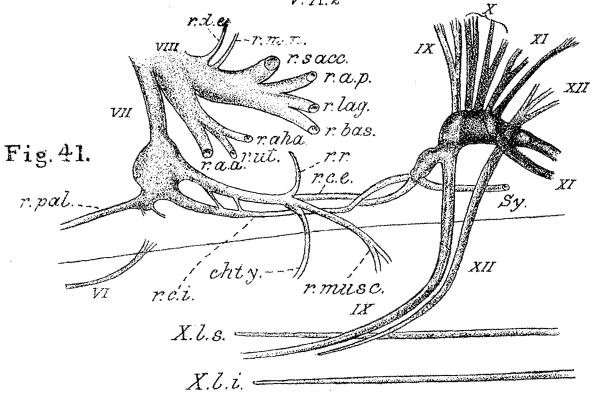
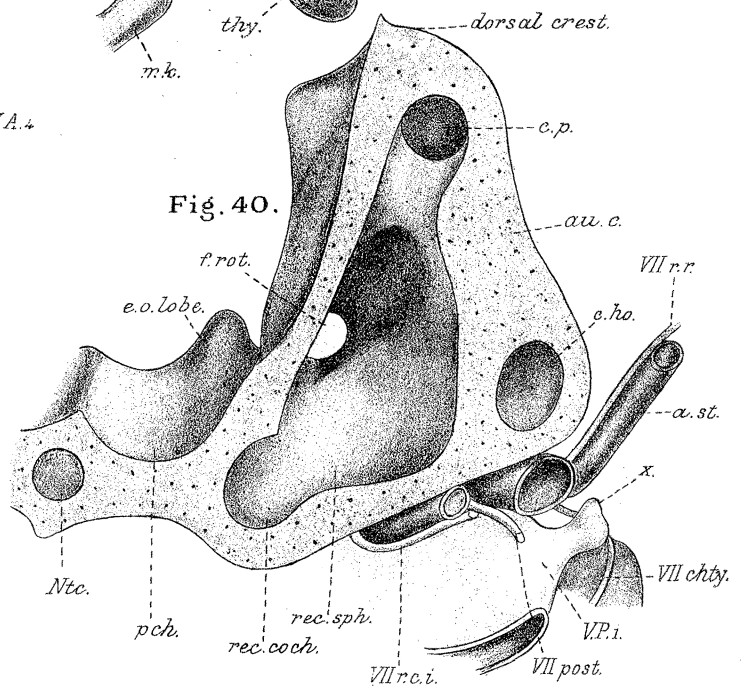
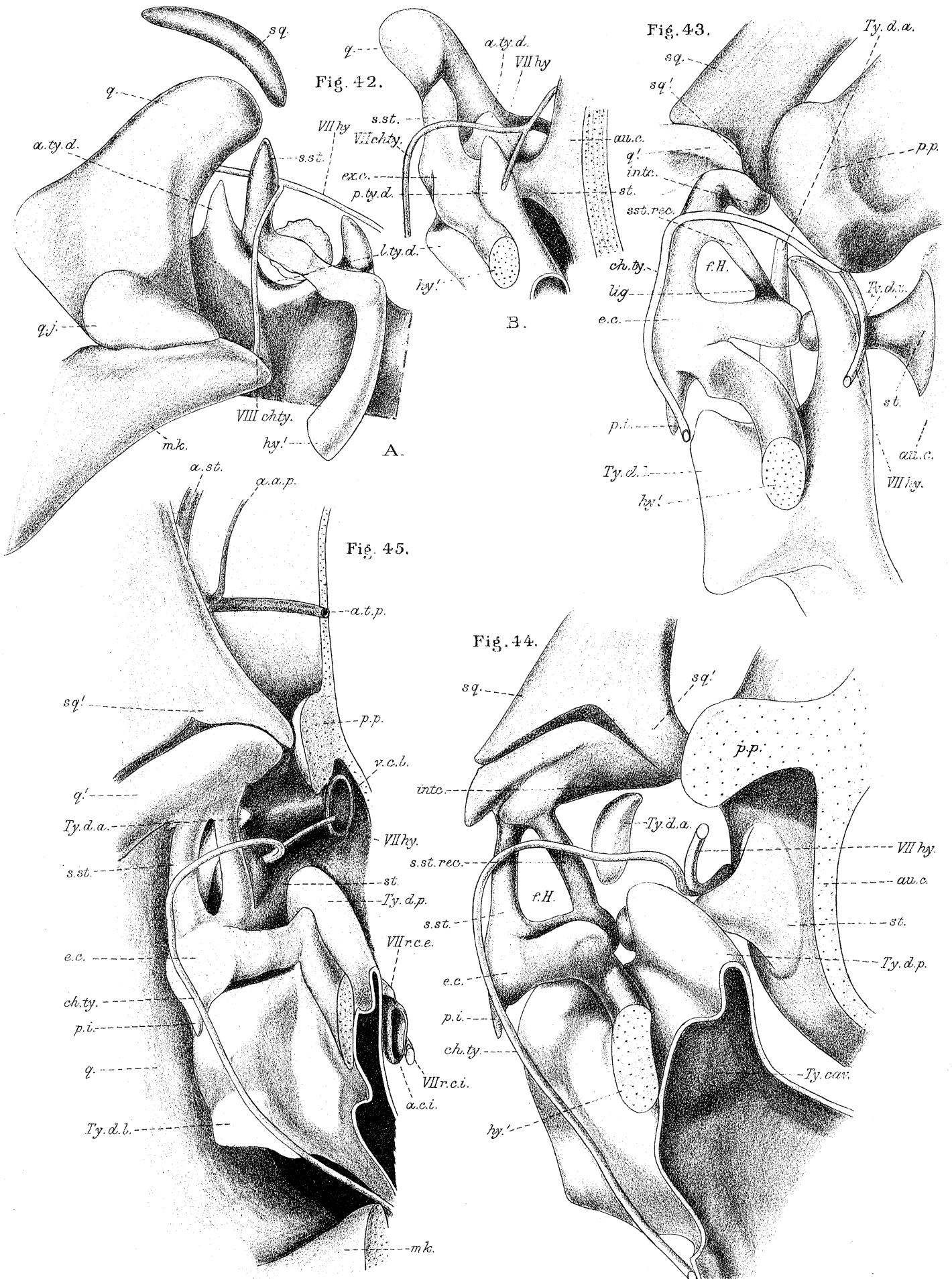


Fig. 41.



## LIST OF REFERENCE LETTERS.

- A.A.1*, 1st Aortic arch; *A.A.2*, 2nd Aortic arch; *A.A.3*, 3rd Aortic arch; *A.A.4*, 4th Aortic arch; *A.A.5*, 5th Aortic arch; *A.A.6*, 6th Aortic arch; *a.a.p.*, Arteria auricularis posterior; *a.bas.*, Arteria basilaris; *a.c.e.*, arteria carotis externa; *a.c.i.*, Arteria carotis interna; *a.ch.*, Arteria choroidea; *a.d.i.*, Arteria dentalis inferior; *a.d.p.*, Antero-dorsal pocket; *a.ling.*, Arteria lingualis; *a.lar.*, Arteria laryngealis; *al.c.*, Alimentary canal; *a.max.*, Arteria maxillaris; *amp.post.*, Ampulla posterior; *amp.ho.*, Ampulla horizontalis; *amp.ant.*, Ampulla anterior; *a.m.p.*, Arteria medullaris posterior; *a.pal.*, Arteria palatina; *ap.c.*, apical crest; *apon.*, Aponeurosis (Membrana tympani); *a.pulm.*, Arteria pulmonalis; *a.sacc.*, Arteria sacculi; *a.st.*, Arteria stapediale; *a.ty.*, Arteria tympanica; *a.t.p.*, Arteria temporalis posterior; *a.th.*, Arteria thyroidea; *Au.*, Auditory pit or organ; *Au.C.*, Auditory capsule; *ax.m.*, Axial mesenchyme.
- B.a.*, Bulbus arteriosus; *Bucc.*, Buccal cavity.
- Caps. prol.*, Capsular proliferation; *c.a.sp.*, Circus arteriosus spinalis; *c.ant.*, Anterior vertical canal; *cb.*, Cerebellum; *c.ho.*, Horizontal canal; *C.H.*, Cerebral hemisphere; *ch.ty.*, Chorda tympani; *conn.tiss.*, Connective tissue; *cochl.*, Cochlea; *col.*, Columella auris; *c.post.*, Posterior vertical canal; *c.p.c.*, Choroid plexus of 4th ventricle; *cr.ac.*, Crista acustica.
- D.Ao.*, Dorsal aorta; *d.a.*, Ductus arteriosus; *d.c.*, Ductus caroticus; *d.e.*, Ductus endolymphaticus; *d.l.g.*, Dorso-lateral groove; *d.per.*, Ductus perilymphaticus.
- E.c.*, Extra-stapedial cartilage; *e.o.*, Exoccipital bone.
- F.H.*, Huxley's foramen; *f.m.*, Foramen magnum; *F.B.*, Fore-brain; *f.s.c.*, Foramen sacculo-cochleare; *f.ut.s.*, Foramen utriculo-sacculi; *f.ut.*, Fundus utriculi; *f.end.*, Foramen sacci endolymphatici; *f.rot.*, Foramen rotundum; *f.fac.*, Foramen facialis; *f.a.a.*, Foramen acustici anterior; *f.a.p.*, Foramen acustici posterior; *f.d.e.*, Foramen ducti endolymphatici; *f.jug.*, Foramen jugulare.
- G.g.*, Ganglion geniculatum; *g.pet.*, Ganglion petrosum.
- H.B.*, Hind-brain; *H.C.*, Head cavity; *Ht.*, Heart; *H.C.m.*, Mandibular head cavity; *H.C.pm.*, Premandibular head cavity; *H.C.c.*, Canal of head cavity; *Hy.prol.*, Hyoid proliferation; *hy'*, *hy''*, *hy'''*, Cornua of hyoid.
- Interc.*, Intercalare.
- L.t.g.*, Laryngotracheal groove; *l.a.d.g.*, Lateral antero-dorsal groove; *l.p.d.g.*, Lateral postero-dorsal groove; *l.p.*, Lateral pocket; *lig.*, Ligament.
- Mk.*, Meckel's cartilage; *memb.lim.*, Membrana limitans; *m.a.d.g.*, Medial antero-dorsal groove; *m.p.d.g.*, Medial postero-dorsal groove; *mac.negl.*, Macula neglecta; *mac.utr.*, Macula recessus utriculi; *mac.sacc.*, Macula sacculi; *mac.bas.*, Macula basilaris; *mac.lag.*, Macula lagenæ; *mth.*, Mouth.
- Ntc.*, Notochord; *n.ep.*, Neuro epithelium; *nct.*, neurencygium.
- Pcdm.*, Pericardium; *pch.*, Parachordal cartilage; *p.rec.*, Processus recurrens of supra-stapedial; *p.i.*, Processus inferior of extra-stapedial; *phx.*, Pharynx;

*p.p.*, Parotic process; *par.*, Parietal bone; *p.d.p.*, Postero-dorsal pocket; *p. sup.*, Pars superior; *p. inf.*, Pars inferior; *px.l.*, Periaxial layer; *p. lag.*, Pars lagenæ; *p. bas.*, Pars basilaris; *pl. semil.*, Planum semilunatum.

*Q.*, Quadrate; *q'*, Posterior process of quadrate; *qj.*, Quadrato-jugal.

*R.p.*, Rathke's pouch.

