XX. *On the Development of the Ossicula auditus in the Higher Mammalia.*

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INTRODUCTION.

SINCE the discovery by MECKEL of the cartilage which bears his name and the subsequent discovery by RATHKE of the cartilaginous rods immediately succeeding it, anatomists and embryologists have not failed to be intensely interested in the elucidation of their history. HUSCHKE was the first to limit the origin of the ossicula to the cartilages of the first two post-oral arches, but it is to REICHERT that the first full and masterly description of these two cartilages is due. Looking at the wide-spread existence of these two rods in all classes of the Vertebrata, and the differentiation taking place at their proximal extremities, which may result either in the formation of a suspensory apparatus, or in one which, changing its function, is subordinated to the organ of hearing, it can scarcely be wondered at that the opinions concerning the homology of the differentiated parts should be various and conflicting. Nor can it be otherwise, seeing that as yet there is no general agreement as to what parts are or are not derived from or connected with the upper extremities of these two cartilages in any one class of the Vertebrata. This portion of my work refers only to the Mammalia, but I hope soon to complete my observations upon the remaining classes of the Vertebrata.

Before passing to the description of my own work I shall give a brief summary of the various views that have been advanced respecting the origin of the ossicula auditus.

HISTORICAL.

MECKEL (1) described the cartilage of the first post-oral arch as a mere process of the malleus, but did not further refer to the origin of the ossicula. RATHKE and VALENTIN (2) describe the ossicula as having their origin in two nodules of cartilage which made their appearance in the tympanic cavity; one, the earlier and larger of the two, formed the elements of the incus, malleus, and MECKEL's process; while the other, which appeared later, formed the stapes.

HUSCHKE (3) describes the malleus as arising from the cartilage of the first post-oral arch, the incus from the cartilage of the second, while the two cartilages united at their proximal extremities to form the stapes.

BURDACH (4), while accepting with some doubts the last-mentioned origin for the malleus and incus, thought the stapes ought to be considered as a bud from the wall of the labyrinth.

REICHERT (5) divides the first post-oral cartilage into three portions, the posterior of which connected the cartilage to the cranial vertebræ, and did not undergo any further change, but finally disappeared; the median division formed the incus with its processes; the anterior, the malleus, and MECKEL's process.

The second post-oral cartilage was at first connected to the base of the cranium in the region of the post-sphenoid; this part, however, soon disappeared, and the remainder of the cartilage formed in succession the stapes, stapedius muscle, eminentia pyramidalis, styloid process, stylo-hyoid ligament (generally), and lesser cornu of the hyoid bone.

GÜNTHER (6) while in the main accepting REICHERT's views respecting the cartilage of the first arch, considered his description of the second, so far as it referred to the stapes, to be untenable. He described the origin of the stapes as follows: from the median of the three divisions of the first post-oral cartilage a nodule arose which applied itself to the wall of the labyrinth; formed a depression there—the future fenestra ovalis; this nodule, by the growth of the parts, chiefly the cochlear part of the labyrinth, became more remote from its place of origin, and formed a process, which process becoming bent on itself, formed a horizontal part—the stapes, and a vertical part—the long crus of the incus; this division formed also the incus with its processes. Malleus, incus, and stapes were thus derivatives of the first post-oral cartilage.

MAGITOT et ROBIN (7) describe the malleus as arising from the intra-tympanic portion of the Meckelian cartilage. The incus and stapes they consider to arise independently, but in what manner they do not make clear; they mention that the stapes is a perforated and not a solid ball of cartilage at its first appearance, as had been described by REICHERT. BRUCH (8) describes the mandibular cartilage, with the malleus and the incus, as forming one continuous strip of cartilage; but he also mentions that he has seen the malleus and incus take their origin in a special cartilage which soon united with the mandibular one.

The stapes appears at the upper end of the hyoidean cartilage as a somewhat square-shaped cartilage, whether continuous with it or not he does not state; it is the latest of the ossicula to appear.

HUXLEY (9) in his earlier writings accepted the views advocated by REICHERT, but at a later period he has advanced views of his own based upon comparative anatomical work, and more especially on the condition of parts found in "sphenodon punctatum." He describes the malleus as forming the proximal extremity of the mandibular cartilage. He divides the hyoidean into a part above and a part below the stapes; the former becomes the incus or supra-stapedial, which is connected by a distinct ossification—the orbicular bone—to the stapes; the latter becomes the infra-stapedial or stylo-hyal of the Mammalia, which may be connected to the supra-stapedial either by means of the stapedius muscle, which passes to the orbicular bone, or by means of a ligament which passes to the short crus of the incus.

He mentions also that in many Fishes and Amphibia the proximal ends of the two cartilages are united into a single plate.

PARKER (10) describes the malleus also as the proximal end of the mandibular cartilage, the apex of which grows downwards over the first visceral cleft and forms the manubrium mallei, the shoulder of the bend forming the head with its articular surface; the hyoidean cartilage undergoes segmentation; the upper part becomes the incus, the apex of the bar growing downwards forms an attachment by its capitulum (which becomes the orbicular bone) with the stapes; the shoulder of the bend becomes the body and articular surface of the incus, which unites with the corresponding part of the mandibular cartilage. From the shoulder or bend a little boss grows backwards which becomes the short process of the incus. The rest of the cartilage is carried backwards and downwards, but is connected to the previously described part by a ligament, the inter-hyal, in which a nodule of cartilage appears, one end of which becomes attached to the head of the stapes, the other is buried in the substance of the stapedius muscle. The head of that part of the cartilage carried downwards is bifurcated; the outer division becomes attached to the tegmen tympani, the inner to the ear sac immediately in front of the exit of the cranial nerve. The stapes is derived from the median of three projections, which appear on the external surface of the wall of the labyrinth; it frees itself from the wall, leaving a gap, the future fenestra ovalis, which is closed by the separated nodule; externally, the nodule is covered by delicate indifferent tissue ready to become cartilage, and union takes place between it and the orbicular apex of the hyoidean rod.

SEMMER (11) corroborates REICHERT'S conclusions respecting the origin of the malleus and incus. He describes the stapes as appearing in the form of an oval group of cells situated immediately behind and above the proximal end of the stylo-hyal and only indistinctly separate from it.

It is, however, clearly separated from the long crus of the incus by the upper wall of the tympanic sulcus, and by a thick layer of indifferent tissue. It is in all probability developed out of the second visceral arch; but it is impossible to prove that, owing to the second visceral cleft having already disappeared.

HUNT (12) considers them to arise in embryonic connective tissue elements. He does not mention whether they are continuous with any cartilage or not; he cannot accept Mr. PARKER'S views respecting the stapes, but describes it as arising, like the other ossicles, in embryonic connective tissue elements.

GRUBER (13) agrees with PARKER as to the stapes and fenestra ovalis. He does not accept the view that the cartilages give origin to the other ossicles, but considers them to be developed, like the stapes, from the original substance of the head vertebræ.

LÖWE (14) describes all three ossicles as having been at one time continuous; also, as having their origin in a visceral cartilage, but from which cartilage he does not make clear.

KÖLLIKER (15) accepts REICHERT'S conclusions respecting the malleus and incus, but differs from him and from more recent workers respecting the origin of the stapes. He describes the hyoidean cartilage as being at its commencement a thin, elongated rod, stretching from, and continuous with, the cartilaginous petrous bone to the middle line in front, the cartilages of opposite sides failing, however, to meet there. The changes that take place at a later period are that the upper and the lower ends ossify to form the styloid process and the lesser cornu of the hyoid bone, while the connexion between these may be fibrous, cartilaginous, or bony. The origin of the stapes he leaves doubtful, but he denies altogether the contentions of PARKER and GRUBER that it springs from the labyrinth in the cartilaginous condition, as well as those of REICHERT, that it forms a part of the hyoidean cartilage, although the cartilage and the stapes are very close to one another.

SALENSKY'S (16) papers form the last contribution to the working out of this subject in the Mammalia (Pig and Sheep embryoes to which his observations were restricted), and I shall therefore state them in detail. In 2 centim. embryoes the mandibular and hyoidean cartilages are cylindrical in shape and limit the hyomandibular cleft, the one above, the other below. They attach themselves to the ear capsule and their extremities are connected by embryonic tissue. The changes that rapidly take place at the proximal extremity of the mandibular cartilage are, that it thickens and bends downwards, two furrows making their appearance, which divide the extremity into three parts, the posterior of which forms the elements of the body and long crus of the incus, the latter being attached by embryonic tissue to the upper extremity of the hyoidean cartilage. The short crus, later in its appearance, is described as growing backwards from the body. The median thickening forms the malleus, while its down-growing process forms the neck and manubrium. The anterior thickening soon disappears and has no significance. The separation between the posterior and median thickenings is complete in embryoes measuring 2·7 centims. The union between the long crus of the incus and the upper end of the hyoidean cartilage is described as being secondary. The part of the mandibular cartilage which remains after the separation of the incus forms the malleus and MECKEL'S process.

The stapes is described as making its appearance first in embryoes measuring 2·7 centims. At first it forms an accumulation of cells, in the middle of which is seen the cross-section of a vessel which he names the arteria mandibularis. He describes this as a branch of a vessel which is situated dorsally to the facial nerve, and which he calls carotis interna. This I shall show further on to be the primitive jugular vein, and I shall further demonstrate that the arterial branch does not go to the mandible. The stapes is also described as being independent of the cartilages of the two first post-oral arches and of the periotic capsule.

These various and conflicting opinions may be reduced to order as follows :—All observers are agreed that the malleus has its origin in the mandibular cartilage ; that the incus is either the proximal extremity of the mandibular cartilage or the proximal extremity of the hyoidean cartilage ; that the stapes has its origin in the mandibular or the hyoidean cartilage, or is a bud from the periotic capsule, or built independently round a small artery.

PERSONAL WORK.

METHODS OF PREPARATION, AND GENERAL STATEMENTS.

The embryoes were prepared after the manner of KLEINENBERG ; that is, they were placed in his solution of picric acid for periods varying from five to forty-eight hours according to size. They were then placed in 50 per cent. alcohol for twenty-four hours, then in 75 per cent. for a similar period, and finally in absolute alcohol ; stained in his solution of hæmotoxylin, placed again in absolute alcohol, then in bergamot oil ; embedded in a mixture of spermaceti and castor oil, cut, cleared in a mixture of creosote and turpentine, and finally mounted in Canada balsam. The embryoes were measured by placing their most projecting parts (mid brain and curve of tail) between the limbs of a compass, and the length read off on a centimetre scale.

The work was intended primarily to settle the relation of the incus to the cartilages of the mandibular and hyoidean arches, and the relation of the stapes to the hyoidean cartilage and the periotic capsule.

It has been done upon embryoes of the following Mammals.

Rat embryoes.—The earliest under 8 millims ; then at 8 millims., 1 centim., 1·3 centim., 2 centims., 2·2 centims., 2·5 centims., 3·5 centims., 4 centims., and at the last stage just before birth.

Pig embryoes.—1 centim., 1·5 centim., 2 centims., 2·3 centims., and at 2·6 centims.

Dog embryoes.—1 centim., 1·3 centim., and at 2·5 centims.

Sheep embryoes.—For a series of these I have to thank Dr. ALLEN THOMSON. 1 centim., 1·4 centim., 1·6 centim., 2 centims., and at 4 centims.

Rabbit embryoes.—1 centim., and at 1·5 centim.

Human embryoes.—1 centim., fully, and at 4 centims. The head and body of the last embryo measured about the length stated.

In addition to these I have made observations upon the embryoes of the Mouse and Calf, but these were not complete.

In the embryoes, and at the stages mentioned above, I have made complete series of sections (in many cases several complete series), in the long vertical (the plane being either parallel to the middle line of the head or along the obliquity of the post-oral arches, in order to cut their cartilages along their whole length), transverse vertical (with reference to the ossicula), and obliquely transverse approaching the horizontal planes. These were numbered so that I had corresponding sections at different stages for study and comparison. During the course of the work I soon learned that the incus was quite as distinct from both cartilages when they could properly be called so, as it was at birth or at adult age, so that I had to work upon embryoes at a stage preceding the true cartilaginous one, that is, at a stage between that in which there was not the slightest trace of cartilage to be detected, and that in which the cartilages of the arches were sharply and clearly defined, and in which the cartilage cells had acquired the characteristic hyaline appearance. In order that I should have abundance of material for the study of this particular stage, I cut in the long vertical direction the heads of seven embryo Pigs, five Dogs, five Rabbits, four Sheep, seven Rats, and one Human embryo. But here again the difficulty arose that although the cartilages could be roughly distinguished, yet they were not limited by any sharp line of demarcation, but faded gradually away into the adjacent mesoblastic or embryonic tissue, from which they differed only in greater aggregation of round cells; hence it is that there is room for difference of opinion among rival homologists, especially those who, resting their claims solely upon the condition of the embryonic cartilages at this immature stage, fail to recognise the value of a knowledge of their form and relations throughout their entire distribution in the vertebrate series, and of the great importance of the relation of the nerves in determining the true homology of the parts in dispute. As I shall show further on, the value of the mandibular branch of the seventh nerve (chorda tympani) in the solution of this particular question is considerable. In the endeavour to make the embryonic history of these parts clear, I shall first of all describe the parts coming into more or less close connexion with the ossicula auditus, but more in a morphological than in a histological sense; then, secondly, I shall give a description of the proximal extremities of the first two post-oral cartilages, which is in effect a description of the malleus and incus, and compare the embryonic condition of these ossicles with their form in the adult. I shall also give under this heading a separate description of the embryonic history and adult condition of the stapes and the artery with which it is connected, and finally, briefly summarise the results which may be drawn from the work.

Description of the Work.

First.—The parts entering into more or less close connexion with the ossicula are the gasserian ganglion and maxillary and mandibular branches of the fifth nerve, the ganglion, trunk, and mandibular (chorda tympani) branch of the facial nerve, the primitive jugular vein, the hyomandibular cleft, the meatus auditorius externus, the auditory vesicle and its capsule, the dorsal aorta, and its branch passing towards the stapes, and lastly the tympanic annulus.

The gasserian ganglion is situated dorsad of the cleft of the mouth, over which its maxillary and mandibular branches are placed. In the earliest embryoes figured (Plate 54, fig. 1; and Plate 55, fig. 11) the nerves and ganglia are of large relative size, in the older ones they are less conspicuous.

The mandibular branch of the fifth divides into two parts which come into close relation with the cartilage of the arch a little distance in front of its proximal extremity, one part runs internal to the cartilage and is joined by the mandibular branch of the seventh, the other passes obliquely external to the cartilage (Plate 54, figs. 1, 4, 5 ; Plate 55, fig. 11 ; and Plate 58, fig. 39). The ganglion of the seventh is situated posterior to and near the ventral border of the gasserian ganglion, compared with which it is very small (Plate 54, fig. 6 ; Plate 55, fig. 12 ; Plate 56, figs. 22, 24, 26 ; and Plate 58, fig. 39). The trunk of the nerve at first runs in an antero-posterior direction, lying with the primitive jugular vein, between the canal portion of the labyrinth and the dorsal and external portion of the hyomandibular cleft (Plate 54, fig. 6 ; Plate 55, figs. 11, 12 ; and Plate 56, fig. 24). At the level of the lower border of the periotic capsule it turns almost at right angles to its former direction, turning round and passing external to the hyoidean cartilage on its way to the face.

Where the above change in the direction of the axis of the trunk takes place the mandibular or chorda tympani branch is given off; in older embryoes this branch passes off the trunk of the nerve after it emerges from under the cover of the periotic process (a process given off from the periotic capsule to join the hyoidean cartilage); it is of large size in very young embryoes (Plate 54, fig. 1 ; and Plate 55, fig. 11), and passes between the hypoblast and epiblast forming the closed dorsal and external portion of the hyomandibular cleft, then runs in a ventral direction and joins the internal branch of the mandibular division of the fifth nerve. In older embryoes it comes into relation with the cartilages of the first two post-oral arches passing external to the hyoidean, internal to the proximal extremity of the mandibular (Plate 54, figs. 4, 5, 8 ; Plate 55, figs. 10, 16 ; Plate 56, figs. 19, 21, 25 ; and Plate 58, figs. 39, 40).

This relation to the cartilages is common to the embryoes of the human subject and the lower animals; but while in the embryoes of the lower animals the nerve never comes into relation with the incus; in the human embryo it has the same relation to the long crus (Plate 55, fig. 16) as to the hyoidean cartilage. This relation, if not secondary or acquired, points suggestively to the origin of the incus. The mandibular branch and the trunk of the seventh have been described as being homologous to the maxillary and mandibular branches of the fifth, but the mandibular branch of the seventh differs from the maxillary division of the fifth in not being ganglionic at its origin and in joining the mandibular division of that nerve.

In sections of embryoes before birth the trunk of the seventh has acquired its characteristic adult course (Plate 58, fig. 36); that is to say, the anterior portion of the trunk is pushed in a ventral direction by the growth chiefly of the cochlear part of the labyrinth.

The primitive jugular vein in the earliest embryoes is of very large size, being the most conspicuous feature in the sections. It returns the blood from the entire head. It lies dorsad of the gasserian ganglion and seventh nerve, ventrad of the periotic capsule, and then passes backwards towards the heart (Plate 54, figs. 3–6; Plate 55, figs. 17, 18; Plate 56, figs. 20, 22, 24; and Plate 58, fig. 39). This is the vein that SALENSKY names arteria carotis interna. It has the same relations as the cardinal vein in the Chick's head. When the ossicula begin to develope it commences to disappear, and is soon replaced by the internal and external jugular veins.

In the earliest condition of the hyomandibular cleft in the dorsal region, the hypoblast lining approaches and touches the external epiblast. I feel convinced that this cleft never actually forms a perforation in this region (region of membrana tympani), although it is perforated ventrad of this. Should the above supposition be correct, the formation of the membrana tympani would be very easy to understand; the hypoblast lining forming the mucous lining of the adult membrane, the epiblast the cuticular covering, while the fibrous layer is derived from the ingrowth of mesoblast, which along with the proximal extremity of the mandibular cartilage separates these two layers from each other (Plate 55, fig. 18; Plate 56, figs. 23, 26; and Plate 57, fig. 29). In the oldest embryoes the manubrium mallei occupies the entire space between the dorsal part of the cleft and the bottom of the meatus auditorius externus (Plate 55, fig. 13; and Plate 57, fig. 31).

HIS (17) has recently raised doubts as to the correctness of the usually accepted statements first advanced by RATHKE and HUSCHKE regarding the open condition of the clefts. These authors passed bristles from the external surface through the clefts, and as they appeared in the cavity of the pharynx, they concluded that the clefts were open. HIS, on the contrary, states that the bristles were passed through the delicate epiblast and hypoblast, which come into close contact with each other. He does not press his observations, but leaves them as matter for future determination.

The dorsal and external part of the cleft, following MOLDENHAÜER (18), may be called the sulcus tympanicus, while the ventral and internal portion opening into the pharynx may be termed the tubal portion of the sulcus. This sulcus does not expand until after birth, when the fœtus begins to breathe air; the walls of it, even in the oldest embryoes, being close together, although in some of the figures, owing to the obliquity of the sections, they are a little distance apart (Plate 57, figs. 29, 30, 31, 32, and 34).

There is at first no external auditory meatus; it is formed later on by the growth outwards of the side walls of the head (Plate 55, figs. 17, 18; Plate 56, fig. 23; Plate 57, figs. 29 and 31), leaving a gap leading towards the dorsal part of the hyomandibular cleft (region of membrana tympani). The growth outwards of the wall of the head incloses a median thickening, which contains the ventrally curved extremity of the mandibular cartilage (Plate 55, fig. 18); the dorsal region of this growth becomes bent upon itself, forming a fold of the integument, which unfolding after birth becomes the long dorsally directed pinna of the Rodents (Plate 57, fig. 31).

The auditory vesicle, after it has been shut off from the external epiblast, has an oval form (Plate 54, figs. 2 and 3), and is situated between the hind brain and the external epiblast. Ventrad of the vesicles runs the seventh nerve, the primitive jugular vein and dorsal aorta. The ganglion acusticum and auditory epithelium are very intimately connected, a fact already noticed by BALFOUR and MARSHALL (Plate 54, fig. 2; and Plate 55, fig. 17). The ganglion has two well marked divisions, corresponding to the cochlear and vestibular portions of the nerve (Plate 54, fig. 9; Plate 55, fig. 18; and Plate 56, fig. 23), although in embryoes near the period of birth it is single (Plate 57, fig. 32).

In slightly older embryoes the vesicle has undergone the ordinary Mammalian complications (Plate 55, fig. 17; and Plate 56, figs. 20 and 23); the ventral end of the vesicle passes inwards towards the base of the skull, forming the canalis cochlearis and sacculus hemisphericus; in the hollow of the canal lies the ganglion acusticum; from the dorsal end of the vesicle, on the side nearest the brain cavity, there passes off an elongated diverticulum, the recessus labyrinthi, external to which, and running for some distance parallel with it, lies the superior semicircular canal.

The external semicircular canal passes from the vestibular cavity outwards, dorsad of the seventh nerve and primitive jugular vein towards the epiblast (Plate 55, fig. 17; Plate 56, figs. 20 and 23). The complicated vesicle becomes surrounded by a thickened layer of densely packed cells, which follows the outlines of the several parts of the vesicle, with the exception of the recessus vestibuli. This layer of cells is laid down at the same time as the elementary cartilages in the arches, and the changes by which it is converted into hyaline cartilage go on simultaneously with those occurring in the cells of the cartilages.

The points of interest in connexion with the periotic capsule are that it is deficient on its internal surface, for the ganglion acusticum and its vestibular and cochlear branches; it is also deficient externally, for the fenestra ovalis and fenestra rotunda.

These fenestræ differ in their development in the following manner: in sections from rat embryoes 8 millims. in length, in which the wall surrounding the labyrinth can first be said to be roughly differentiated from the adjacent mesoblast, a gap for neither fenestra exists; but in sections from embryoes 13 millims. in length, while the wall is continuous at the position of the future fenestra ovalis (Plate 57, fig. 27), a well marked deficiency exists for the fenestra rotunda (Plate 57, fig. 28).

The primitive jugular vein and seventh nerve divide the auditory region on an external view into two parts. Ventrad of these structures are the proximal extremities of the first two post-oral cartilages; dorsad of them lies the semicircular canal portion of the labyrinth; this portion of the periotic capsule is roughly circular in outline, but flattened ventrally, and more or less pointed dorsally. Along the anterior and posterior borders run in a dorsal direction the superior and posterior semicircular canals; these turning ventrally unite together, and open by a common aperture into the vestibular portion of the labyrinth; the external semicircular canal lies between the ventral extremities of the last two, and has a direction parallel to the vessel and nerve (Plate 54, fig. 6; Plate 56, figs. 19, 21, and 22; Plate 57, figs. 33 and 34; and Plate 58, fig. 39).

I shall describe the dorsal aorta and the branch passing from it in connexion with the stapes.

The tympanic annulus can first be detected in Rat embryoes 2 centims. in length; it lies within the proximal extremities of the mandibular and hyoidean cartilages, ventrad of the external wall of the sulcus tympanicus, and internal to the bottom of the meatus auditorius externus; it is deficient dorsally, the proximal extremity of the mandibular cartilage appears to bend round and be supported by it (Plate 55, fig. 15). In the oldest Rat embryoes and especially in the young of carnivorous animals at birth (Cat, Dog, Leopard), a membranous splint intrevenes between it and the mandibular cartilage (Plate 57, fig. 34); this, however, soon unites with the periotic, or the annulus.

In the oldest embryoes examined there is no trace of the papery bulla or bony meatus auditorius externus, which are continuous with and lie internal and external to the annulus in the adult (Plate 55, figs. 13, 14, and 16; Plate 57, fig. 31; Plate 58, figs. 35, 37, and 40).

Second.—Embryonic history of the proximal extremities of the first two post-oral cartilages, being in effect a description of the malleus and incus, and a comparison between the embryonic and adult form of these ossicles.

I have never been able to detect, notwithstanding the large number of embryo heads which I cut for the study of the earliest condition of the cartilages, a stage in which these could be described as being straight.

There was always a slight bending of the proximal extremities of both cartilages, that of the mandibular depressing the dorsal wall of the meatus auditorius externus towards the ventral, and forming the elements of the neck and manubrium of the malleus, while that of the hyoidean had its concavity directed towards the mandibular, to which it closely applied itself. The proximal extremity of this cartilage forms the head of the incus, the long crus in the majority of embryoes, those of the Pig especially, being continuous with the rest of the cartilage (Plate 54, fig. 5), but in some Dog and Rabbit embryoes there was a slight gap between the long crus and the remainder of the cartilage (Plate 54, fig. 4); passing dorsally from the head of the incus is a short process (slightly exaggerated in Plate 54, fig. 5) which eventually becomes the short crus of the incus.

The long crus has at this stage no bend inwards towards the stapedial ring (Plate 56, fig. 24). The distal end of the hyoidean cartilage is closely connected to the cartilage of the first branchial arch (thyro-hyal), so much so that if microscopic sectional appearances were alone to be considered they could be described as being continuous.

The drawings do not do justice to the immature condition of these cartilages, there being no sharp limiting lines in nature. In older embryoes there is a striking similarity in the appearance of the cartilages in the different embryoes (at the same developmental stage), Plate 54, figs. 8 and 9; and Plate 55, fig. 10, for the Pig; Plate 55, fig. 18; and Plate 56, fig. 19, for the Sheep; Plate 56, fig. 21, for the Dog; and Plate 56, figs. 25 and 26; and Plate 57, fig. 27, for the Rat. In the entire series the several parts of the malleus and incus can be readily distinguished; the apex of the long crus of the incus has but a slight turn inwards towards the stapedial ring (Plate 54, figs. 7 and 9; Plate 55, fig. 18; and Plate 57, fig. 27), and it is separated from the remainder of the cartilage (which joins the periotic process of the periotic capsule) by a slight interval, but it agrees with the cartilage both in its form and general direction in a very marked manner. It also, and this is equally important, agrees with the hyoidean cartilage in every histological particular; it takes up the colouring matter in the same way, and its cells assume the hyaline character at the same period of time—those of the mandibular cartilage having undergone that change at an earlier date.

The seventh nerve and its chorda tympani, or mandibular branch, have the relations to the cartilages already described. In still older embryoes (Plate 55, figs. 13, 14, 15, and 16, for Human embryo; Plate 57, figs. 29, 30, 31, 32, 33, 34; and Plate 58, figs. 35, 36, 37, 38, for the Rat) the individual parts of the adult ossicula are fully developed. The joint between the malleus and incus is now for the first time clearly evident, and its V-shape is worthy of notice (Plate 58, fig. 36). The manubrium is large, and of the same shape as in the adult; it occupies the entire space between the sulcus tympanicus and the meatus auditorius externus (Plate 55, fig. 13; and Plate 57, fig. 31); at its junction with the neck is a well marked process, which I have called posterior (DORAN'S (19) orbicular process or apophysis—a bad name, because of the orbicular apophysis of the incus). The processus muscularis of HYRTL and the tensor tympani muscle are well developed.

The cartilages of the Human embryo are very massive (Plate 55, figs. 15 and 16), but have otherwise much the same shape as those of other animals.

On comparing these embryonic parts with those of the adult malleus and incus (Plate 58, fig. 40), the derivation of these can be understood at a glance. The head of the malleus in the adult Rat articulates with the incus, and from it pass two bony processes of considerable size—one has a direction forwards, and soon tapers to a point; this may be called the mandibular process, because it is ossified from the cartilage (DORAN (19) calls it process head of malleus); the other, with a direction downwards, is the neck. From the lower part of this passes in a forward, downward, and inward direction, a long sabre-shaped process, with its edges looking inwards and outwards, the manubrium mallei. At the lower part of the neck on its internal surface, is the processus muscularis of HYRTL; while at the junction of the neck with the manubrium are three other processes, one of which looking backwards is very constant and called posterior, another looks outwards, like the processus brevis of the Human malleus, and the third looks forwards. Passing from this last to the tapering point of the mandibular process, is the free edge of a papery lamina of bone, the extent of which depends chiefly on the length of the neck; it bears the same relation to the mandibular cartilage that the papery bulla does to the tympanic annulus, and it developes mainly after the fœtus has begun to breathe air, when the tympanic cavity expands. The processus gracilis of the adult Human malleus must be formed by the atrophy of the mandibular cartilage along the dotted line in Plate 55, fig. 15, the head and short neck of the Human malleus corresponding to the entire thickness of the cartilage, the lower margin of which persists as the processus gracilis. A study of the plates illustrating DORAN's (19) paper, which show the various forms of mallei throughout the Mammalian orders, will make clear at once the morphological significance of the mandibular process, which is the true remnant in the adult of the mandibular cartilage of the embryo; the whole thickness of the cartilage may ossify, as in the Rat (Plate 58, fig. 40), or its lower margin only, as in the Human embryo, while there may be all grades of persistence in the thickness of the ossified cartilage between these two extremes. The adult incus (Plate 58, fig. 40) corresponds in every particular save one with its appearance in the embryo. When looked at from the outside, the body and the two crura are at once recognised; the short crus is but little, if at all, inferior in size to the long crus; the latter stands over the upper end of the ossified hyoidean cartilage (tympano-hyal of FLOWER), seen better after the removal of the bulla. The seventh nerve lies behind the tympano-hyal and the bulla; its mandibular branch passes external to the first-named, and is found with the greatest difficulty in the adult, as also in fine sections of the older embryoes, the nerves being less conspicuous because of the development of the surrounding parts. It is on looking at the incus from the anterior view that the only difference is seen to exist between its embryonic and adult form. In the adult (Plate 58, fig. 40, B) the orbicular apophysis has a pedicular attachment to the apex of the long crus on its internal surface. In the older embryoes the distal extremity of the long crus of the incus is flexed inwards, but has not any trace of the characteristic adult constriction. The orbicular apophysis cannot therefore be longer spoken of as a bone distinct from the long crus of the incus before or after birth, but is simply a small portion of the long crus separated by constriction from, and assuming a direction at right angles to it, accommodating itself in this way to the stapes.

Embryonic history and adult condition of the stapes, together with the artery in connexion with it.