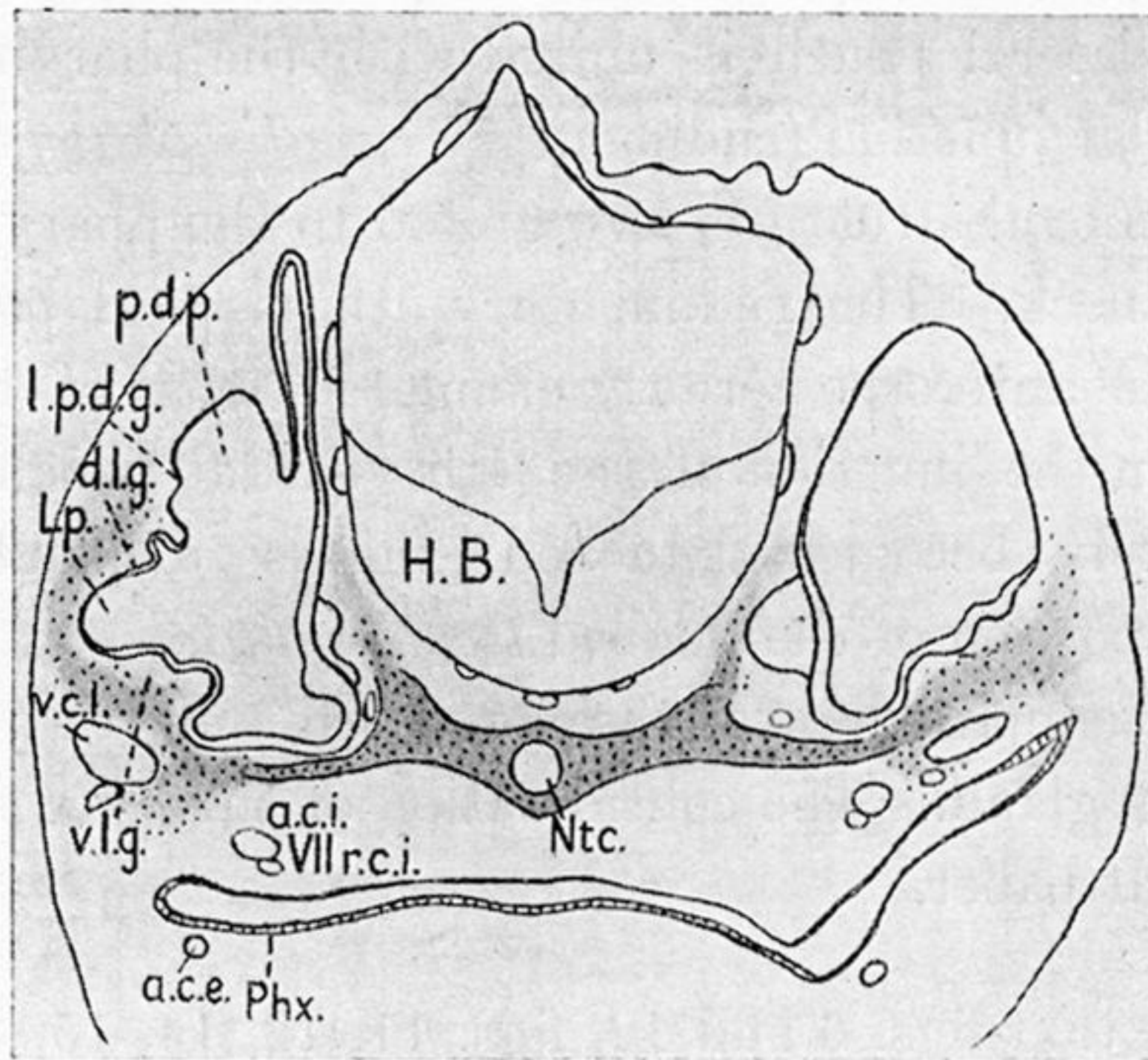
*S.p.*, Seessel's pouch; *Stm.*, Stomodæum; *S.L.*, Sinus longitudinalis; *S.O.p.*, Sinus occipitalis posterior (Sinus longitudinalis posterior); *s. tr.*, Sinus transversus; *s.o.v.*, Supra-occipital vein; *s. st.*, Supra-stapedial process; *sq'*, Squamosal; *sq''*, Postero-ventral process of squamosal; *st.*, Stapes; *s. ex. col.*, Extra-columellar sinew; *S.S. Ut.*, Sinus superior utriculi; *Sacc.*, Sacculus; *s. per.*, Saccus perilymphaticus; *s.l.*, sinus longitudinalis; *s.o.c.*, Supra-occipital cartilage; *s.o.p.*, Supra-occipital process; *S.t.*, Sinus transversalis.

*Ty. d.a.*, Anterior tympanic diverticulum; *Ty. d.l.*, Lateral tympanic diverticulum; *Ty. d.p.*, Posterior tympanic diverticulum; *Thy.*, Thyroid gland; *tr.*, Trachea; *thm.*, Thymus; *t.h.*, Torcular Herophili.

*V.x.*, Unnamed vein (DENDY).

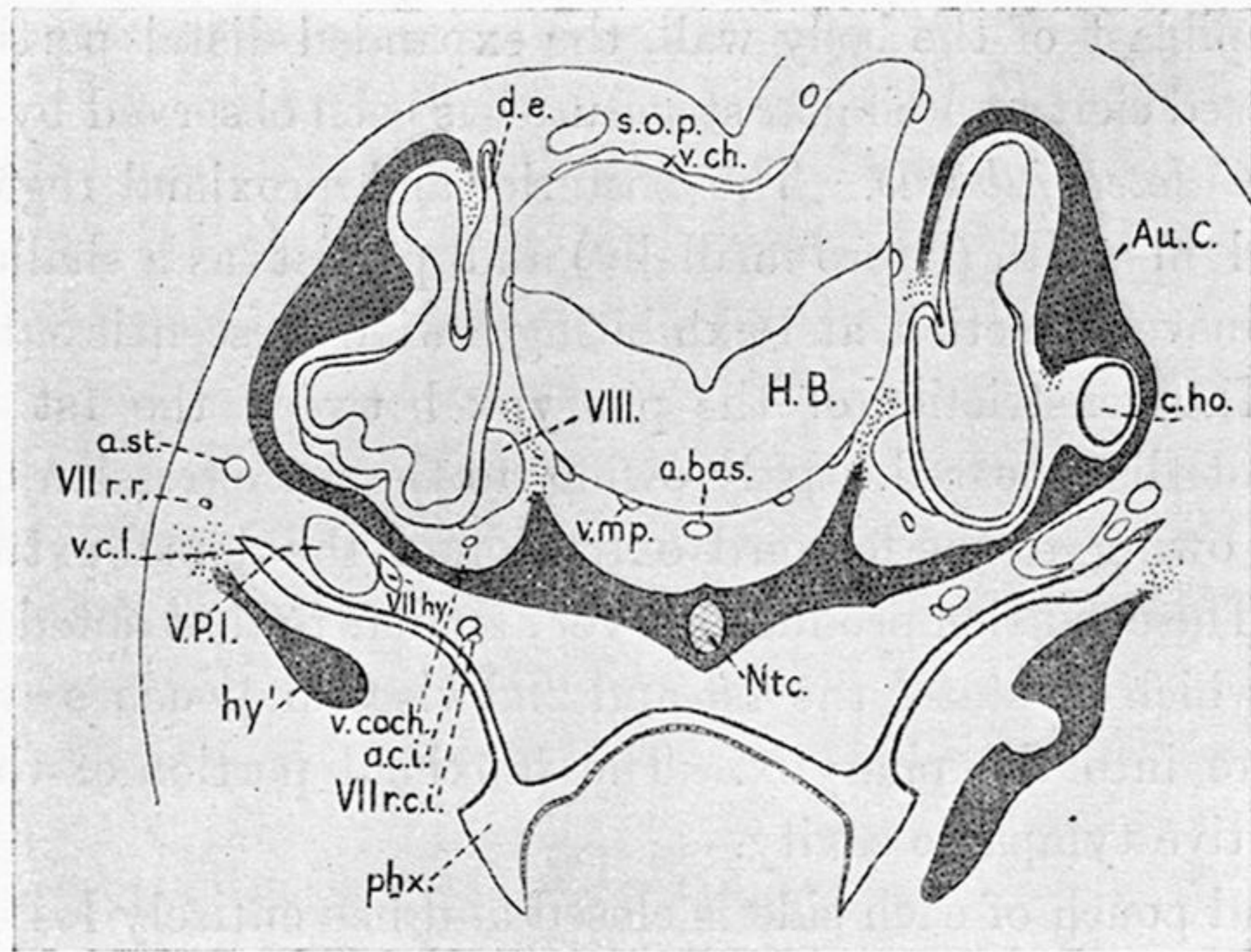
*V. Ao.*, Ventral aorta; *V.P.1*, 1st Visceral pouch; *V.P.2*, 2nd Visceral pouch; *V.P.3*, 3rd Visceral pouch; *V.P.4*, 4th Visceral pouch; *V.P.5*, 5th Visceral pouch; *V.C.1*, 1st Visceral cleft; *V.C.2*, 2nd Visceral cleft; *v. sp.*, Vena spinalis; *v.m.p.*, Vena medullaris posterior; *v.m.a.*, Vena medullaris anterior; *v.c.l.*, Vena capitis lateralis; *v. ce. m.*, Vena cephalica media; *v.o.c.*, Vena occipitalis communicans; *v. ce. p.*, Vena cephalica posterior; *v.c.m.*, Vena capitis medialis; *V. porb.*, Post orbital venous sinus; *v.l.g.*, Vento lateral groove; *v. th.*, Vena thyroidea; *v.j.e.*, Vena jugularis interna; *v. lar.*, Vena laryngealis; *v.j.i.*, Vena jugularis interna; *v.f.*, Vena facialis; *v.t.*, Vena tympanica; *v. coch.*, Vena cochlearis; *v. ch. m.*, Vena choroidea media; *v. chl.*, Vena choroidea lateralis; *V.*, Nervus Trigemini; *Vg.*, Gasserian ganglion; *VI.*, Nervus Abducens; *VII.*, Nervus Facialis; *VII. pret.*, pre-trematic branch; *VII. posttr.*, post-trematic branch; *VII. pal.*, palatine branch; *VII. post.*, posterior main stem; *VII. hyomand.*, hyomandibular branch; *VII. musc.*, muscle-branch; *VII. r.r.*, ramus recurrens; *VII. r.c.i.*, ramus communicans interna; *VII. r.c.e.*, ramus communicans externa; *VIII.*, Nervus acusticus; *VIII. r.a.*, ramus anterior; *VIII. r.p.*, ramus posterior; *VIII. sacc.*, ramus sacculi; *VIII. r. coch.*, ramus cochlearis; *VIII. r. bas.*, ramus basilaris; *VIII. r. lag.*, ramus lagenæ; *VIII. r. uti.*, ramus utriculi; *VIII. d.e.*, ramus ducti endolymphatici; *VIII. r.m.n.*, ramus maculæ neglectæ; *VIII. r.a.a.*, ramus ampullaris anterior; *VIII. r.a.ho.*, ramus ampullaris horizontalis; *VIII. r.a.p.*, ramus ampullaris posterior.

*IX.*, Nervus glossopharyngeus; *X.*, Nervus vagus; *X.l.i.*, ramus laryngealis inferior; *X.l.s.*, ramus laryngealis superior; *XI.*, Nervus Spinalis accessorius; *XII.*, Nervus hypoglossus; *X.*, closed distal extremity of 1st visceral pouch.