This ossiculum appears contemporaneously with the cartilages in the arches and the cartilage surrounding the labyrinth; it lies dorsad of the sulcus tympanicus, ventrad of the seventh nerve and primitive jugular vein, external to the unperforated wall of the labyrinth with which at first it is not even in contact, and internal to the long crus of the incus (Plate 54, figs. 6, 7; Plate 55, figs. 12, 18; and Plate 56, fig. 24), with which it is much more closely connected, although from the different direction of its cells it cannot be described as being actually continuous with the hyoidean cartilage; it has the form of a circular ring of cells of uniform thickness. Through the centre of the ring passes a vessel (Plate 54, figs. 2, 6, 7, 9; Plate 55, figs. 12, 18; Plate 56, figs. 22, 23, 24; Plate 57, fig. 27; and Plate 58, figs. 35, 36), which has never yet been described in the embryonic condition nor its value recognised in the formation of this ossiculum. True, SALENSKY has seen the vessel, but he describes it as being a branch of a vessel which he calls carotis interna, but which I have shown to be the primitive jugular or anterior cardinal vein. He also mentions that it ends in the mandibular arch. OTTO (20) was the first to describe and figure this artery in the adult. He found it in the hybernating animals and imagined that some connexion existed between the course pursued by this vessel and the peculiar function of hybernation. HYRTL (21) described it (at first unaware of OTTO's previous observations) in the Cheiroptera, Insectivora, the genus Lemur, and many Rodents. He named it the "Steigbügelarterie"; he found that it supplied part of the brain, the orbit and its contents, and the whole of the superior maxilla; he described also the homologue of this vessel in Man, which might have one of three sources—(*a*) the accessory middle meningeal, pursuing an unusual course; (*b*) the stylo-mastoid artery; or (*c*) a small branch from the anastomosis formed usually between the stylo-mastoid and vidian arteries. It has also been described by MECKEL (22) in the Hedgehog and Dormouse, but called by him carotis interna, although doubtless it was this same vessel. This artery may be either free between the crura so that in the macerated skull no trace of it is left, or it may be surrounded by a bony canal which may have osseous union to one of the crura, so that a vertical bolt may occupy the space between the crura. This has been figured and named the pessulus by CARLISLE (23) in the Marmot and Guinea Pig. He considered that the function of the pessulus was to prevent the stapes from falling into the vestibule.

In the Mammalian embryoes from which my sections have been made, there are two forms of this artery, one which disappears very early represented by the embryoes of the Pig, Dog, Sheep, Calf, and Human subject; the other which persists throughout life as in the embryoes of the Rat—the former may be called arteria stapedialis, the latter arteria stapedio-maxillaris, a name already applied to it by HYRTL in the adult. In embryoes of the Rat the artery has the following course (Plate 56, figs. 22 and 24):—The carotis communis, when it approaches the ventral part of the cartilaginous wall of the cochlea, divides into two branches, one considerably in front of the other, passes internal to the cochlear wall on its way to the brain cavity, and corresponds to carotis interna; the other passes external to the wall of the cochlea, dorsad of and slightly internal to the sulcus tympanicus, through the embryonic ring of the stapes, threading it, as it were, then passes ventrad of the seventh nerve, external to its ganglion, internal to the mandibular division of the fifth nerve, then comes into relation with its maxillary division, and runs underneath this nerve in the whole of its extent until it terminates in branches to the face. During this course it gives off several small branches, which pass in various directions, one of which, however, passes into the mandibular arch. The artery in the embryoes of the Pig, which may be taken to represent those in which it early disappears, has the same course from the carotis communis through the ring of the stapes upwards as far as the ganglion of the seventh nerve, where it divides into two small branches (Plate 54, fig. 6), which pass external to the gasserian ganglion, and beyond which I have failed to trace them. In the adult Rat it is a large and important artery and has the following course:—The carotis communis is a long straight artery, and runs from the aorta to the upper part of the air tube; it there divides into two branches, the external of which passes up over the outer surface of the mandible, forming the arteria facialis; the internal is a short vessel, which soon divides into two branches, the internal of which passes between the anterior Eustachian thickened portion of the bulla and the basisphenoid on its way to the brain cavity, and corresponds to carotis interna; the external and larger of the two branches passes through a foramen formed in the line of articulation between the hinder part of the bulla and the petrosal into the tympanic cavity, then passes up in front of the fenestra rotunda, grooving the cochlear wall, between the crura of the stapes, over the cerebral surface of the bulla, through a foramen in the alisphenoid, then runs under the maxillary division of the fifth nerve in the whole of its length until it terminates in branches to the face, corresponding, in the latter part of its course, to the infra-orbital artery in the human subject. This artery, then, plays a very important part in the formation of this perforated ossiculum; in truth, it bears the same relation to the stapes that the embryonic vertebral artery does to the cartilaginous transverse processes of the cervical vertebræ, or that any artery bears to a cartilaginous mass through which it has to pass, that is, it leaves a foramen. Hence it is a fair deduction that in all Mammalia possessed of a perforated stapes this artery exists always in embryonic and occasionally in adult life. It has some particular relation to RATHKE'S arches, which I have not as yet thoroughly worked out. I had thought at first that it was the artery to the hyoidean arch, in which case it would have afforded strong presumptive evidence in favour of the stapes being a part of the cartilage of this arch; but the careful tracing of the artery in the embryo Rat and its distribution to the maxillary arch made me forego the idea.

In older embryoes the stapes approaches and appears to indent the periotic wall (Plate 54, fig. 9; and Plate 57, fig. 27), the cellular ring being as yet uniform in its dimensions. In Rat embryoes 2 centims. in length the ring has lost its uniform character, the basal portion being much larger than that which comes into relation with the long crus of the incus; it is also in a line with the cartilaginous wall of the labyrinth, with which it appears to be almost continuous (Plate 57, fig. 30); it is separated from the vestibular portion of the membranous labyrinth by the remains of its primitive wall. The stapes in embryoes before birth has assumed somewhat of the appearance and proportions of the adult stapes—it has a well-marked head, two crura and a base, which is still separated from the membranous labyrinth (vestibular portion) by connective tissue (Plate 58, fig. 37); there is also a well-marked articulation between its head and the long crus of the incus, similar to what exists between the malleus and incus; the wall of the cochlea ventrad of the stapes is circular in outline and bulges externally, so that the stapes appears to be buried in the wall (Plate 57, fig. 32; and Plate 58, fig. 35).

On examining the stapes of the adult Rat with the lens it is found to bear a very close resemblance to the form of the human stapes, differing only in point of size (Plate 58, fig. 40, A).

It has a well-marked head, at the junction of which with the posterior crus is a slight tubercle for the attachment of the stapedius muscle. Of the two crura the anterior descends from the head to the base almost vertically, the posterior being the more curved; the base projects beyond the crura and it is wider, the head, crura, and base are fluted internally so that the adult stapes is the merest outside form or semblance of bone, a change which takes place after birth.

The stapedius muscle agrees in its development with the tensor tympani muscle, or with any other in the region of the head. The tubercle on the posterior crus has the same relation to this muscle that the processus muscularis of HYRTL has to the tensor tympani (the muscle is seen in Plate 57, fig. 34; and Plate 58, figs. 37, 38); it lies some distance internal to the hyoidean cartilage, from which it is separated by the seventh nerve. The nucleus in its tendon, named inter-hyal by Professor PARKER, is not present in any of the embryoes from which my sections have been made; moreover, it cannot have any relation to the hyoidean cartilage, or it would agree with it in its developmental history. When the nucleus in the tendon of this muscle is present it may be looked upon as comparable to the nuclei found in the tendons of other muscles.

Summary and Results.

Summarizing this work the following conclusions can with safety be drawn.

First.—That the malleus is the proximal extremity of the mandibular cartilage, and that its manubrium is the last part to be developed.

Second.—That the incus is the proximal extremity of the hyoidean cartilage. That this is determined not only by continuity of embryonic cartilage (which is not always present) and its morphological and histological agreement with the remainder of the cartilage, but also by the relation which the chorda tympani nerve (mandibular branch of the seventh) bears to its long crus. That its orbicular apophysis is the last to develope; its pedicular form of attachment appearing after birth.

Third.—That the stapes is developed as a circular ring of cells round the artery which has been described. That its connexion with the hyoidean cartilage is at first more close than with the periotic capsule; that of its individual parts the head and margins of the base are the last to appear, and that the fluted condition of the head, crura, and base is developed after birth.

In conclusion, I have to express my warmest acknowledgments to my former teacher, Dr. Allen Thomson, but for whom this paper could not possibly have been in its present form. I am also much indebted to Professor Parker for information concerning the form and modifications of the two cartilages in the lower Vertebrates.

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Explanation of the Figures.

All the figures were drawn (with the exception of the last two) with a Zeiss' camera (Oberhäuser) and Hartnack objective. The numbers attached indicate in diameters the magnifying power employed. Some of the drawings are from single sections, but the majority have been made by combining consecutive sections.

The outlines in such cases were generally drawn from a single section, and are strictly accurate. The details were filled in from the appearances seen with a Zeiss Obj. A, Ocul. 2 × 55, or with Obj. D, Ocul. 2 × 235.

They have been restricted to those essential to the work in hand.

Alphabetical List of Reference Letters.

au.v. Auditory vesicle.
a.st. Arteria stapedialis.
ao. Aorta.
a.st.m. Arteria stapedio-maxillaris.
a.c.c. Arteria carotis communis.
a.c.i. Arteria carotis interna.
a.v. Arteria vertebralis.
art.i.st. Articulation between incus and stapes.
art.b.p. Articulation between bulla and petrosal.
B. Bulla.
Br[1]. First branchial arch.
Br[2]. Second branchial arch.
b.cr. Basis cranii.
ch.t. Chorda tympani.
ch. Chorda dorsalis.
c.co. Canalis cochlearis.
c.he. Cerebral hemispheres.
ce. Cerebellum.
e.s.ca. External semicircular canal.
f.br. Fore brain.
f.l. Fore limb.
fe.r. Fenestra rotunda.
G.ga. Ganglion gasserii.
g.v.ac. Vestibular portion of ganglion acusticum.
g.c.ac. Cochlear portion of ganglion acusticum.
h.br. Hind brain.
hy.c. Hyoidean cartilage.
Hy. Hyoid arch.
H. Heart.
in. Incus.
in.m. Investing mass.
la. Lamina of papery bone between mandibular process of malleus and tubercle at the junction of the neck with the manubrium (the free edge of which is called by Doran processus gracilis).
m.au.e. Meatus auditorius externus.
mn.c. Mandibular cartilage.
mn. Mandible.
m. Malleus.
ma.h. Head of malleus.
ma.n. Neck of malleus.
m.ma. Manubrium mallei.
m.obl. Medulla oblongata.

m.br. Mid brain.
Mx. Maxillary arch.
Mn. Mandibular arch.
mn.pr. Mandibular process.
op. Optic.
olf.p. Olfactory pit.
oc.c. Occipital cartilage.
or.ap. Orbicular apophysis of the incus.
olf.n. Olfactory nerve.
pe.c. Periotic capsule.
p.s.ca. Posterior semicircular canal.
pe.pr. Periotic process.
p.v.au. Vestibular portion of auditory nerve.
p.c.au. Cochlear portion of auditory nerve.
p.pr. Posterior process.
pe. Periotic.
p.eust. Eustachian portion of bulla.
pt.i. Pterygoideus internus.
pt.c. Pterygoid cartilage.
r.v. Recessus vestibuli.
r.ce. Recessus cerebelli.
s.ty. Sulcus tympanicus.
s.s.ca. Superior semicircular canal.
st. Stapes.
s.hem. Sacculus hemisphericus.
st.a.c. Anterior crus of stapes.
st.m. Stapedius muscle.
s.p.s.ca. United portion of superior and posterior semicircular canals.
th.hy.c. Thyro-hyoid cartilage (cartilage of first branchial arch).
t.ty. Tensor tympani.
ty.a. Tympanic annulus.
th.c. Thyroid cartilage.
t.p. Tubal portion of sulcus tubo-tympanicus.
tub. Tubercle on posterior crus of stapes for stapedius muscle.
th. Vesicle of the third ventricle.
v.j.pv. Vena jugularis primitiva.
v.j. Vena jugularis.
v.c. Vertebra cervicalis.
ve. Vestibule.
v.j.ex. Vena jugularis externa.
V^1. Ophthalmic branch of fifth nerve.
V^2. Maxillary branch of the fifth.
V^3.*ib.* Mandibular branch of fifth (internal division).
V^3.*e.b.* Mandibular branch of fifth (external division).
VII. Seventh (nervus facialis).
VIII. Auditory.
IX. Glossopharyngeal.
X. Pneumogastric.
XI. Spinal accessory.
XII. Hypoglossal.

Forty Figures in all: Of these there are 11 in Pig embryoes, 6 in the Human embryo, 3 in the Sheep, 2 in the Dog, and 18 in the Rat.

PLATE 54.

Figs. 1–3. Sections through Pig embryoes 1 centim. in length × 25.

Fig. 1. Longitudinal vertical section, showing gasserian ganglion, maxillary and mandibular branches of the fifth, the latter dividing into two; the seventh nerve, with its mandibular (chorda tympani) branch joining the inner of the two branches of the mandibular division of the fifth.

Fig. 2. Longitudinal vertical section, showing auditory vesicle, ganglion acusticum, dorsal aorta with the origin of the arteria stapedialis. Both figures have been cut along the obliquity of the arches.

Fig. 3. Transverse vertical section, showing the auditory vesicle, primitive jugular vein, facial nerve, and dorsal aortæ; the section is very oblique, shows on one side the open cleft.

Figs. 4–7. Sections through Pig embryoes 1·4 centim. in length × 25.

In the first three figures the sections are made along the obliquity of the arches. In all the figures a large number of consecutive sections have been used to fill in the outlines of the cartilages and periotic capsule.

Fig. 4. Longitudinal vertical section, showing eye, nose, mouth, cartilages of mandibular and hyoidean arches, mandibular branch of the fifth, with its outer and inner divisions, facial nerve with its mandibular (chorda tympani) branch, and meatus auditorius externus.

Fig. 5. Longitudinal vertical section much the same as preceding, but hyoidean cartilage continuous throughout its entire length, short crus of incus commencing to be formed, although too strongly indicated in the diagram.

Fig. 6. Longitudinal vertical section, showing gasserian ganglion, ganglion of olfactory nerve giving off two sets of branches, standing over nose cleft, ganglion and trunk of facial; stapes and stapedial artery, primitive jugular vein, periotic capsule and semi-circular canals, and junction of hyoidean cartilage with cartilage of first branchial arch (thyro-hyoid).

Fig. 7. Transverse vertical section, showing incus, hyoidean cartilage, stapes, and stapedial artery, periotic capsule, basis cranii,

gasserian ganglion, primitive jugular vein, facial nerve, with its mandibular (chorda tympani) branch, mouth cavity, and sulcus tympanicus.

Figs. 8–9. Sections of Pig embryoes 2 centims. in length × 25.

Fig. 8. A stage later than fig. 5.

Fig. 9. A stage later than fig. 7. Shows in addition the cochlear and vestibular divisions of the ganglion acusticum.

PLATE 55.