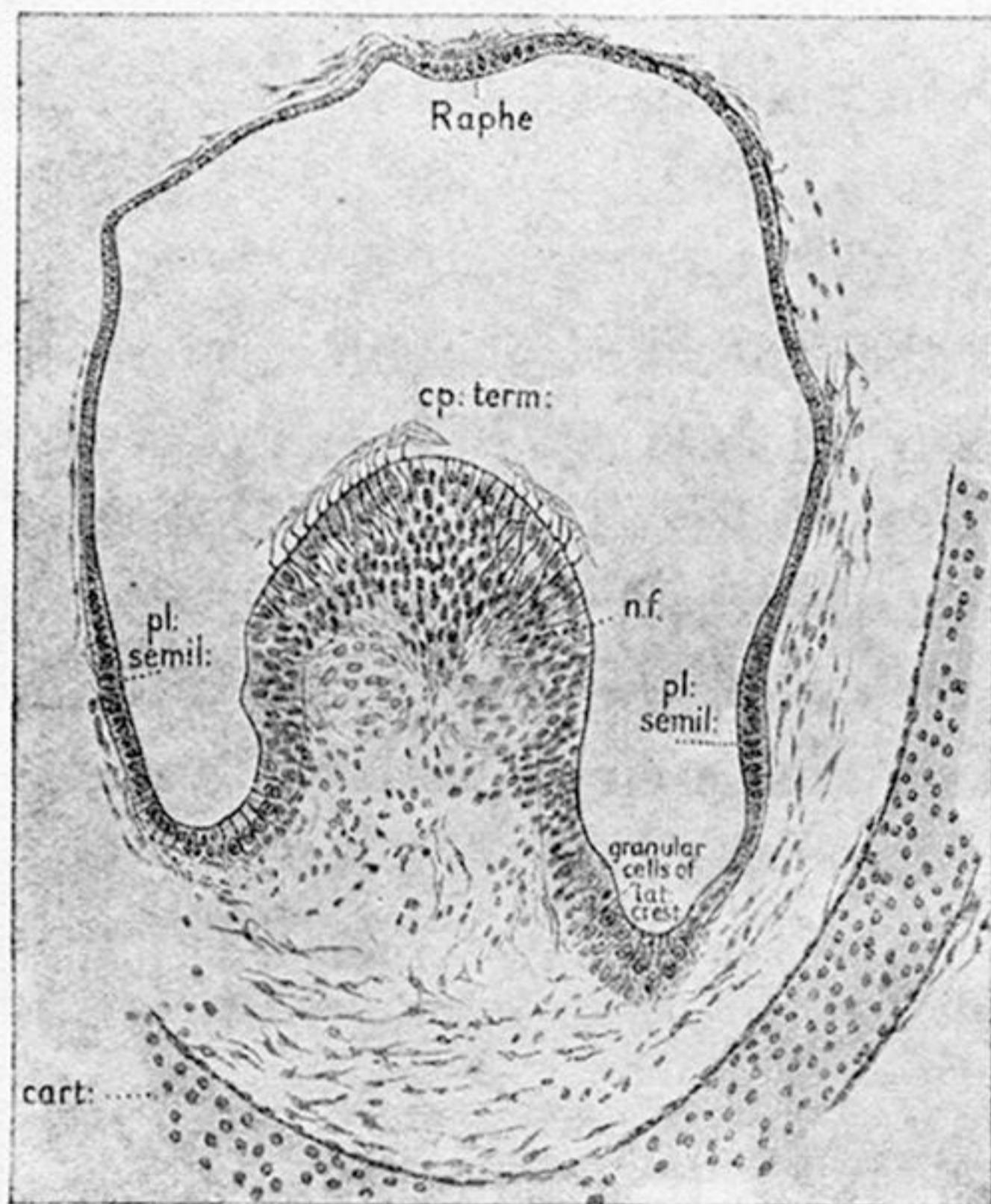


TEXT-FIG. 5.—Stage O-P. Embryo 35*a*. Diagrammatic transverse section through the otocysts.  
(× 33.)

(For explanation of lettering see pp. 367–368.)

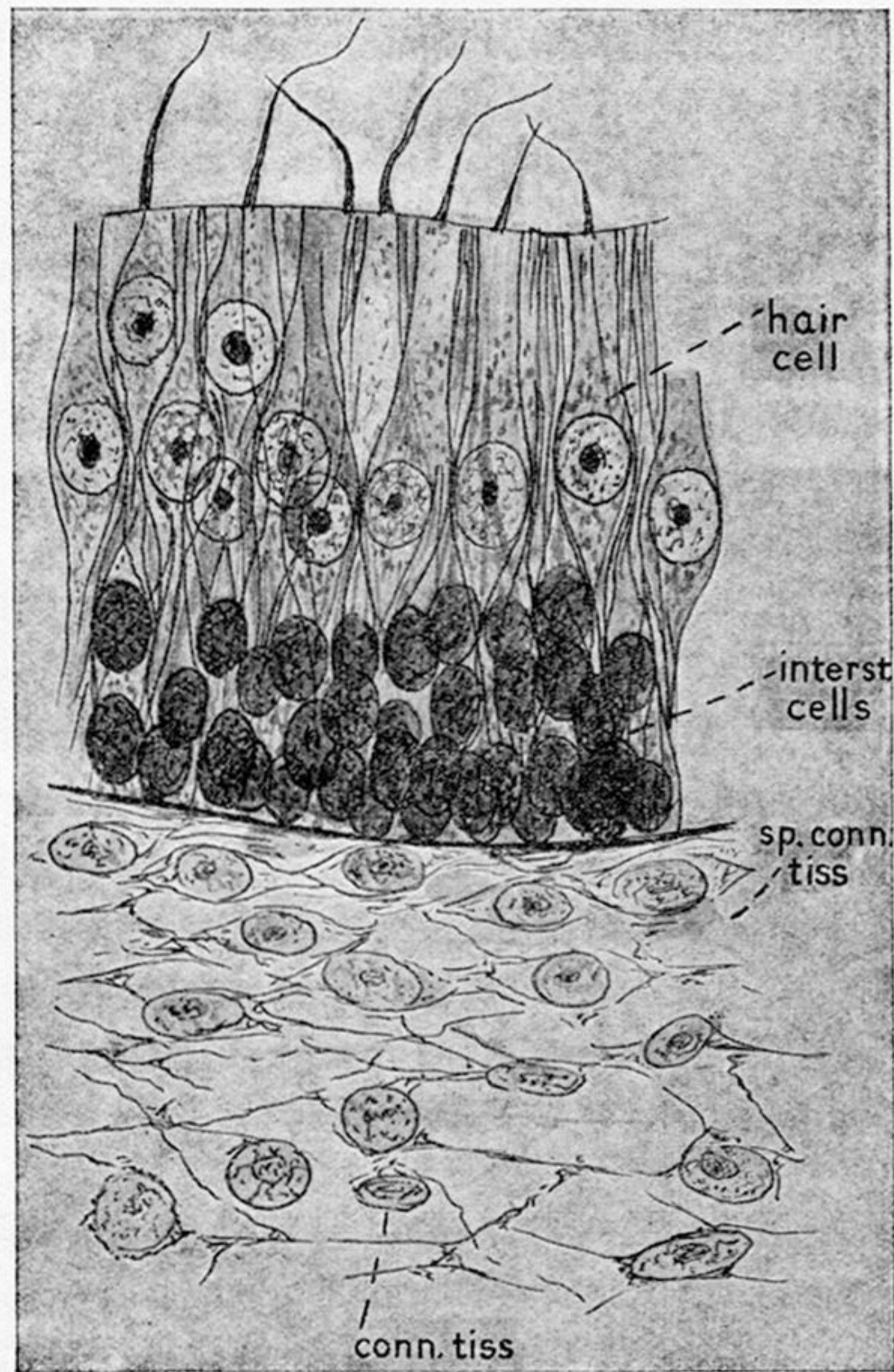


TEXT-FIG. 6.—Stage P. Embryo 45a. Diagrammatic transverse section through the auditory capsules and otocysts [developing membranous labyrinths]. ( $\times 33$ .)  
 (For explanation of lettering see pp. 367–368.)



TEXT-FIG. 7.

TEXT-FIG. 7.—Stage R. Embryo 141. Diagrammatic transverse section through the *Crista acustica* of the ampulla of the left posterior vertical semicircular canal.

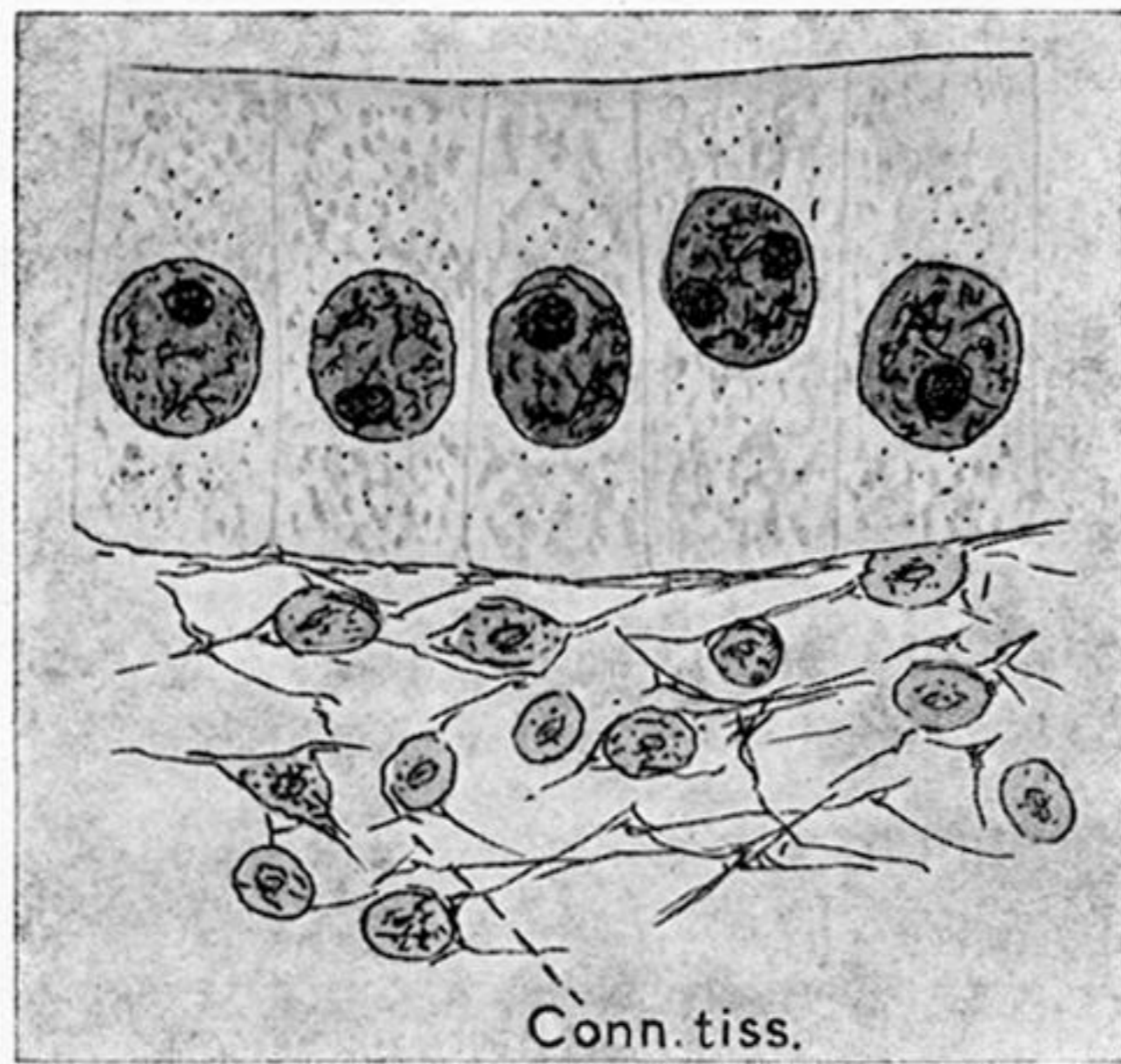


TEXT-FIG. 8.

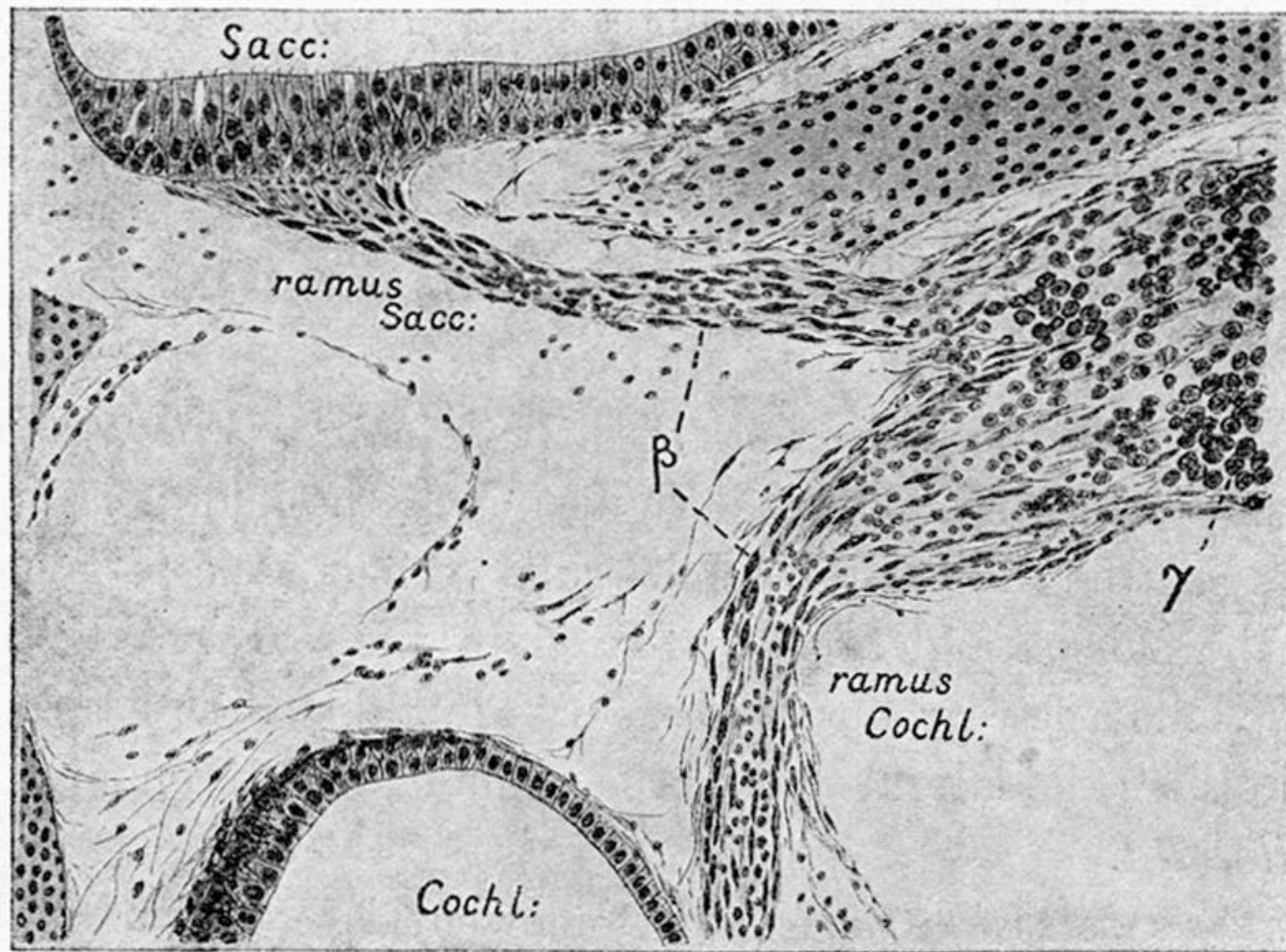
TEXT-FIG. 8.—Stage S. Embryo 9a. Diagram of sensory epithelium and supporting tissue ("spindle cartilage") of the wall of the Sacculus. (Zeiss D, Oc. 2.)

(For explanation of lettering see pp. 367-368).



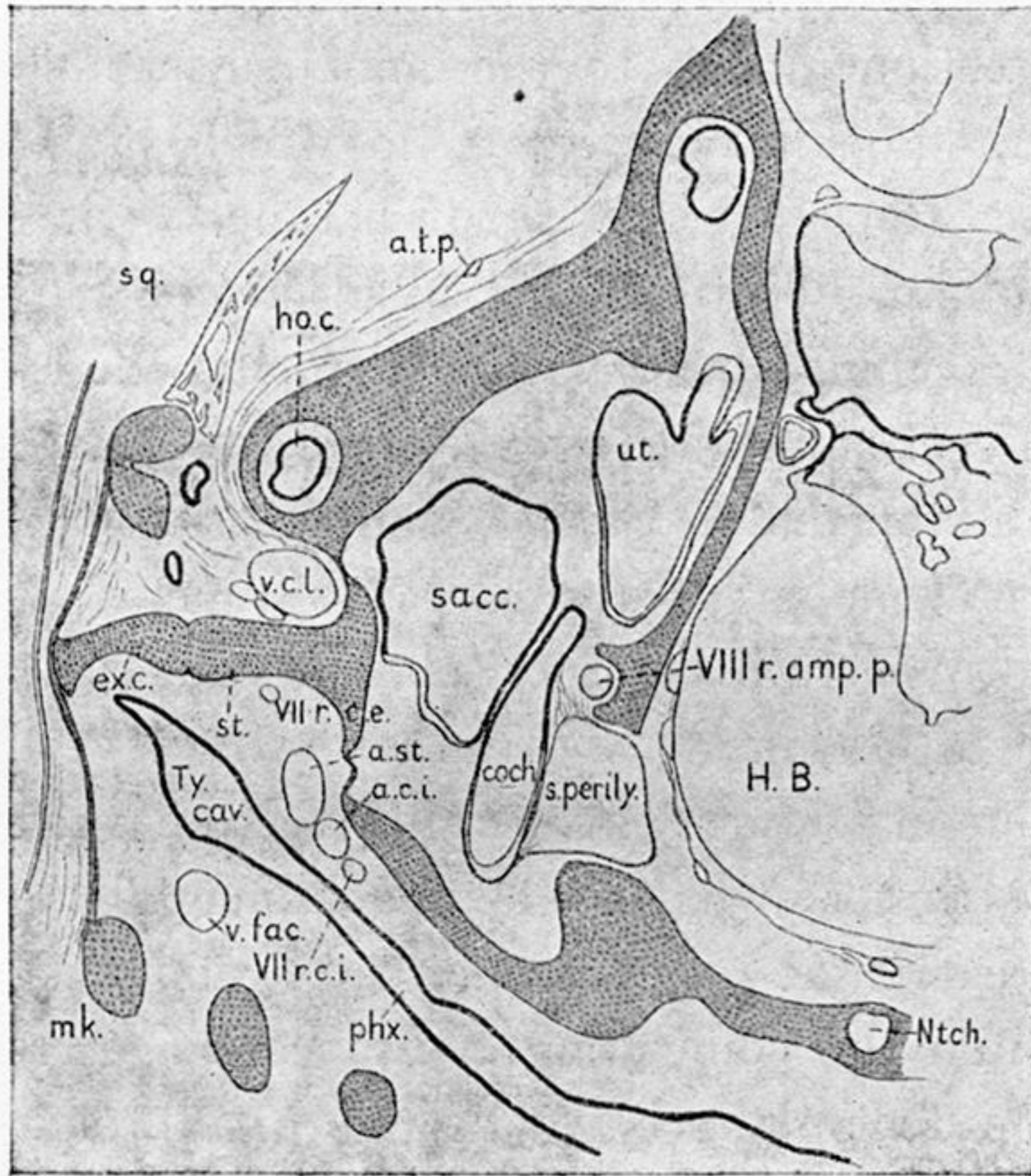


TEXT-FIG. 9.—Diagram of epithelium from the lateral crest of the *Crista acustica* of the ampulla of the left posterior vertical semicircular canal. (Zeiss D, Oc. 2.)  
(For explanation of lettering see pp. 367–368.)



TEXT-FIG. 10.—Stage R. Embryo 141. Diagram of the distal extremities of the saccular and cochlear (Lagenar) rami of the auditory nerve showing  $\beta$  and  $\gamma$  neuroblasts, and sensory epithelium.

(For explanation of lettering see pp. 367–368.)

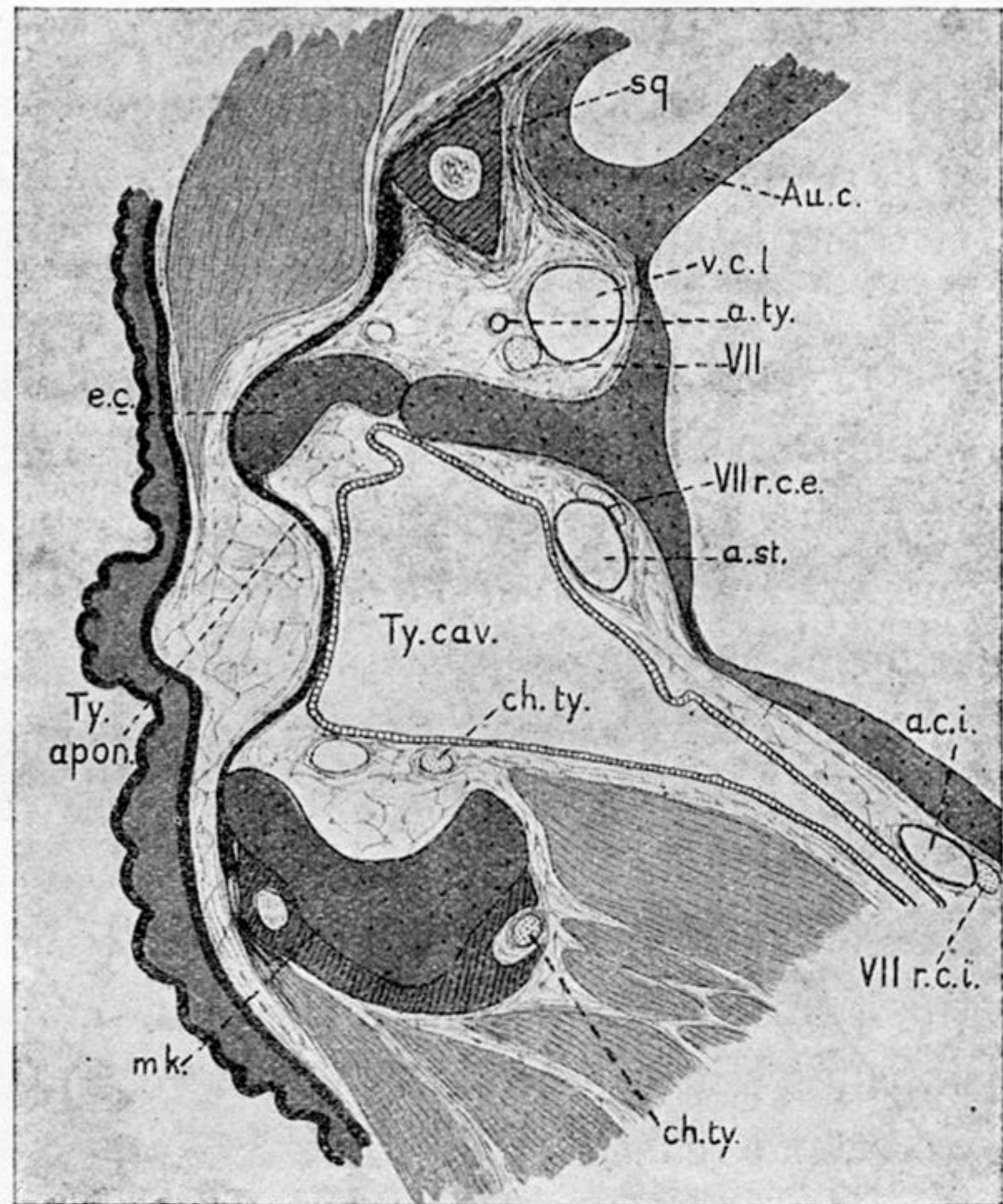


TEXT-FIG. 15.

TEXT-FIG. 15.—Stage R. Embryo 141. Diagrammatic transverse section through the left auditory capsule and associated structures, showing the stapes and extra-stapedial cartilage, together with the developing tympanic diverticula.

TEXT-FIG. 16.—Stage S. Embryo 9a. Diagrammatic transverse section of the left tympanic region showing the stapes, the extra-stapedial cartilage, the tympanic cavity and the tympanic aponeurosis.