Fig. 10. Longitudinal vertical section of Pig embryo 2·6 centims. in length × 25, showing the cartilages of the first two post-oral arches, the periotic capsule with the semicircular canals, and the facial nerve with its mandibular (chorda tympani) branch.

Figs. 11–12. Sections of Human embryo fully 1 centim. in length × 25.

Fig. 11. Longitudinal vertical section, parallel to the middle line of the head, showing maxillary and mandibular branches of the fifth nerve, facial nerve with its mandibular (chorda tympani) branch; outlines of the ganglia of the fifth and seventh; and mandibular and hyoidean cartilages.

Fig. 12. Transverse vertical section showing basis cranii, carotis interna, arteria stapedialis, periotic capsule, stapes, hyoidean cartilage, ganglion and trunk of facial, and ganglion gasserii.

Figs. 13–16. Sections of Human embryo 4 centims. in length × 25.

Fig. 13. Transverse vertical section showing periotic capsule, occipital and hyoidean cartilages, tympanic annulus, sulcus tympanicus, meatus auditorius externus, facial nerve, head, neck (with processus muscularis of HYRTL), and manubrium of the malleus, and tensor tympani muscle.

Fig. 14. Transverse vertical section, through a plane posterior to that of fig. 13, showing head and long crus of the incus, and stapes, no artery (which has disappeared).

Fig. 15. Longitudinal vertical section, showing mandibular and hyoidean cartilages, head, neck, and manubrium of the malleus, incus, tympanic annulus and sulcus tympanicus.

Fig. 16. Longitudinal vertical section, showing part of mandibular cartilage, incus (body and crura), periotic capsule, hyoidean cartilage undergoing segmentation, facial nerve with chorda tympani (mandibular) branch, manubrium mallei, with processus muscularis and tensor tympani muscle, sulcus tympanicus and tympanic annulus.

Figs. 17–19. Sections of Sheep embryoes × 25.

Fig. 17. Transverse vertical section of embryo 1 centim. in length (a little oblique), showing canalis cochlearis, cochlear division of the ganglion acusticum, recessus vestibuli, superior and external semicircular canals, primitive jugular vein, facial nerve, sulcus tubo-tympanicus and arteria stapedialis.

Fig. 18. Obliquely transverse vertical section of embryo 1·4 centim. in length, showing cochlear and vestibular divisions of ganglion acusticum, periotic capsule, primitive jugular vein, facial nerve, stapes, arteria stapedialis, long crus of incus, sulcus tubo-tympanicus, neck of malleus, chorda tympani (mandibular branch of seventh) and hyoidean cartilage.

PLATE 56.

Fig. 19. Longitudinal vertical section of embryo 2 centims. in length, showing cartilages of mandibular and hyoidean arches. Periotic capsule and semicircular canals, facial nerve with its chorda tympani branch and meatus auditorius externus.

Figs. 20–21. Sections of Dog embryoes × 25.

Fig. 20. Obliquely transverse vertical section of embryo 1·3 centim. in length, showing hind brain, canalis cochlearis, sacculus hemisphericus, recessus vestibuli, superior and external semicircular canals, primitive jugular vein, facial nerve, arteria stapedialis, and sulcus tubo-tympanicus. (The cartilage is not represented in this section although it was present.)

Fig. 21. Longitudinal vertical section of embryo 2·5 centims. in length, showing cartilages of mandibular and hyoidean arches, periotic capsule, periotic process, facial nerve with mandibular (chorda tympani) branch, and meatus auditorius externus.

Figs. 22–38. Sections of Rat embryoes × 25.

Figs. 22–24. Sections from embryoes about 9 millims. in length.

Fig. 22. Longitudinal vertical section parallel to middle line of head, showing periotic capsule with semicircular canals, ganglion acusticum, primitive jugular vein, facial nerve with its ganglion, mandibular and hyoidean cartilages, stapes, arteria stapedio-maxillaris, sulcus tympanicus, gasserian ganglion with its maxillary and mandibular branches, eye and olfactory pit.

Fig. 23. Obliquely vertical section showing canalis cochlearis, cochlear and vestibular divisions of ganglion acusticum, recessus vestibuli, superior and external semicircular canals, periotic capsule,

primitive jugular vein, facial nerve, hyoidean cartilage in the whole of its length (partly in outline), mandibular branch of seventh, anterior crus of stapes, part of neck of malleus, basis cranii, sulcus tubo-tympanicus, arteria stapedio-maxillaris, thyro-hyoid cartilage (cartilage of first branchial arch), and thyroid cartilage.

Fig. 24. Nearly horizontal section, showing chorda dorsalis, investing mass, one of the cervical vertebræ, with vertebral artery, arteria carotis communis, arteria carotis interna, arteria stapedio-maxillaris, periotic capsule, stapes, incus, hyoidean cartilage, facial nerve, glosso-pharyngeal, pneumogastric, spinal accessory and hypo-glossal nerves, and gasserian ganglion.

Figs. 25–28. Sections from embryoes 1·3 centim. in length.

Fig. 25. Longitudinal vertical section, showing cartilages of mandibular and hyoidean arches, the various parts of malleus and incus, facial nerve with its mandibular (chorda tympani) branch and external auditory meatus.

Fig. 26. Transverse vertical section, showing malleus, sulcus tympanicus, throat cavity, meatus auditorius externus, periotic capsule, arteria carotis interna, gasserian ganglion, ganglion of facial, hyoidean cartilage, and basis cranii.

PLATE 57.

Fig. 27. Transverse vertical section, from the same series as preceding figure, but through a plane more posterior, showing incus and stapes, arteria stapedio-maxillaris, arteria carotis communis, arteria carotis interna, periotic capsule, basis cranii, hyoidean cartilage, and mandibular branch of seventh nerve.

Fig. 28. Transverse vertical section through a plane posterior to fig. 27, showing periotic capsule with primitive gap for fenestra rotunda, facial, glosso-pharyngeal, and pneumogastric nerves, basis cranii, cervical vertebræ, and primitive jugular vein.

Figs. 29–30. Sections from embryoes 2 centims. in length.

Fig. 29. Transverse vertical section, showing head, neck, and manubrium of the malleus, tensor tympani muscle, basis cranii, periotic capsule, gasserian ganglion, ganglion of the facial, meatus auditorius externus, and sulcus tympanicus.

Fig. 30. Transverse vertical section through a plane posterior to fig. 29, showing incus and stapes, with arteria stapedio-maxillaris.

Figs. 31–38. Sections from embryoes nearly 4 centims. in length.

Fig. 31. Transverse vertical section, showing malleus and its relation to sulcus tympanicus and meatus auditorius externus, tympanic annulus, basis cranii, and thyroid cartilage.

Fig. 32. Transverse vertical section through a plane posterior to fig. 31, showing ganglion acusticum, and the cochlear and vestibular portions of the nerve, basis cranii, thyroid cartilage, tympanic annulus, periotic capsule, incus, stapes and arteria stapedio maxillaris, articulation between incus and stapes; and vestibule of labyrinth.

Fig. 33. Longitudinal vertical section made parallel to middle line of head, showing malleus, incus, periotic process, hyoidean cartilage, facial nerve with its mandibular division, meatus auditorius externus, periotic capsule with the canals partly in dotted outline, recessus cerebelli for flocculus, and exoccipital cartilage.

Fig. 34. Longitudinal vertical section from same series as fig. 33, in a plane more internal, showing mandibular cartilage, and membranous splint of bone immediately underneath it, tympanic annulus, meatus auditorius externus, stapedius muscle in which there is no cartilage, facial nerve, periotic capsule and canals, and hyoidean cartilage.

PLATE 58.

Fig. 35. Longitudinal vertical section in a plane more internal than fig. 34, showing meatus auditorius externus, sulcus tympanicus, manubrium and posterior process of the malleus, hyoidean cartilage, arteria stapedio-maxillaris, and stapes, facial nerve, periotic capsule, and exoccipital cartilage.

Fig. 36. Nearly horizontal section above the level of tympanic sulcus, showing periotic capsule and process, ganglion and trunk of facial, incus and malleus with articulation between them, mandible, pterygoideus internus muscle, gasserian ganglion, and its maxillary and mandibular divisions.

Fig. 37. Nearly horizontal section from same series as preceding figure but cutting tympanic sulcus, showing stapes and its relation to periotic capsule, and long crus of incus, facial nerve, stapedius muscle, neck of malleus, mandibular cartilage, tympanic annulus, tensor tympani muscle, and pterygoid cartilage.

Fig. 38. Nearly horizontal section in a plane ventrad to that of fig. 37, showing meatus auditorius externus in part, sulcus tympanicus,

tensor tympani muscle and neck of malleus, hyoidean cartilage, facial nerve, and stapedius muscle, periotic capsule, mandibular cartilage and mandible.

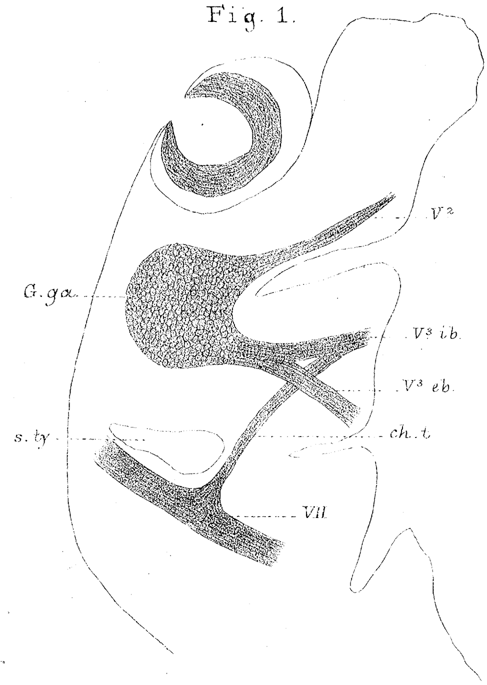
Fig. 39. Head of Pig embryo 1·4 centim. in length × 14, somewhat diagrammatic, designed to show the cartilages of the first two post-oral arches, the periotic capsule and semicircular canals, ganglion and trunk of facial with its mandibular branch, ganglion of ninth nerve, gasserian ganglion with its ophthalmic, maxillary and mandibular branches, primitive jugular vein, cerebral hemisphere, vesicle of third ventricle, midbrain, cerebellum, medulla oblongata, ventricles, auricle and aortic bulb of heart, fore-limb, optic cup, olfactory pit, and maxillary, mandibular, hyoid, and indications of first and second branchial arches.

Fig. 40. Right bulla and periotic bone of adult Rat × 10 (parts of the bony meatus auditorius and periotic have been removed to expose the external ossicles *in situ*), showing mandibular process (what DORAN calls process head) of malleus, lamina of papery bone between this process and tubercle at junction of neck and manubrium (the free edge of which is called processus gracilis by DORAN), posterior process (DORAN'S orbicular apophysis), manubrium mallei, body and crura of incus, ossified hyoidean cartilage (tympano-hyal of FLOWER), facial nerve with its mandibular branch, bulla, and Eustachian portion of bulla, articulation between bulla and petrosal.

Fig. 40, A. Stapes of adult Rat × 10, showing head, crura, and base, with an attempt to show the fluted condition of these, and tubercle on posterior crus for stapedius muscle.

Fig. 40, B. Long crus and orbicular apophysis of incus × 10, showing pedicular attachment of orbicular apophysis to long crus.

Fig. 1.



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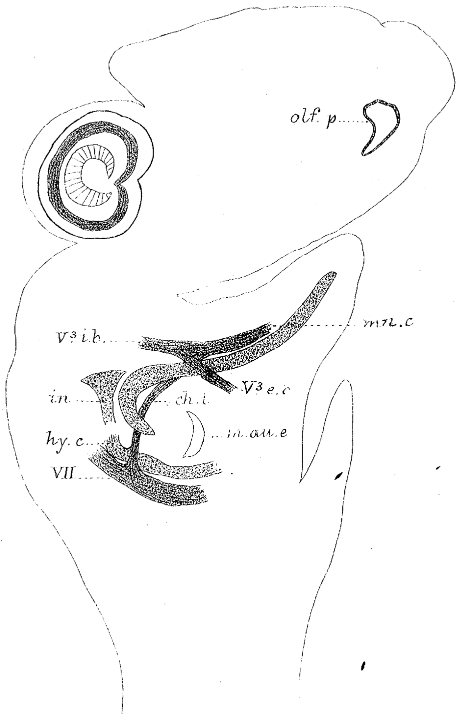

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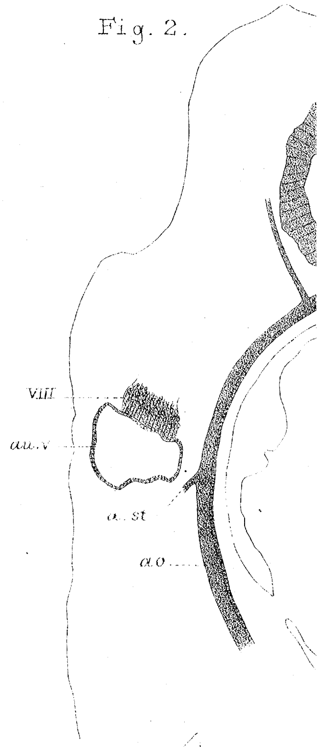

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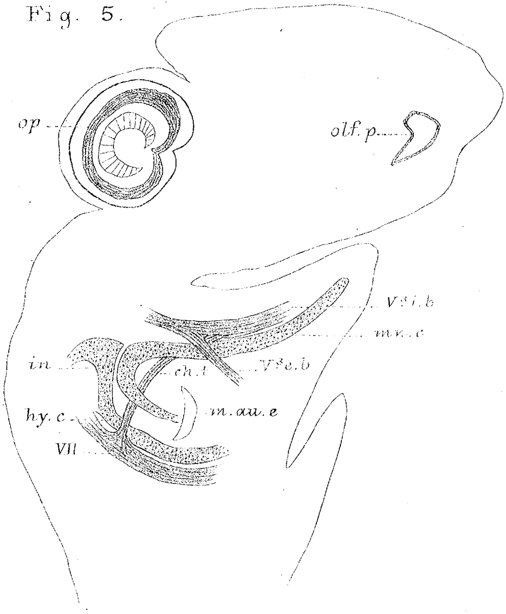

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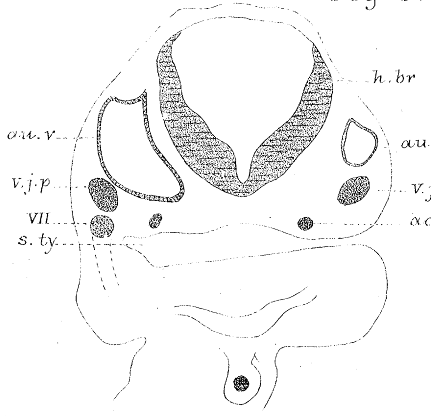