(For explanation of lettering see pp. 367–368.)



TEXT-FIG. 16.

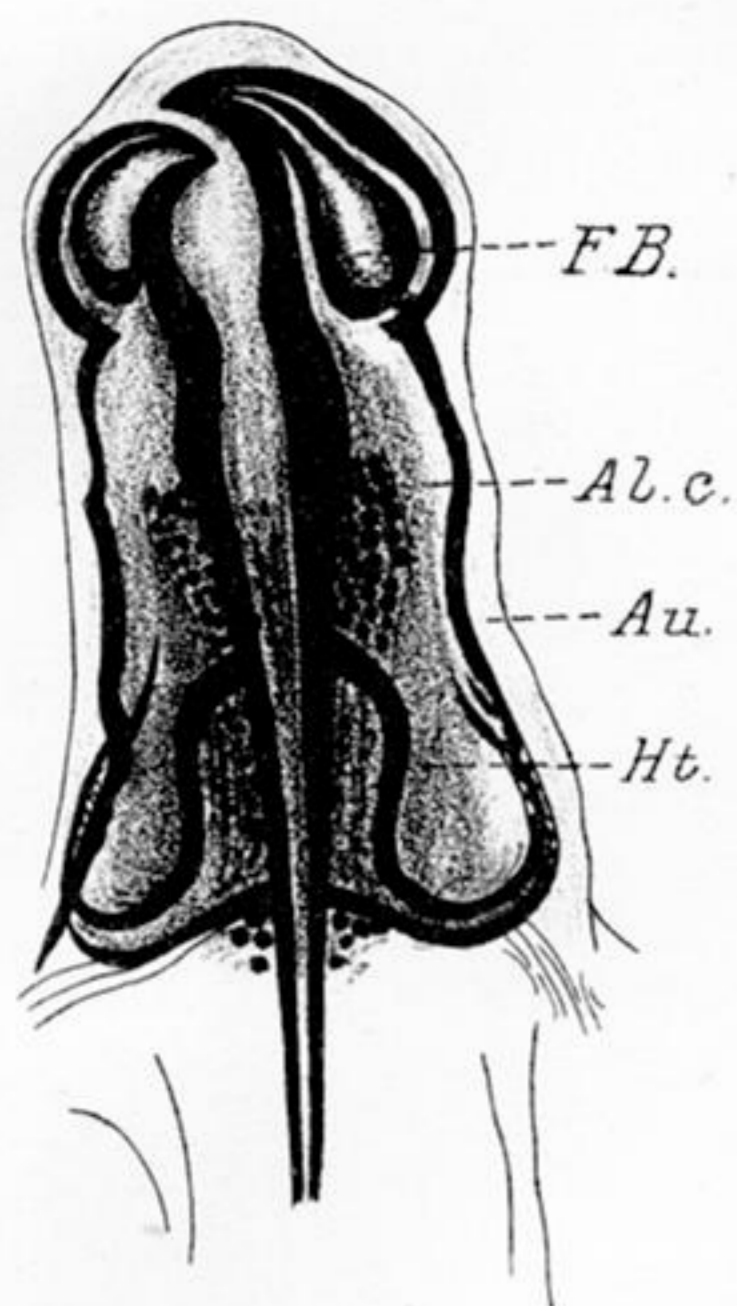


Fig. 1.

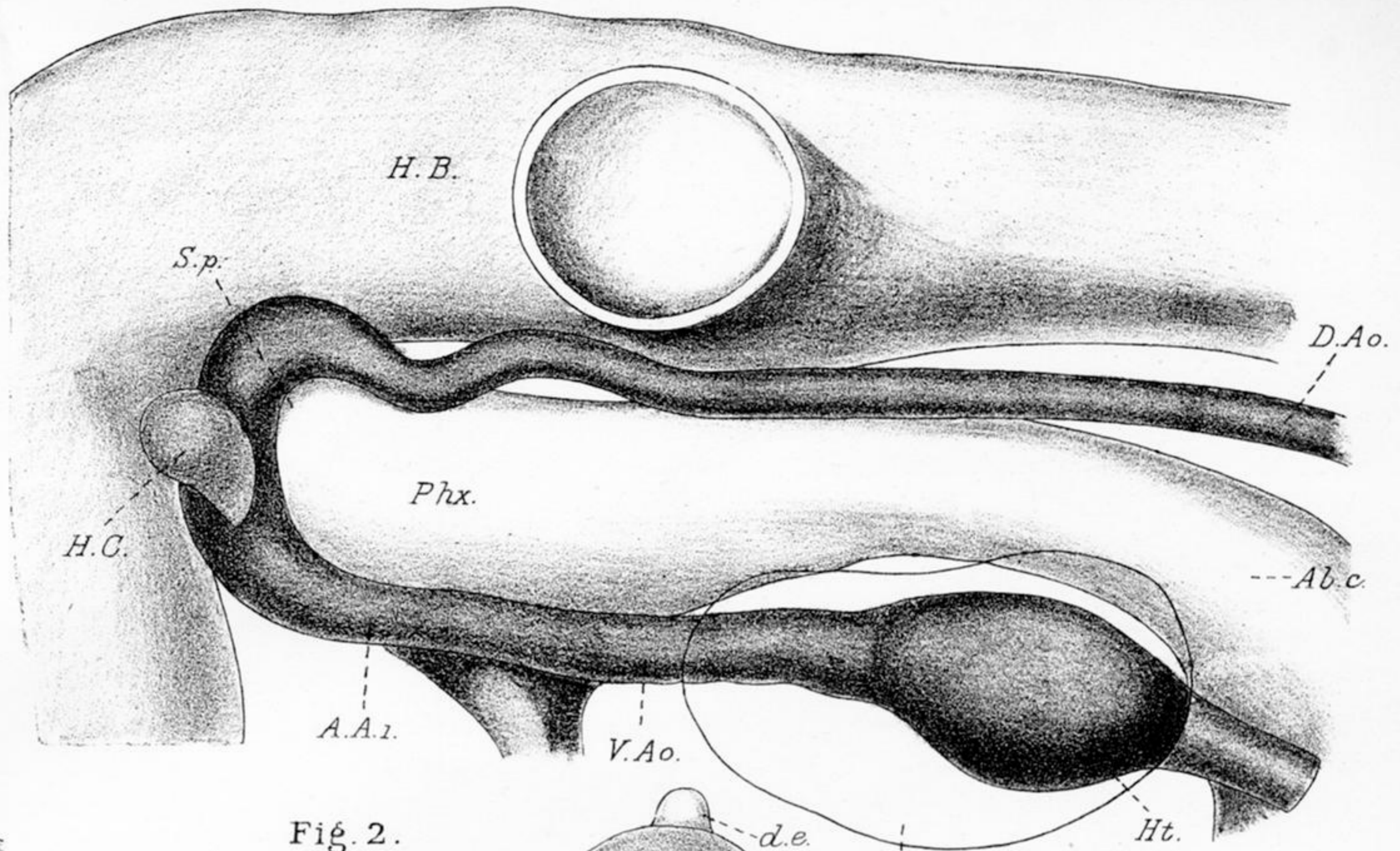


Fig. 2.

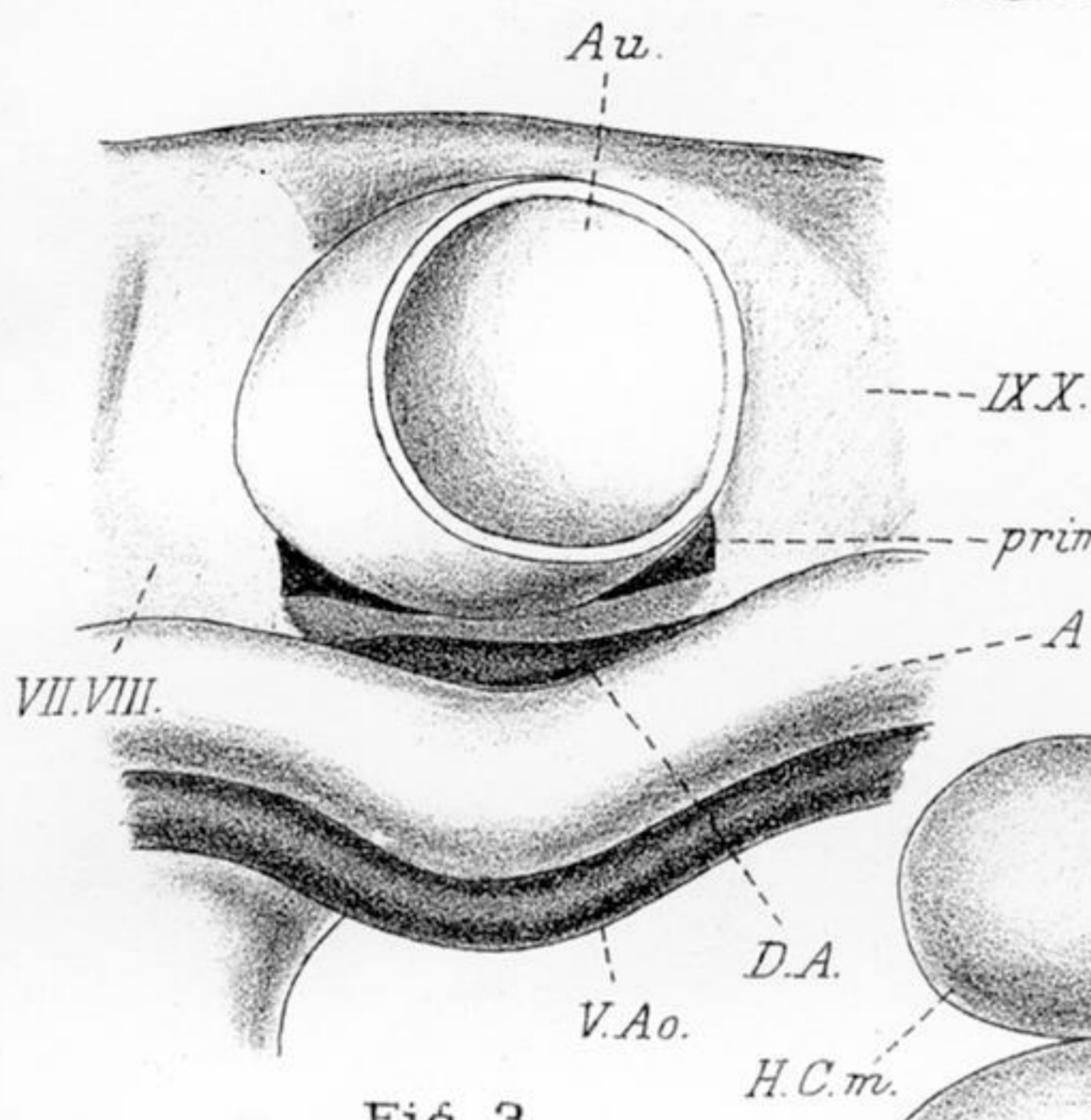


Fig. 3.