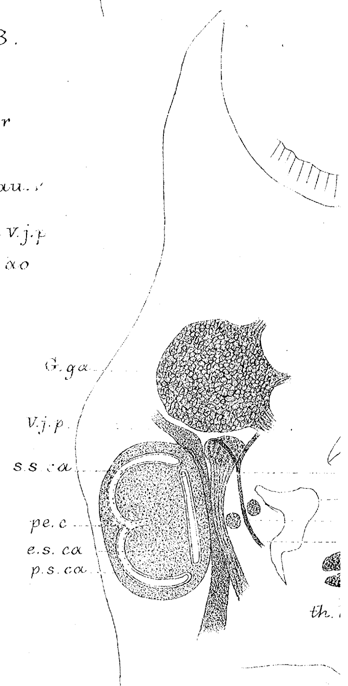

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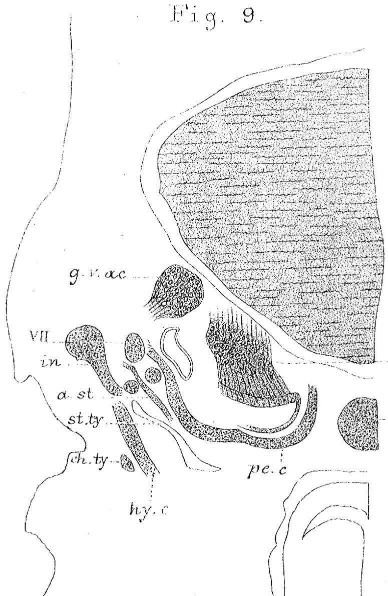

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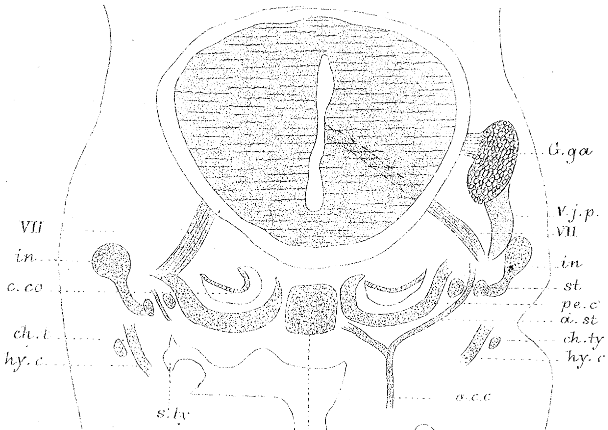

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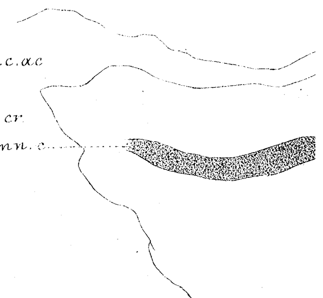

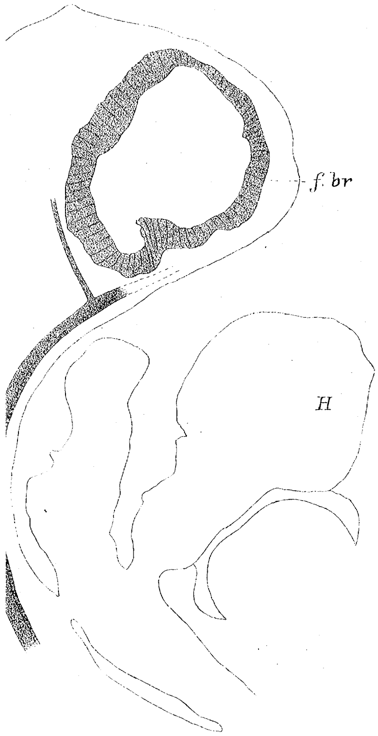
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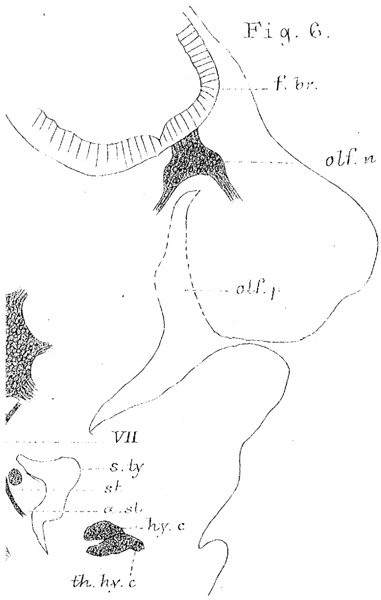
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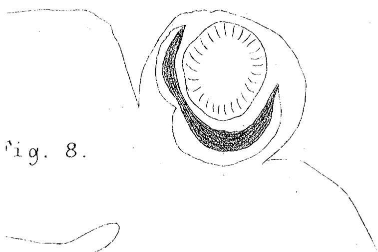

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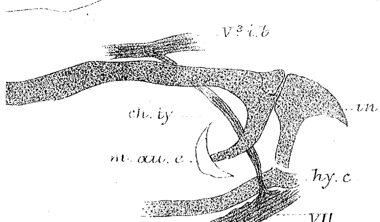
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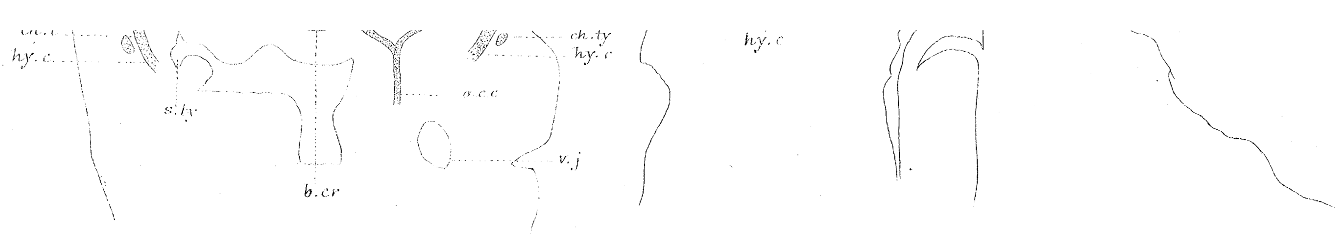

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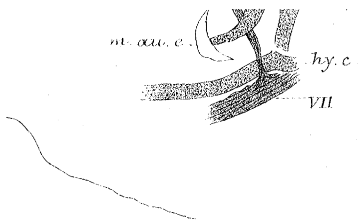

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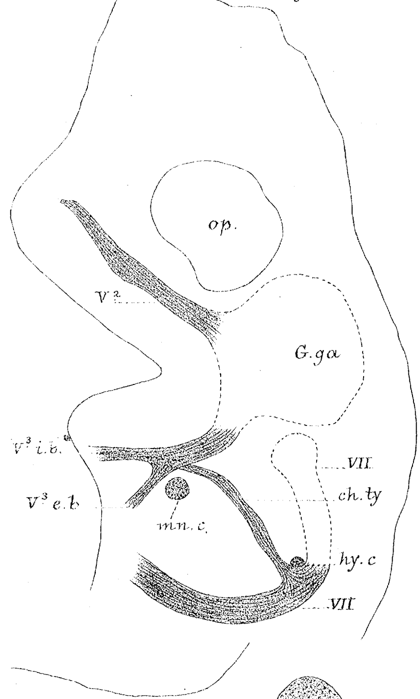

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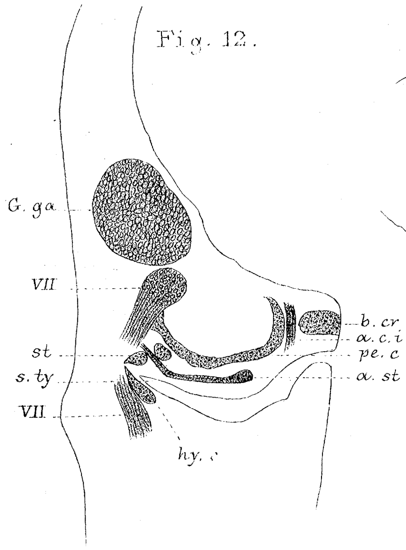

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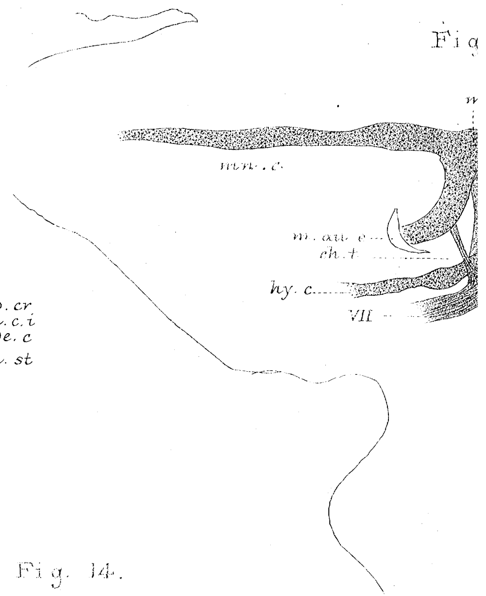

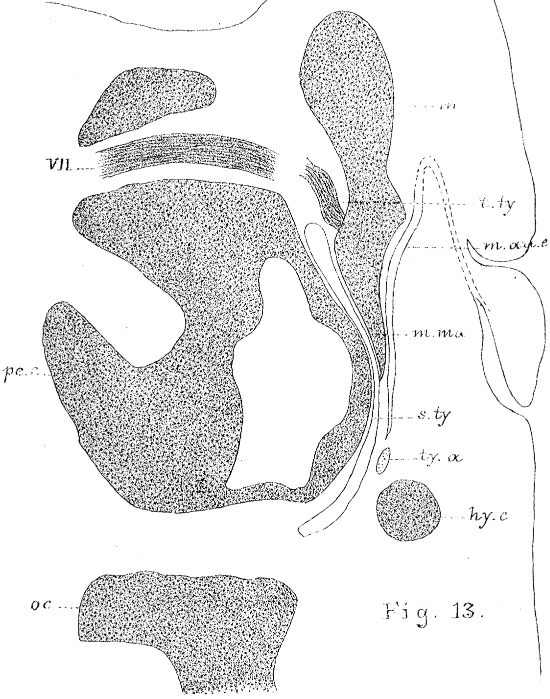

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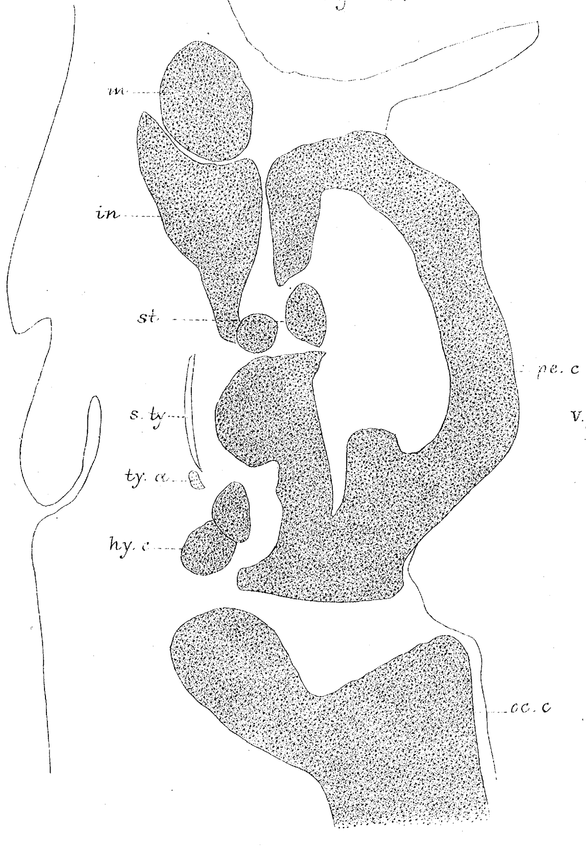

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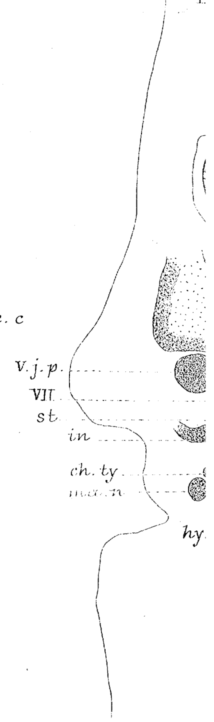

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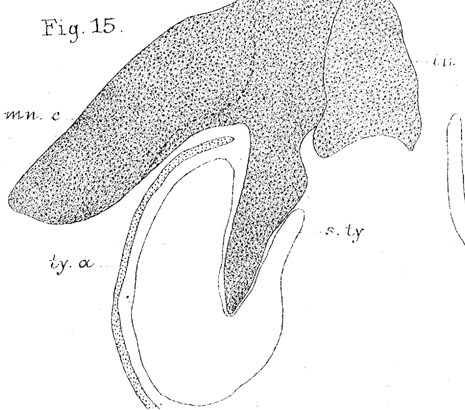

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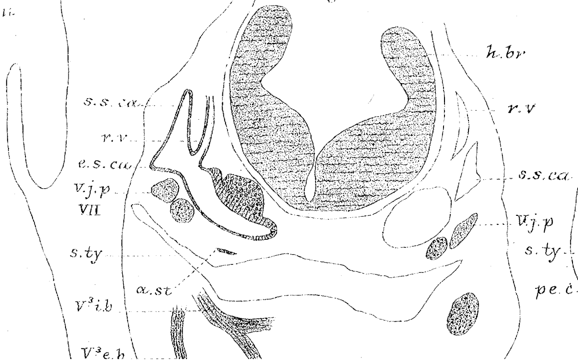

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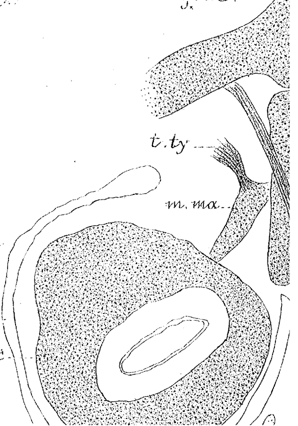

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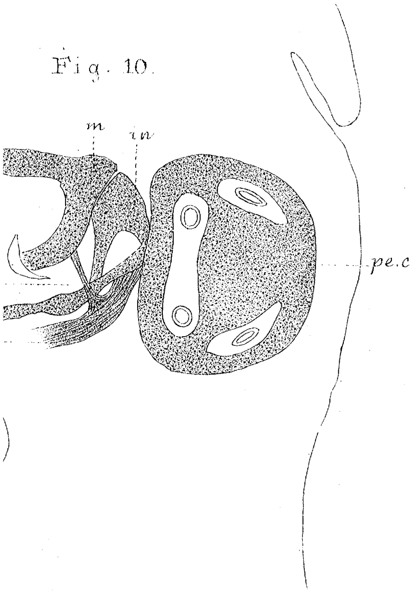

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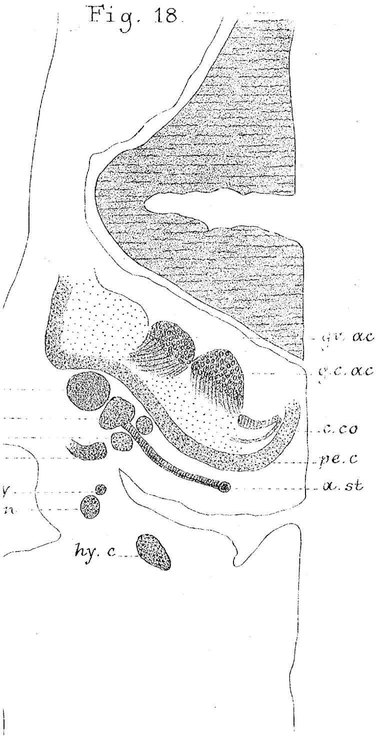

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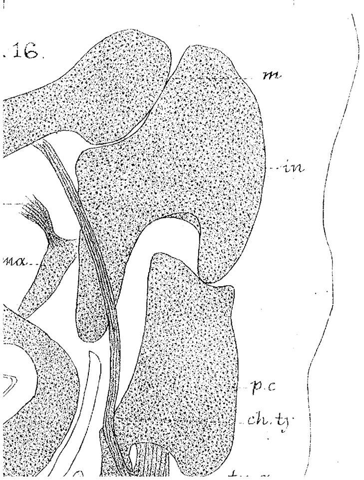

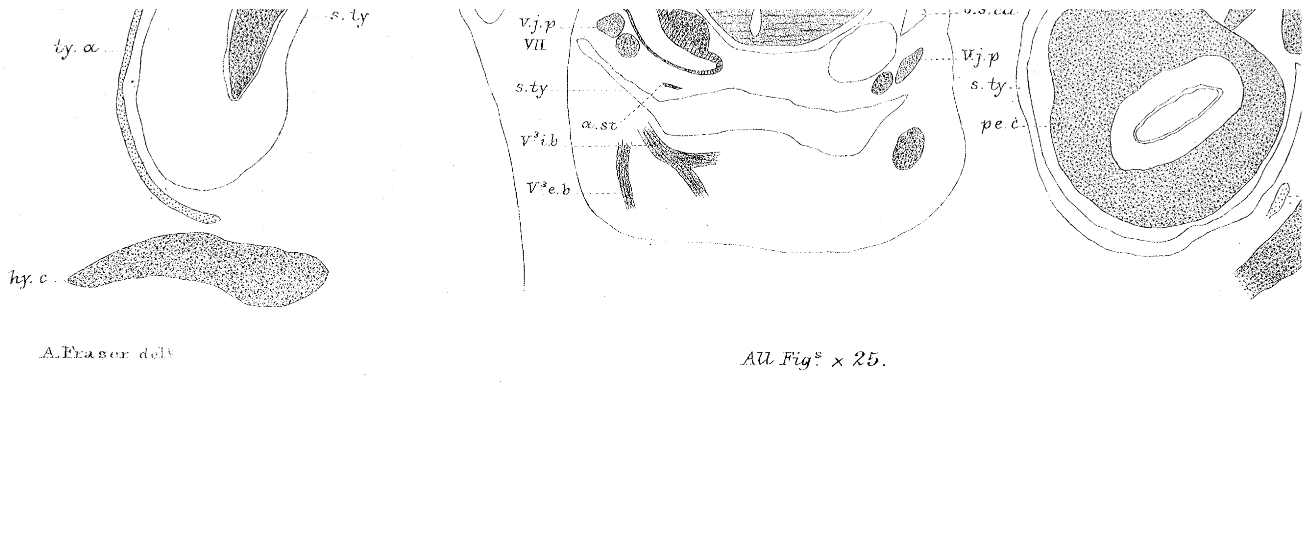

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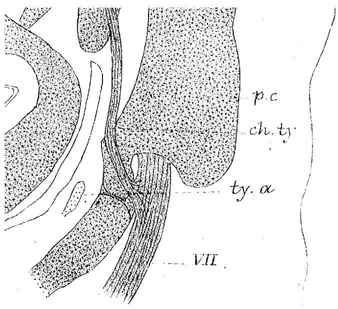

West Newman & Cº lith.

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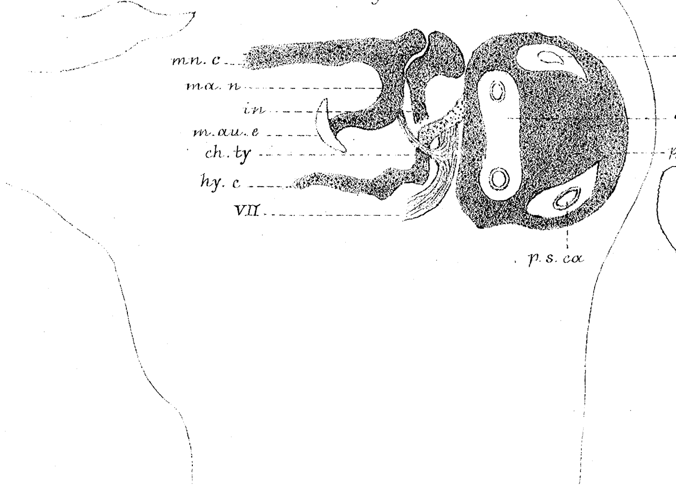

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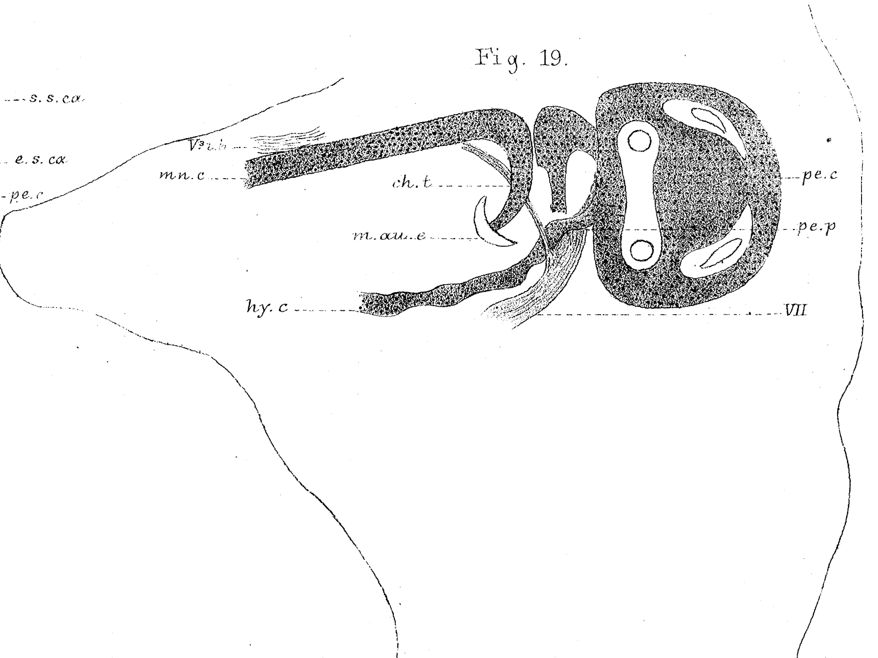

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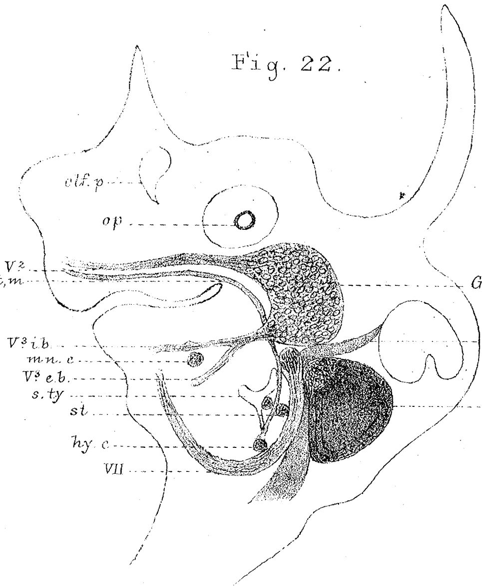

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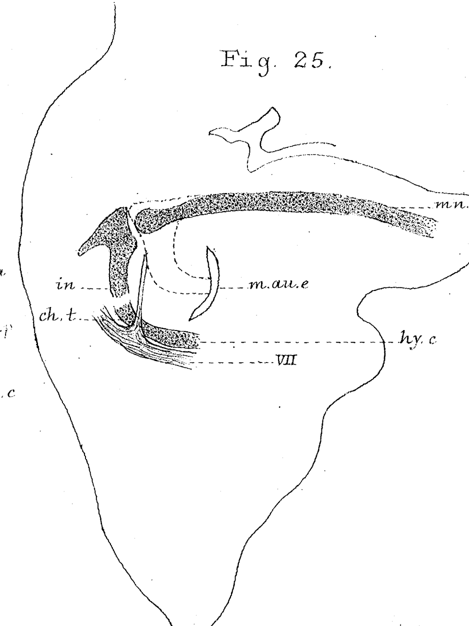

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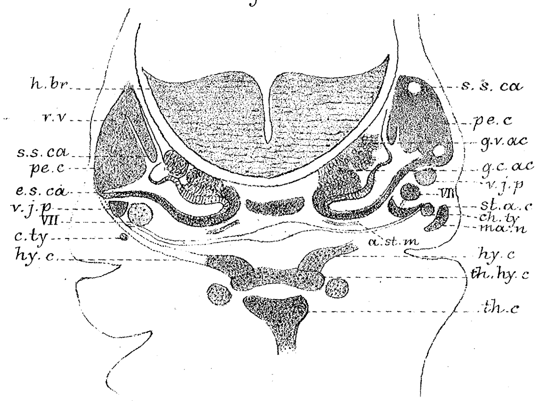

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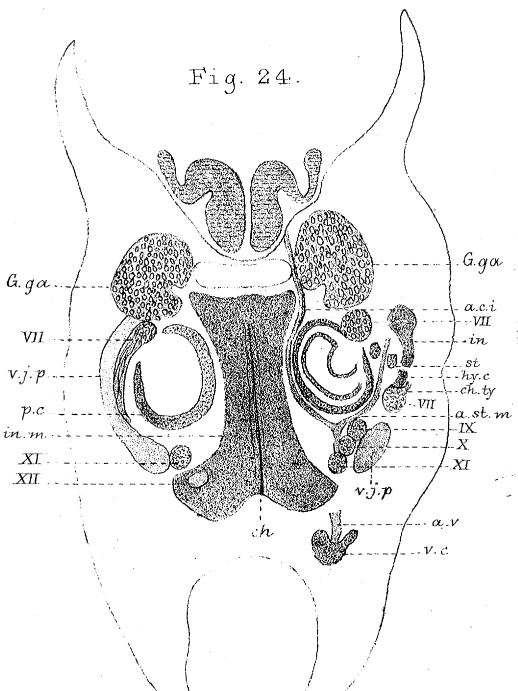

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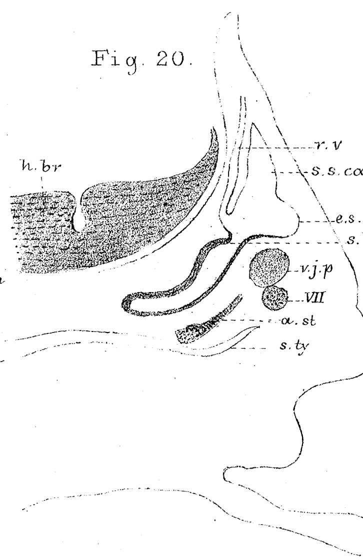

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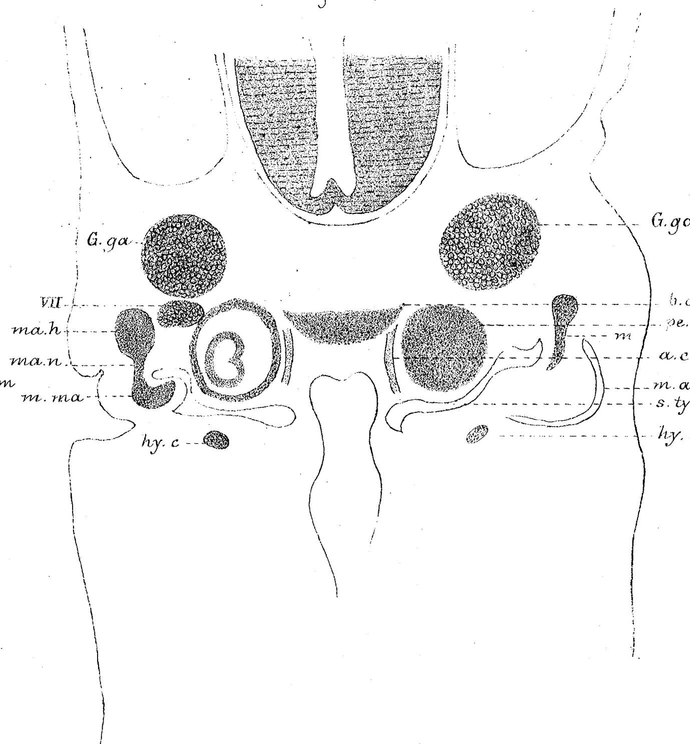

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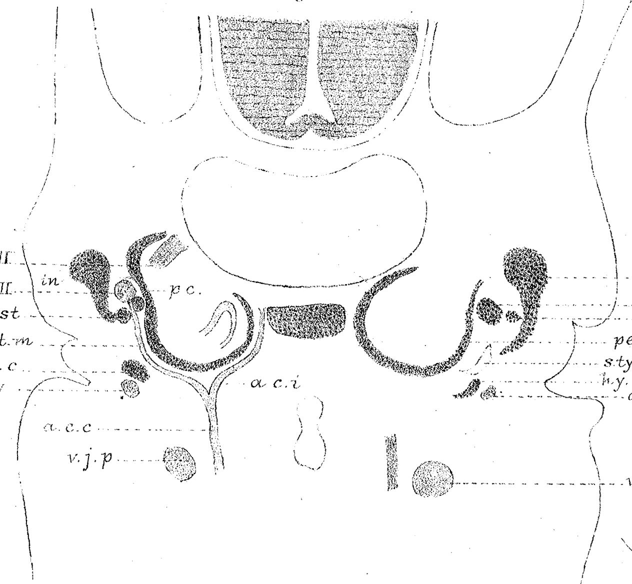

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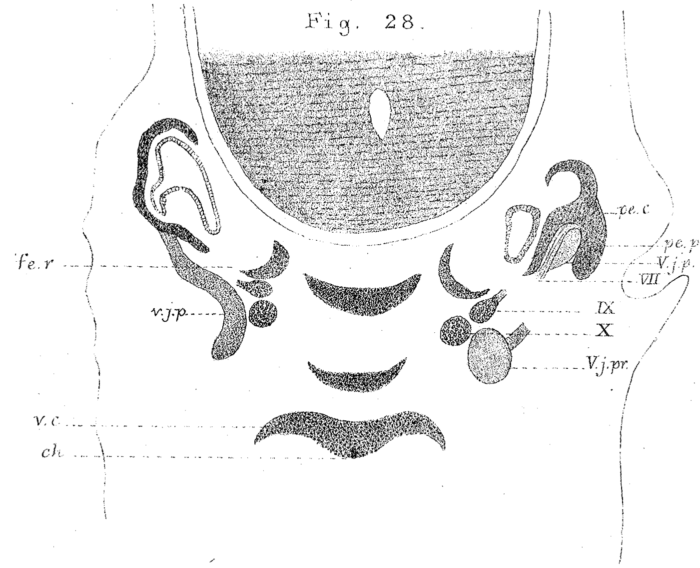