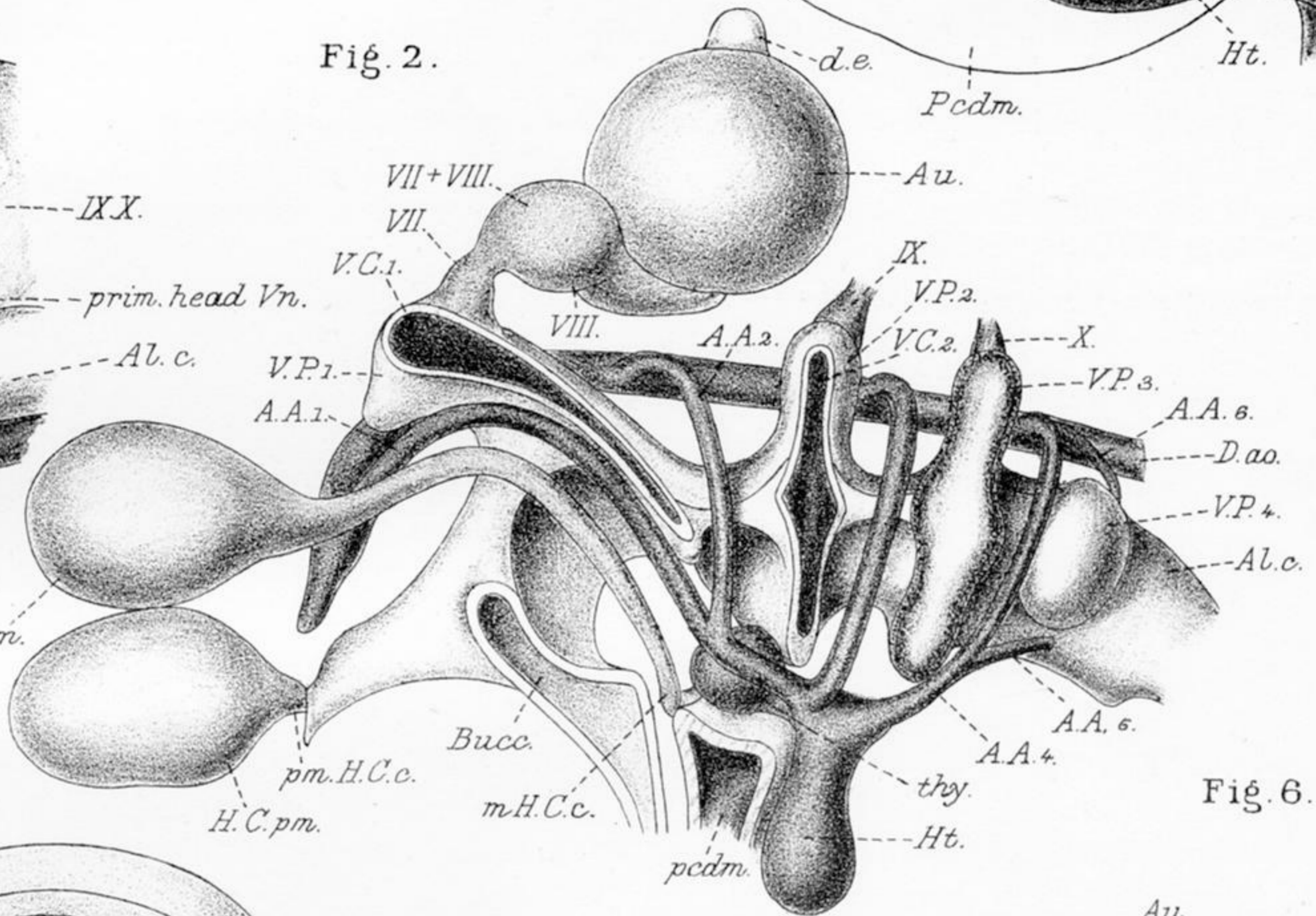


Fig. 6.

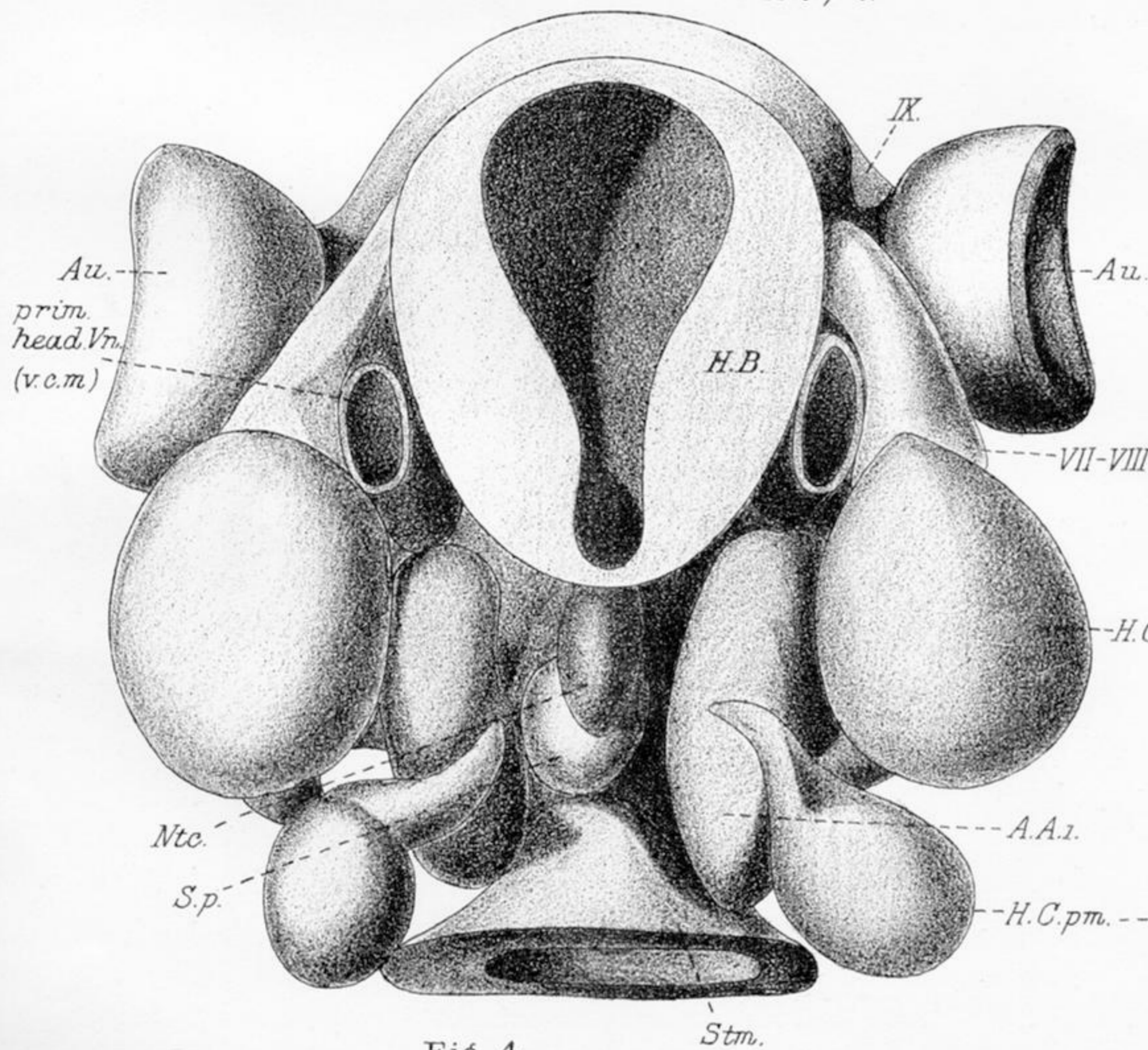


Fig. 4.

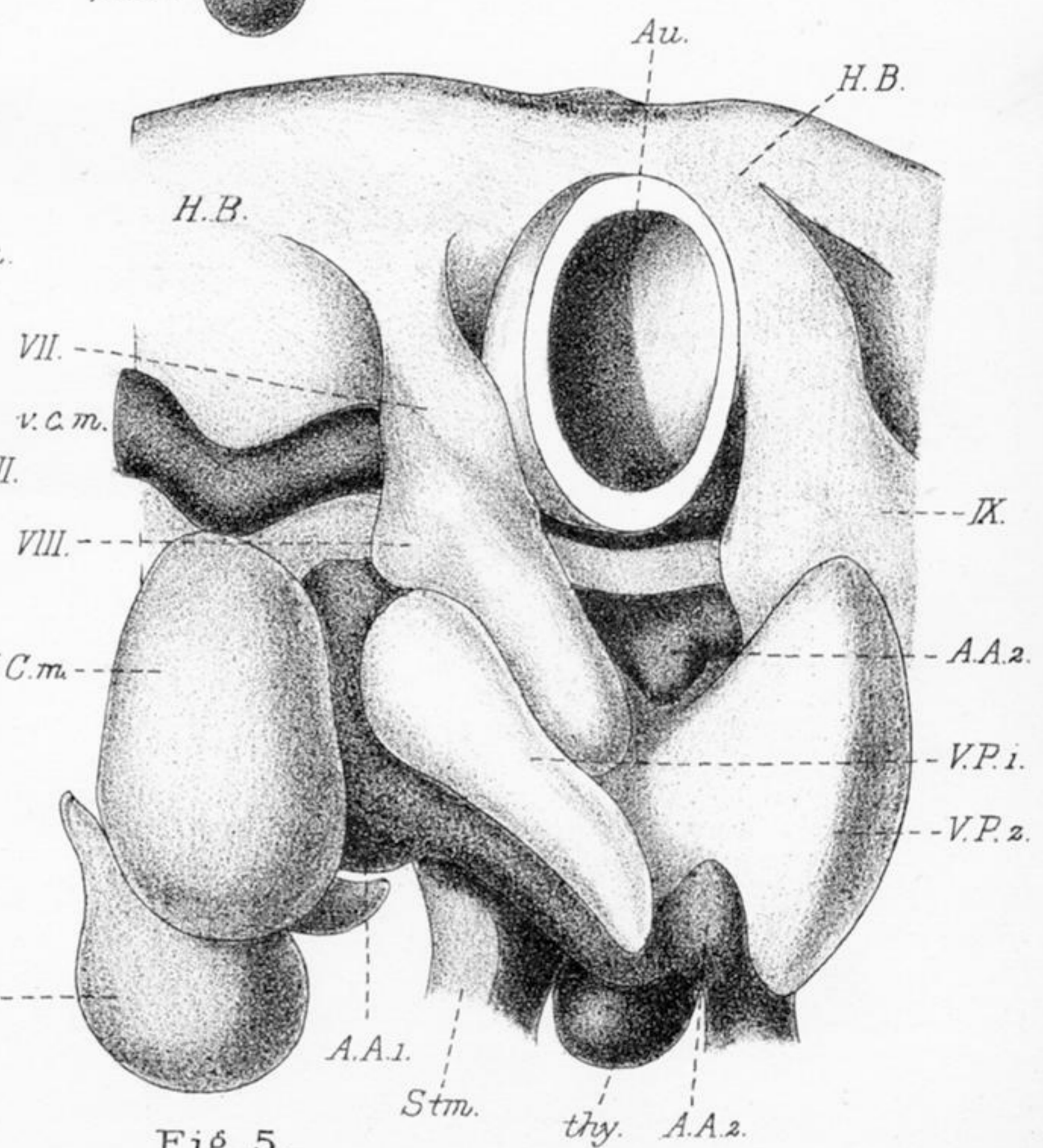


Fig. 5.

PLATE 11.

Stage H.

Fig. 1.—Embryo 78, anterior half, seen from above as a transparent object. ( $\times 25$ .)

Stage J.

Fig. 2.—(Early Stage J), Embryo 44. Reconstruction drawing. Lateral view of auditory region ( $\times 100$ ).

Fig. 3.—(Late Stage J), Embryo 79. Reconstruction drawing. Lateral view of auditory region ( $\times 100$ ).

Stage K.

Fig. 4.—Embryo 39. Model of auditory region ( $\times 100$ ). Frontal view.

Fig. 5.—Embryo 39. Model of auditory region ( $\times 100$ ). Lateral view.

Stage L.

Fig. 6.—Embryo 50. Model of auditory region ( $\times 70$ ). Lateral view. (This model was constructed from longitudinal sections. The hind-brain and veins are not shown.)