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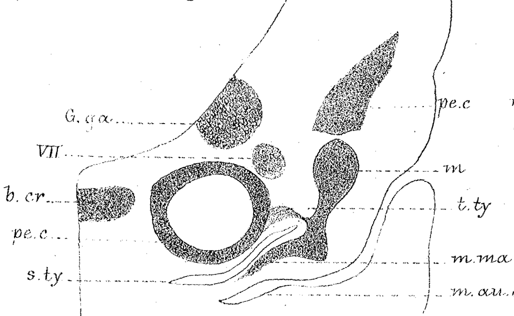

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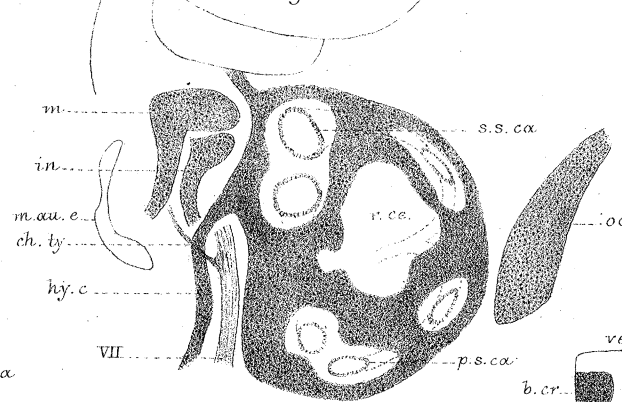

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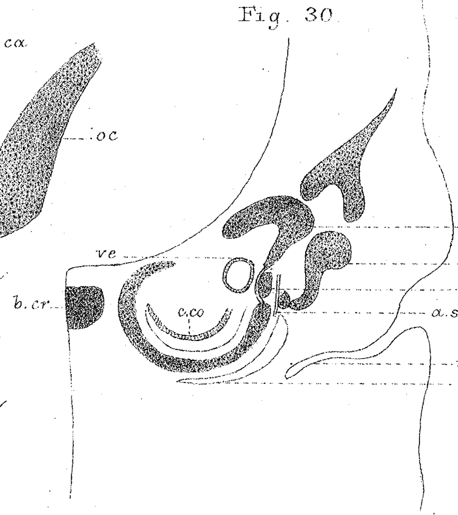

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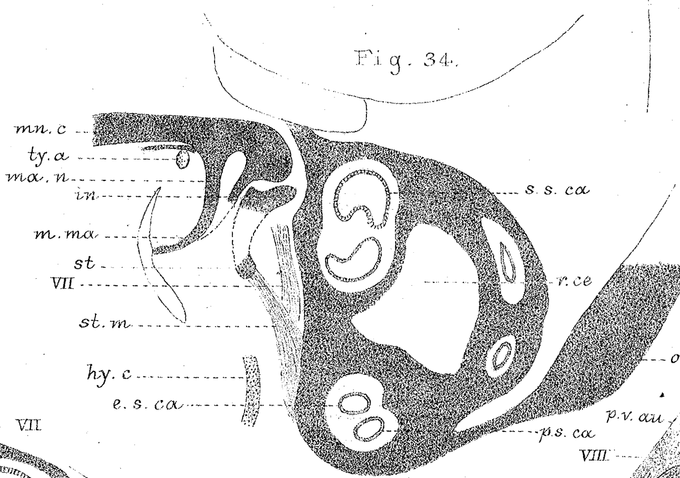

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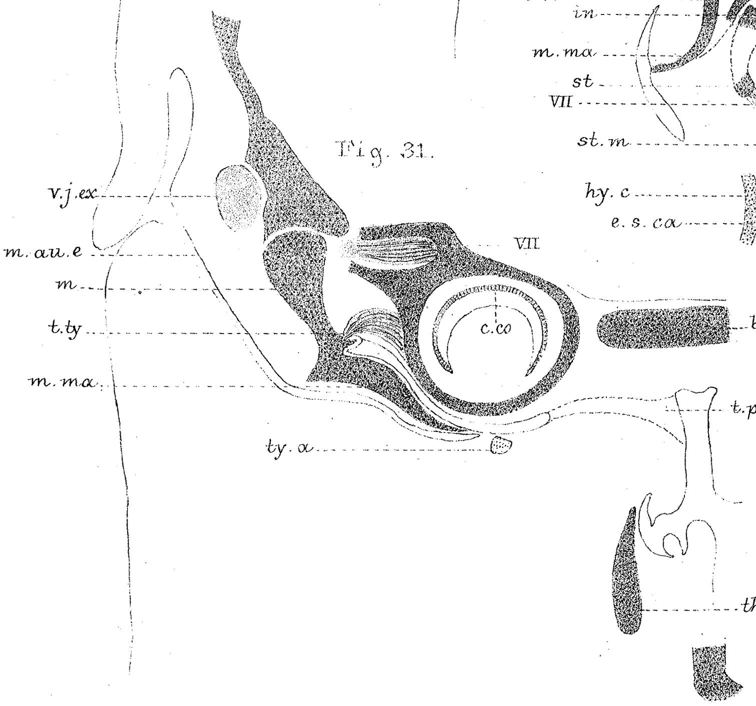

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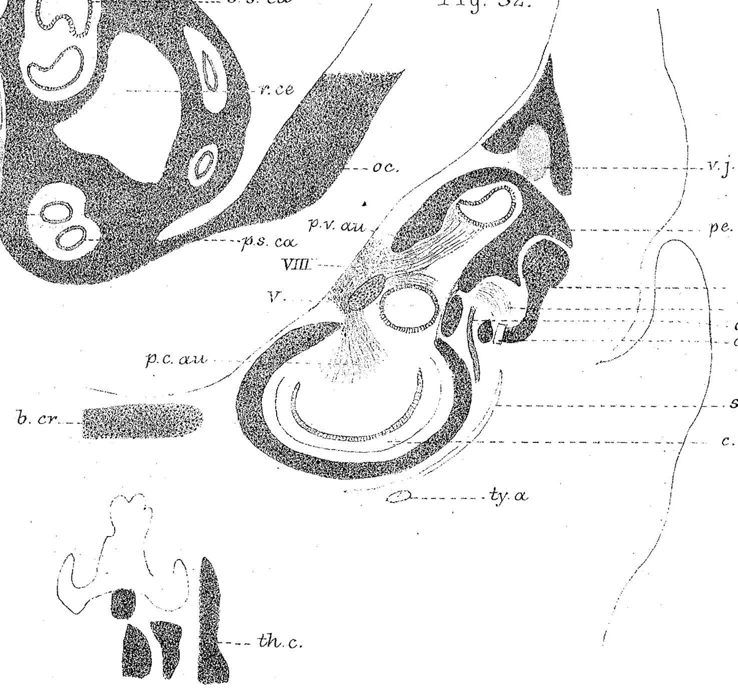

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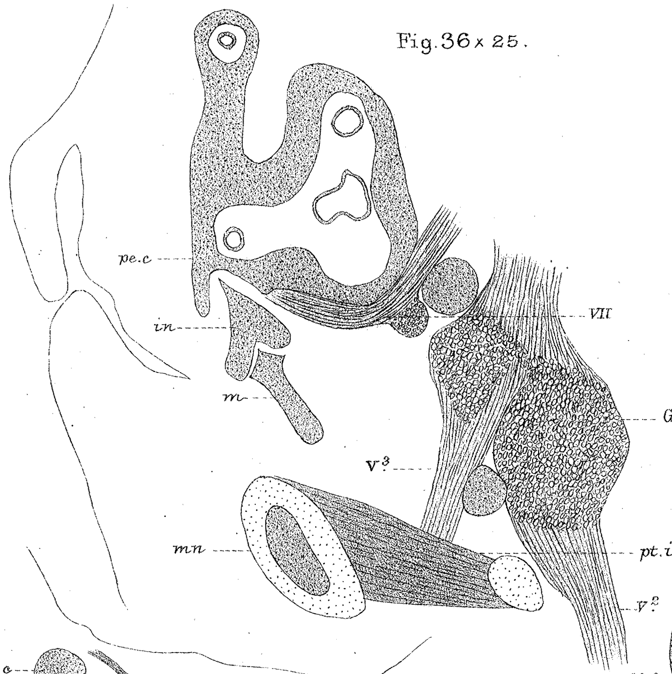

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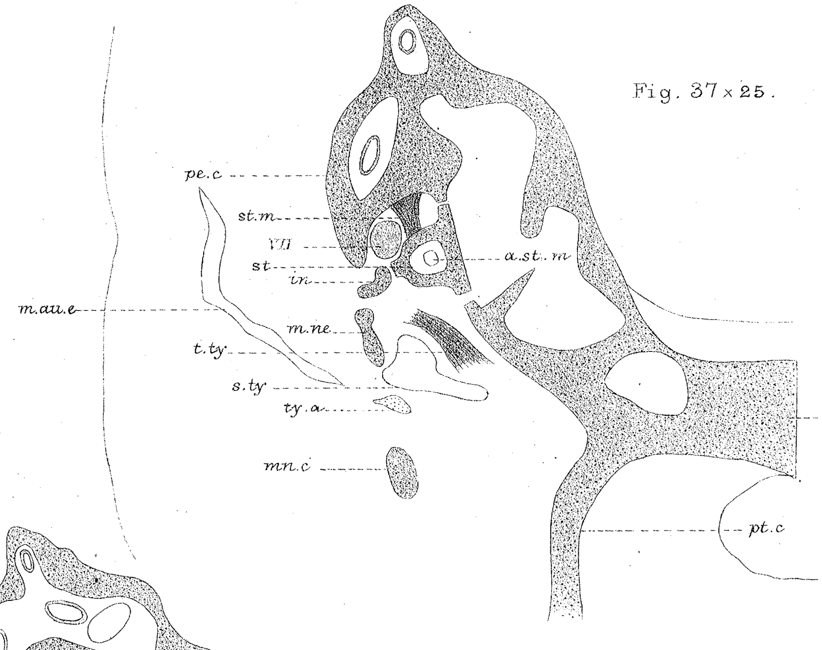

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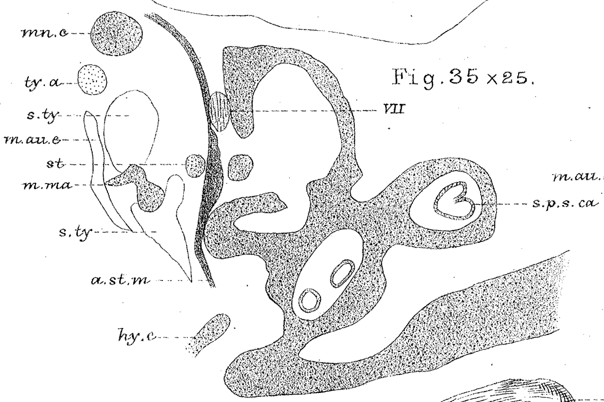

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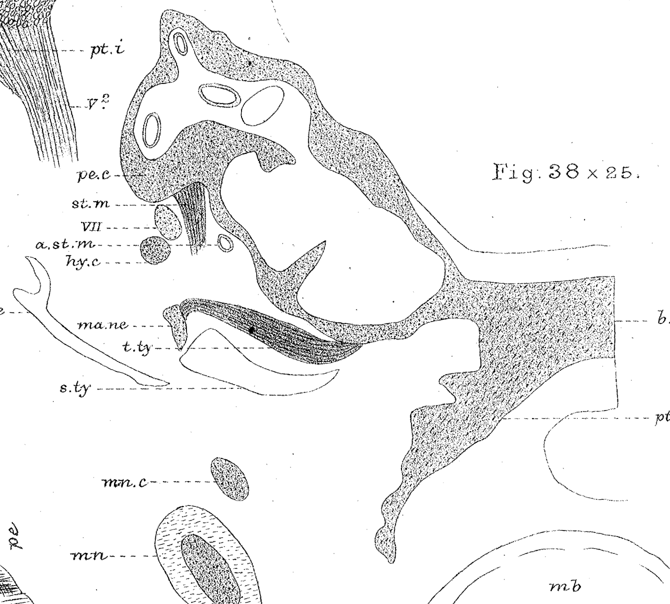

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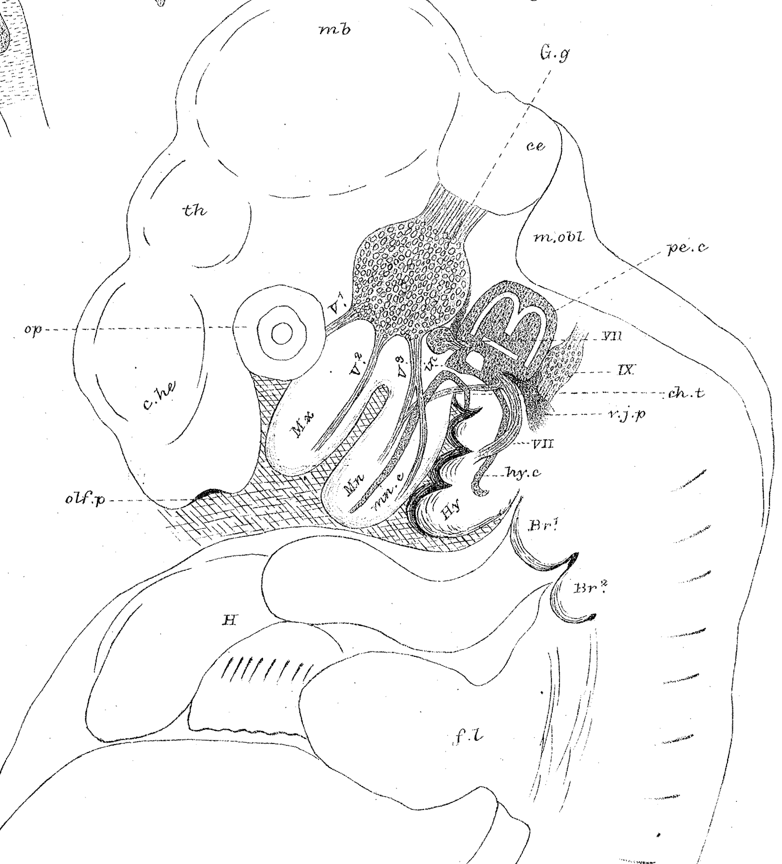

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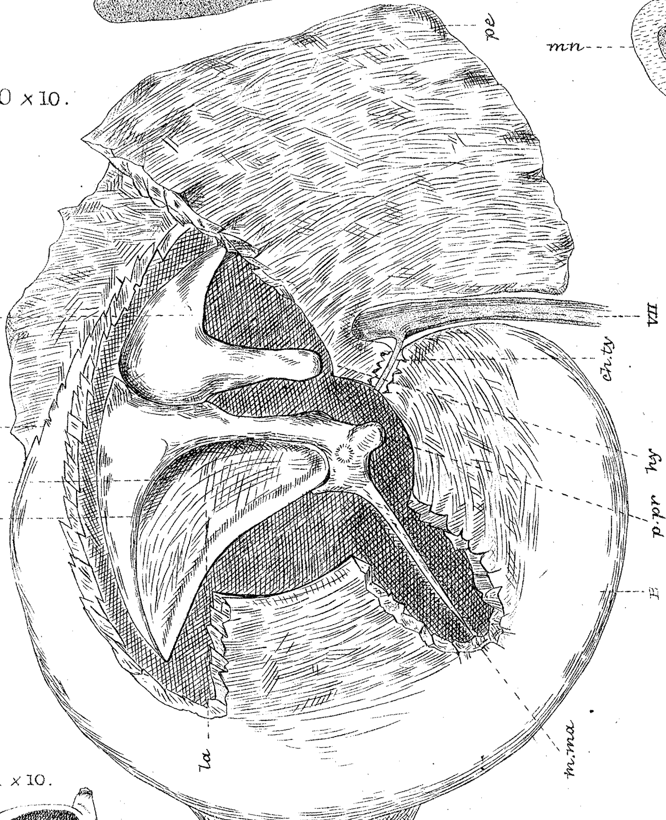

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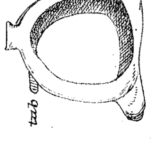

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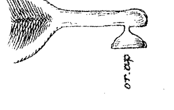

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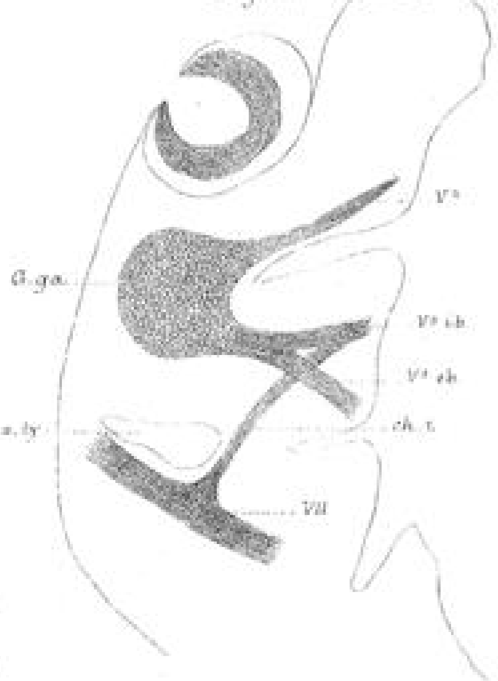

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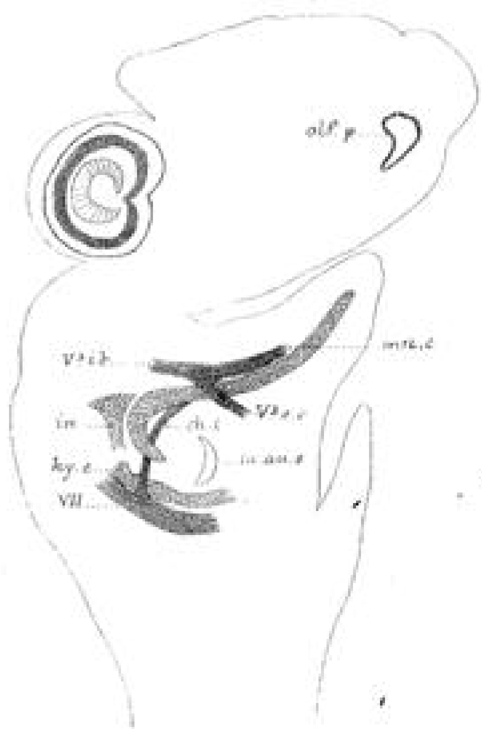

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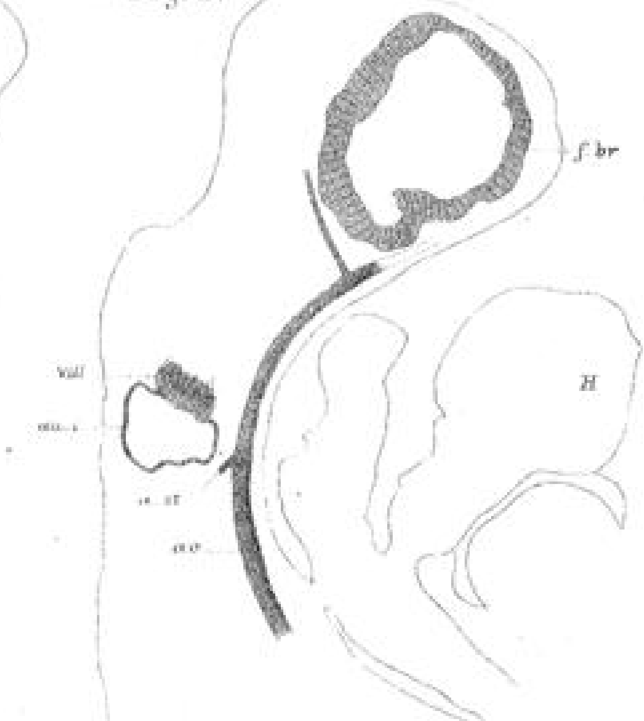

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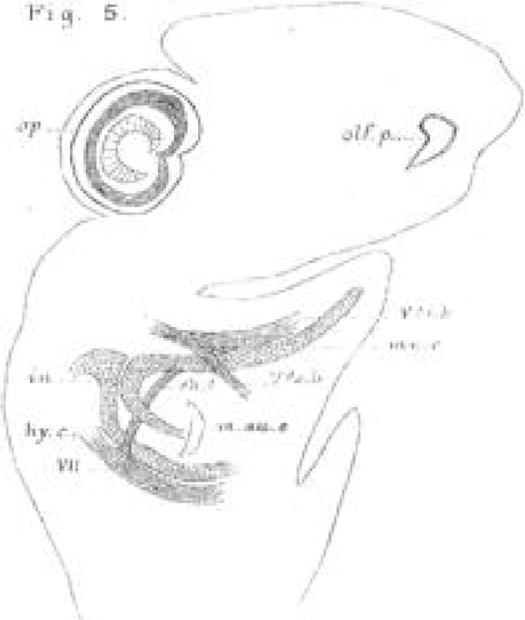


Fig. 3.

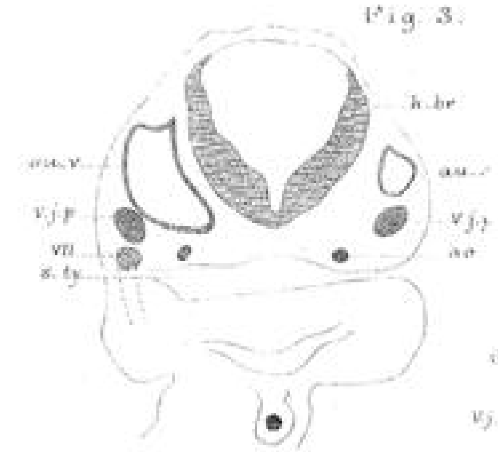


Fig. 6.

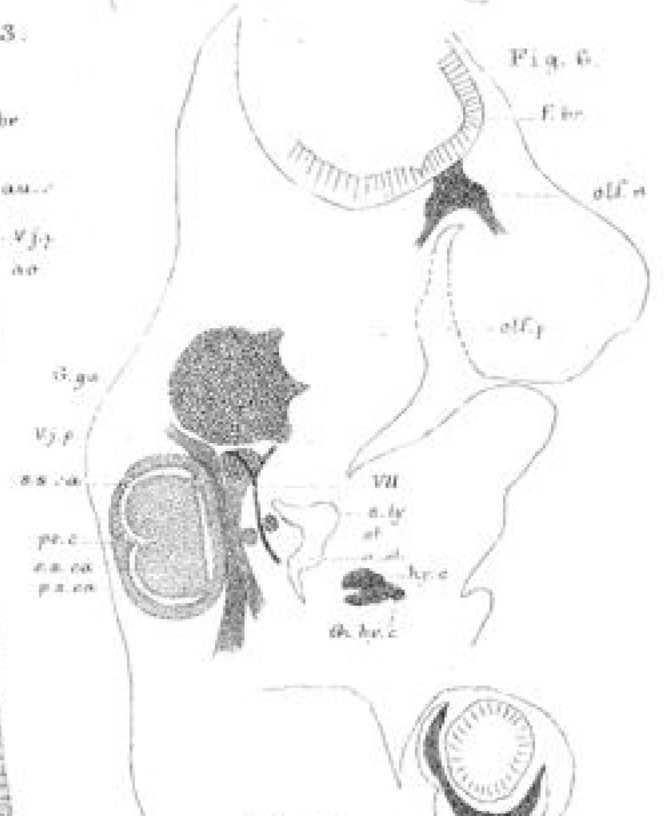


Fig. 9.

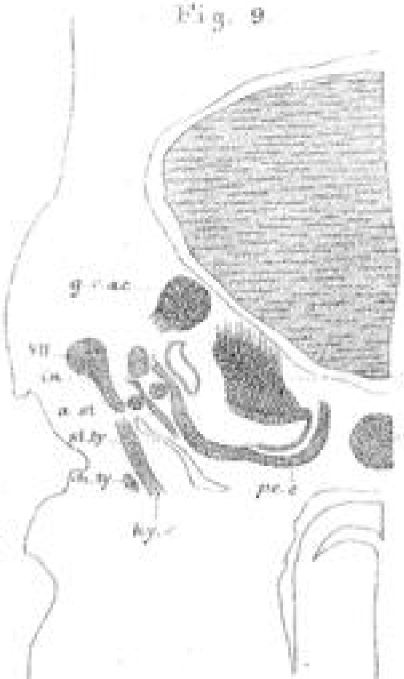


Fig. 7.

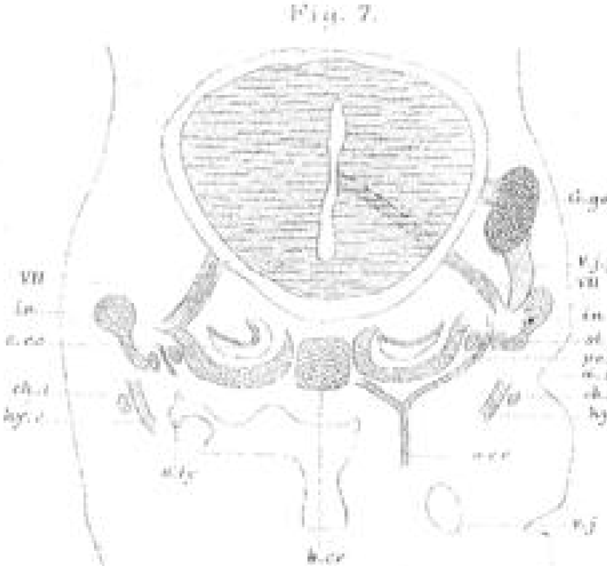
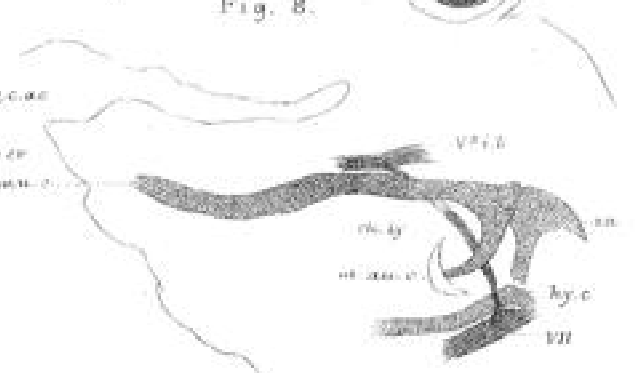


Fig. 8.



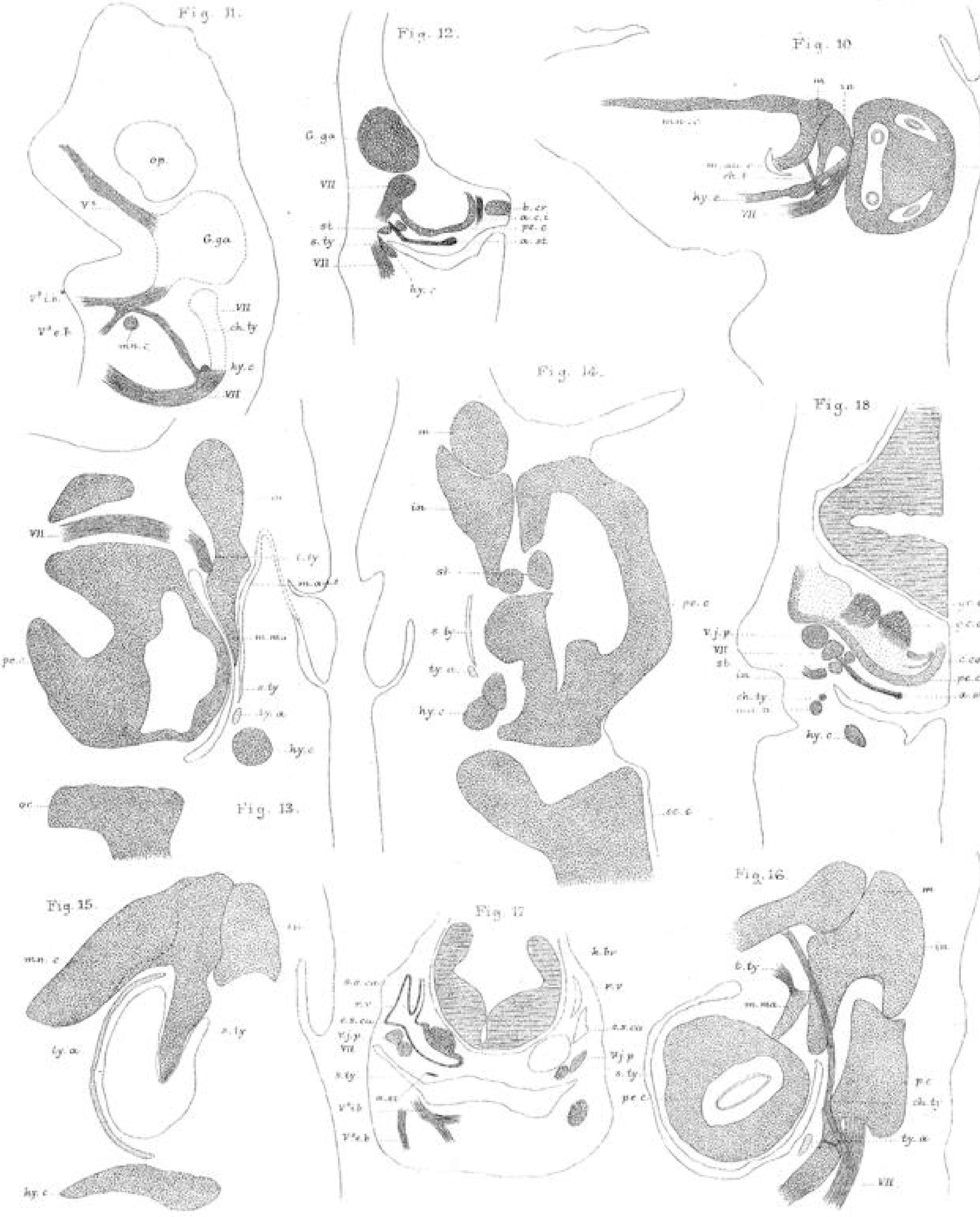


Fig. 11.
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Fig. 12.
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Fig. 10
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Fig. 14.
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Fig. 18
V.j.p.
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Fig. 13.
Fig. 15.
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