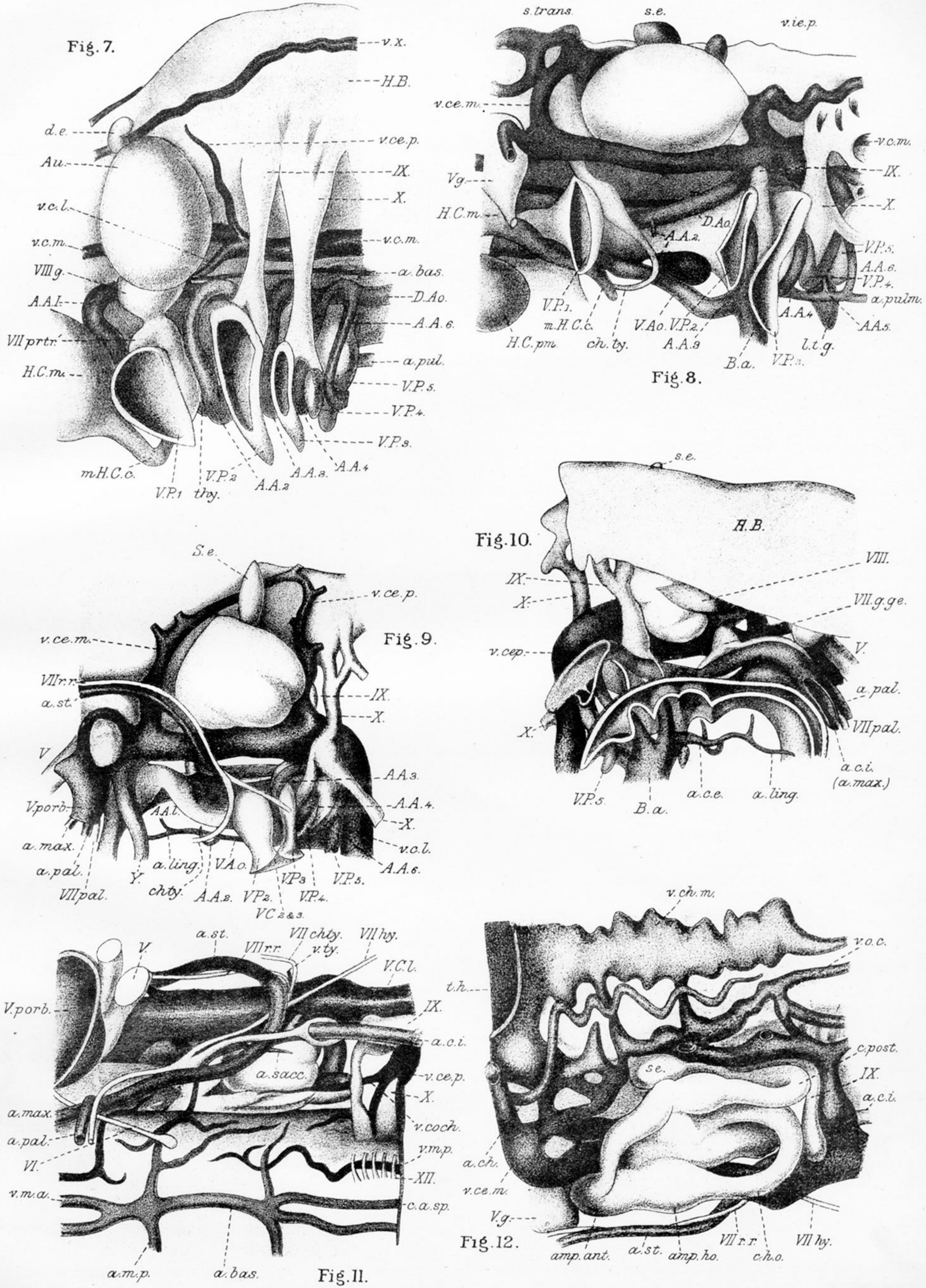


PLATE 12.  
Stage M.

Fig. 7.—Embryo 51. Model of auditory region (×100). Lateral view.

Stage N.

Fig. 8.—Embryo 14a. Model of auditory region (×50). Lateral view.

Stage O.

Fig. 9.—Embryo 32a. Model of auditory region. Medial view. (This model was made from longitudinal sections. Part of hind-brain and its veins omitted.)

Fig. 10.—Embryo 32a. Model of auditory region (×50). Lateral view.

Stage P.

Fig. 11.—Embryo 45a. Model of auditory region, showing nerves and blood-vessels (×35). Seen from below.

Fig. 12.—Embryo 45a. Model of auditory region, showing auditory capsule, blood-vessels and nerves (×35). Seen from above. (The Sinus longitudinalis posterior has been removed.)



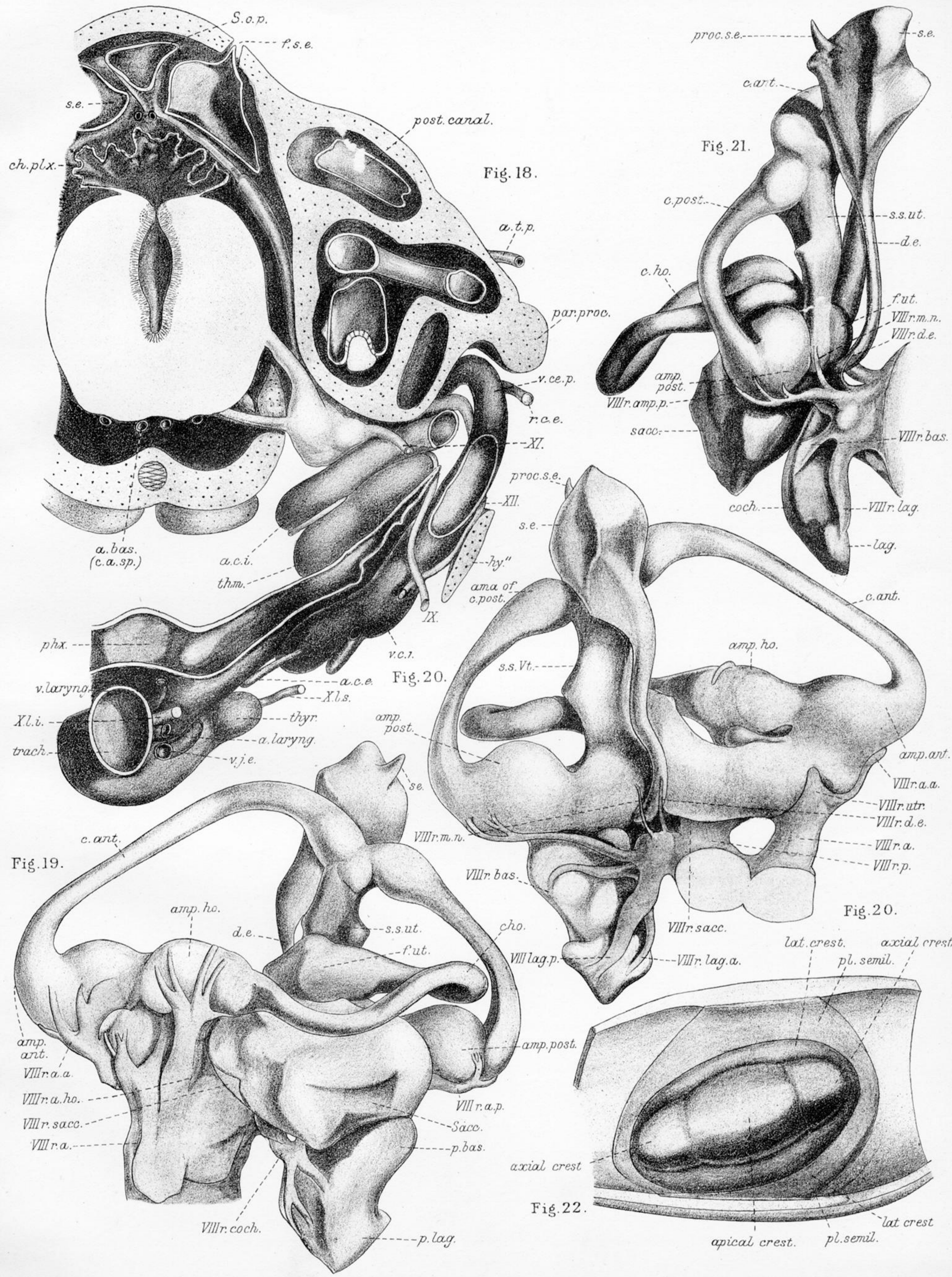


PLATE 14.

Stage R.

Fig. 18.—Embryo 141. Model of posterior portion of auditory region seen from in front. The section passes through the left foramen saccus endolymphaticus ( $\times 33$ ). (Bones and cartilages overlying the auditory capsule omitted.)

Fig. 19.—Embryo 141. Model of left membranous labyrinth and auditory nerve ( $\times 33$ ). Lateral view.

Fig. 20.—Embryo 141. Medial view of same.

Fig. 21.—Embryo 141. Posterior view of same.

Fig. 22.—Embryo 141. Model of the crista acustica and ventral half of the ampulla of the posterior vertical semicircular canal ( $\times 100$ ). (Crista, green; planum semilunatum, red.)

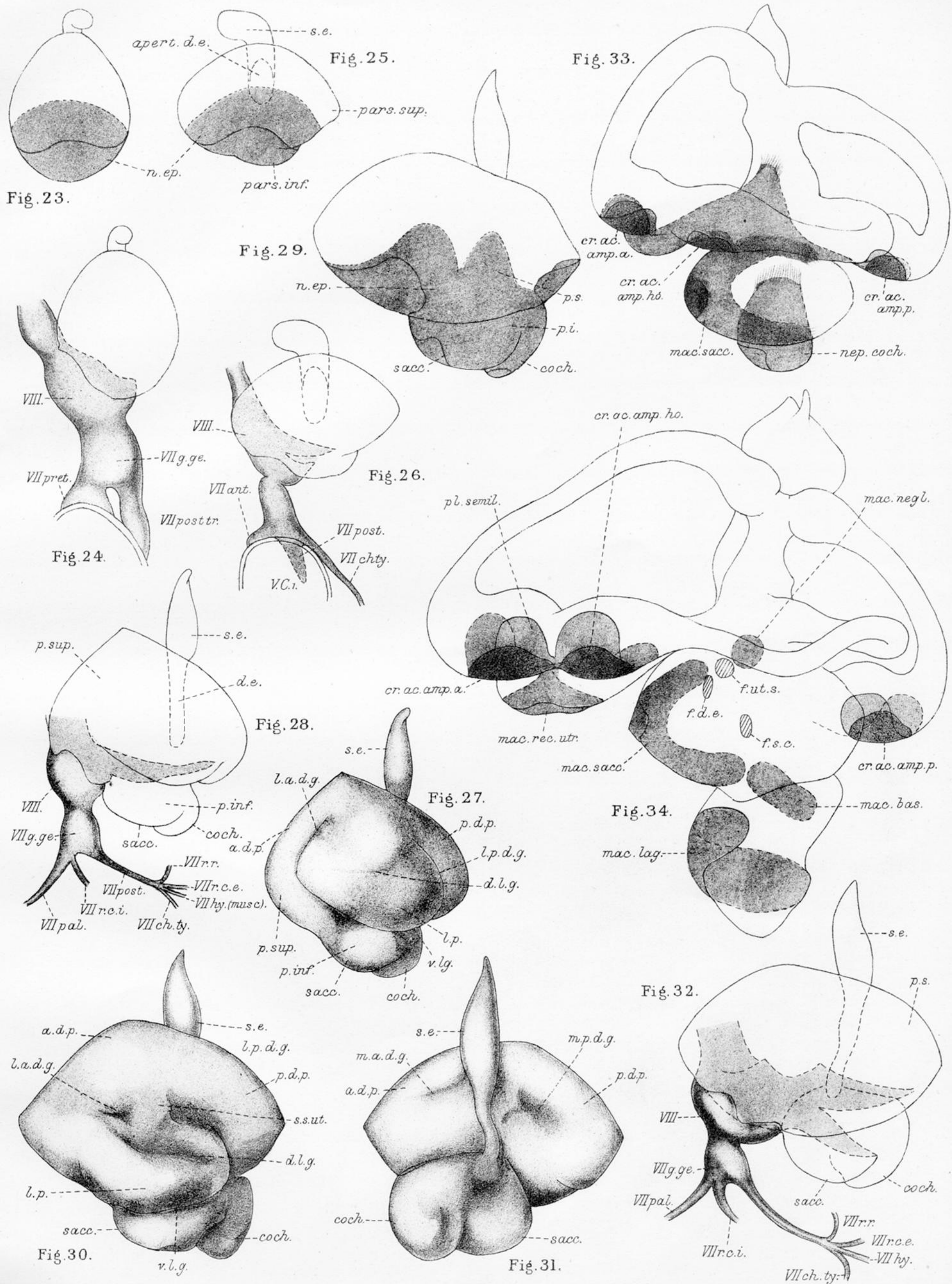


PLATE 15.

Stage M.

Fig. 23.—Embryo 51. Diagram of auditory sac, showing the approximate distribution of the neuro-epithelium, red ( $\times 100$ ).

Fig. 24.—Embryo 51. Diagram of auditory sac and acustico facialis neurencygium ( $\times 100$ ).

Stage N.

Fig. 25.—Embryo 14a. Diagram of auditory sac, showing approximate distribution of neuro-epithelium, red ( $\times 50$ ).

Fig. 26.—Embryo 14a. Diagram of auditory sac and acustico facialis neurencygium, with developing branches of Nerve VII ( $\times 50$ ).

Stage O.

Fig. 27.—Embryo 32a. Auditory sac ( $\times 50$ ). Lateral view.

Fig. 28.—Embryo 32a. Diagram of auditory sac with developing facial and auditory ganglia and nerves ( $\times 50$ ).

Stage O-P.

Fig. 29.—Embryo 35a. Diagram of auditory sac, showing approximate distribution of neuro-epithelium, red ( $\times 50$ ).

Fig. 30.—Embryo 35a. Auditory sac ( $\times 50$ ). Lateral view.

Fig. 31.—Embryo 35a. Auditory sac ( $\times 50$ ). Medial view.

Fig. 32.—Embryo 35a. Diagram of auditory sac and auditory and facial nerves ( $\times 50$ ).

Stage P.

Fig. 33.—Embryo 45a. Diagram of membranous labyrinth with developing sensory patches (Neuro-epithelium, red) ( $\times 50$ ).

Stage R.

Fig. 34.—Embryo 141. Diagram of left membranous labyrinth, showing cristæ and maculæ acusticæ ( $\times 50$ ).



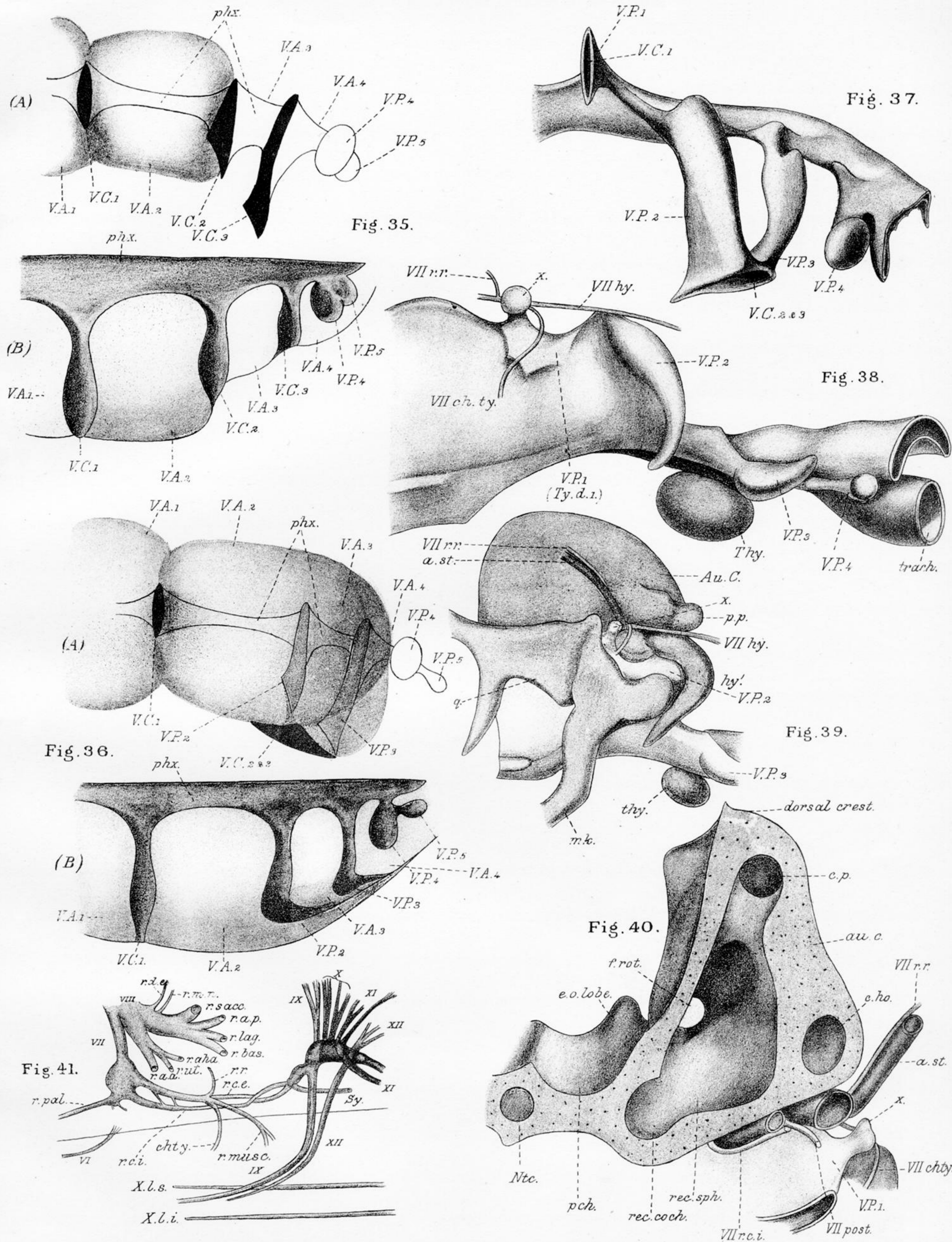


PLATE 16.

Fig. 35.—Diagram to illustrate the relationship of the visceral arches and clefts during Stage N—(A) Lateral view, (B) Seen from above.

Fig. 36.—Diagram to illustrate the early stages of the “overgrowth” (formation of operculum) by which the ultimate closure of the 2nd and 3rd visceral clefts is effected. These clefts are first converted during Stage O into tubes with a common ventral opening—(A) Lateral view, (B) Seen from above. (Thickening visceral arches are coloured: 1st arch, yellow; 2nd arch, green; 3rd arch, red.)

Stage O-P.

Fig. 37.—Embryo 35a.—Model of the pharynx in the auditory region, showing visceral pouches and clefts (×50). Lateral view.

Stage P.

Fig. 38.—Embryo 45a. Model of pharynx in the auditory region, showing visceral pouches and clefts and part of developing trachea (×50). Lateral view. (The lumen of the ventro-medial portion of the 1st visceral pouch forms the rudimentary tympanic cavity. The dorso-lateral portion (x) is a solid neck of tissue, expanded distally.)

Fig. 39.—Embryo 45a. Model of developing cartilaginous auditory capsule, hyoid and mandibular cartilages, pharynx, and thyroid gland (×25). Lateral view.

Fig. 40.—Embryo 45a. Model of posterior half of cartilaginous auditory capsule (×50). Frontal view.

Fig. 41.—Embryo 45a.—Schematic representation of the principal nerves of the auditory region, Stages R and S. Lateral view.

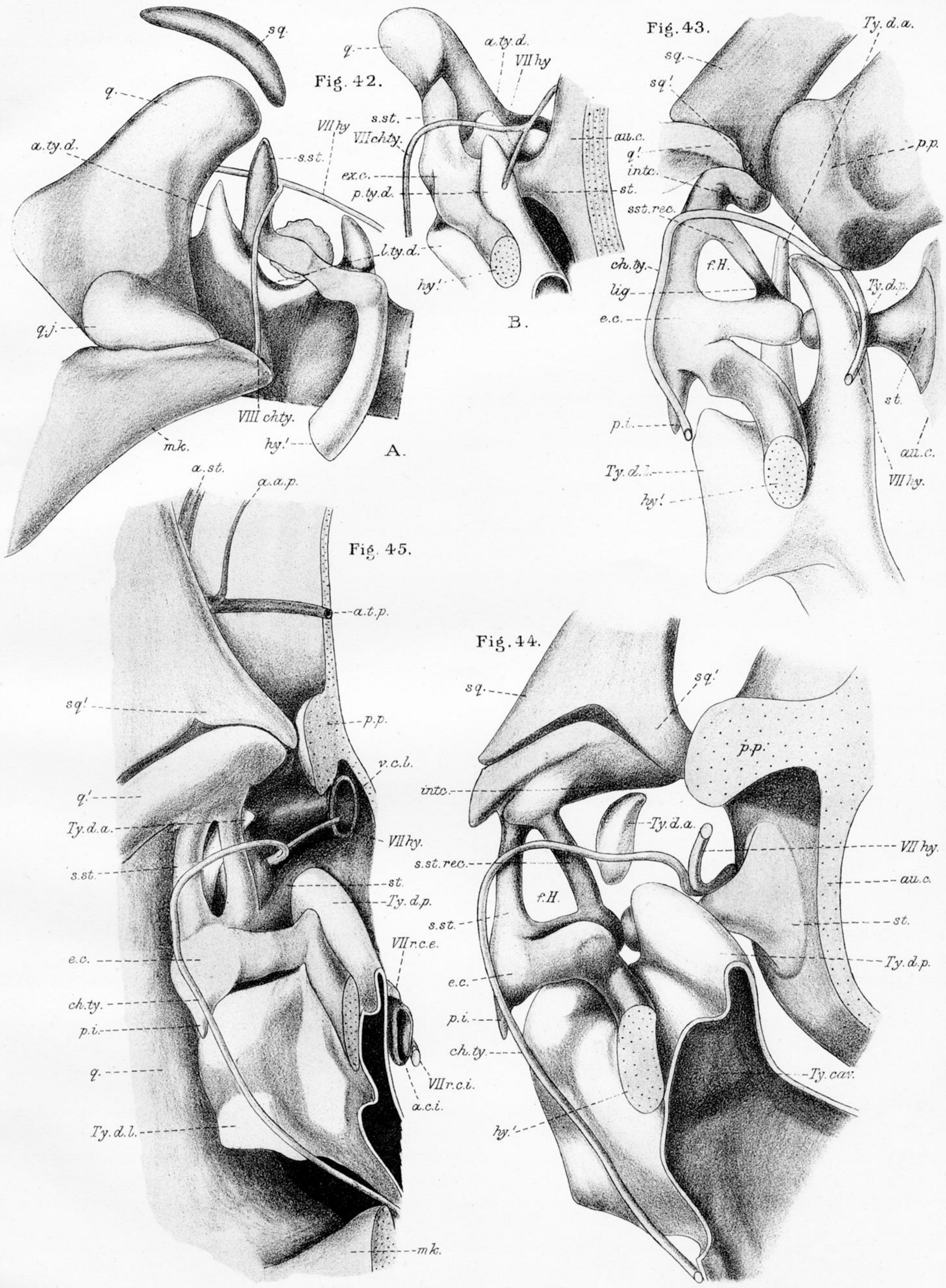


PLATE 17.

Stage Q.

Fig. 42.—Embryo 52a. Model of the developing tympanic diverticula, auditory cartilages (extra-stapedial, supra-stapedial, etc.), chorda tympani, and their relationship to the quadrate and hyoid ( $\times 50$ ). (A) Lateral view. (B) Posterior view.

Stage R.

Fig. 43.—Embryo 141. Model of left tympanic region, including the stapedial cartilages, and chorda tympani (blood-vessels omitted) ( $\times 33$ ). Lateral view.

Stage S.

Fig. 44.—Embryo 9a. Model of left tympanic region (blood-vessels omitted) ( $\times 33$ ). Lateral view.

Fig. 45.—Embryo 9a. The same seen from a position slightly posterior to that of Fig. 57. Principal blood-vessels and nerves shown ( $\times 33$ ).