THE DEVELOPMENT OF THE SCALA TYMPANI, SCALA VESTIBULI AND PERIOTICULAR CISTERN IN THE HUMAN EMBRYO

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NINE FIGURES

The study of the development of the large walled-off connective tissue spaces that surround the membranous labyrinth is particularly interesting in that it shows that they have a very definite morphological individuality. It is evident at least that they are not to be considered as insignificant accessories that merely fill in the waste intervals between the membranous labyrinth and the surrounding cartilage or bone. On the contrary, they have characteristics which are in many respects as definite and constant as those of the ossicles themselves. The individuality of these spaces in all respects is most marked. They make their appearance at a definite stage in the development of the embryo; they are formed at definite places; they pass through a series of definite histogenetic processes; they spread in a definite order and manner and eventually they attain a definite form and structure. The general morphology and relations of these spaces during their developmental period will be described in the following paper, and the opportunity will be taken to point out in the course of the description some of these individualistic features.

Instead of designating the large spaces surrounding the membranous labyrinth as perilymphatic spaces, as has been the general custom since the time of Breschet 1833, they will here be spoken of as perioticular or periotic spaces. The use of the term 'periotic' avoids the confusion arising from the incorporation of the word 'lymphatic' in the terminology. The present ten-

dency is to restrict the use of the word 'lymphatic' to the lymphatic vascular system and its associated structures, with which these particular spaces have no known connection, either in their origin or in their ultimate relations.¹ We shall therefore speak of a periotic connective tissue that everywhere surrounds the epithelial portion of the labyrinth. This connective tissue includes, in part the fine-meshed periotic reticulum, and in part the large walled-off perioticular spaces to which belong the vestibular cistern, the scala vestibuli and the scala tympani with whose development we are primarily concerned.

MATERIAL AND METHODS

The observations that are recorded in this paper are all based on human embryos and cover the period included between embryos 35 mm. and 130 mm. CR length, which is approximately equivalent to the period between the ninth and sixteenth week of fetal life.

To facilitate the determination of the form and relations of the spaces, wax-plate models of the membranous labyrinth and the surrounding spaces were reconstructed after the Born method. Advantage was taken of the improvements in the method recently devised by Lewis 1915.² The serial sections were photographed at a suitable enlargement on bromide paper. By means of a preliminary model of the membranous labyrinth, the necessary reconstruction lines were established and inscribed on the bromide prints. From these prints then the membranous labyrinth and the perioticular spaces were traced on wax-plates. After cutting out from the plates the areas corresponding to these structures, the plates were piled and the resultant cavities were filled with plaster of Paris. The wax was finally melted off and there was left then a permanent plaster cast of the objects desired at a definite enlargement. Views of these models are shown in figures 4 to 9.

In outlining the periotic spaces it was found necessary to

¹ Sabin, F. R. Harvey Society Address. *Science*, vol. 44, 1916, p. 145.

² Lewis, W. H. The use of guide planes and plaster of Paris for reconstructions from serial sections. *Anat. Rec.*, vol. 9, 1915.

make an arbitrary rule as to how much should be included in the model. The smaller spaces of the reticulum that surrounds the main cavities can be seen coalescing to form larger spaces and these in turn coalesce with the main cavity as it advances into new territory. Thus in a given section there is a considerable range in the size and completeness of the spaces. The main spaces and the larger adjacent ones that communicate with them are outlined by a membrane-like border. This characteristic was utilized as the guide for determining which spaces to admit into the model; only those possessing a more or less complete border of this kind were included.

HISTOGENESIS OF THE PERIOTIC RETICULUM

Although this communication is more concerned with the process of conversion of the periotic reticular tissue into the larger walled-off spaces, yet for the purpose of completeness a brief survey will be taken of the earlier history of this tissue and the nature of its histogenesis.

The tissue in which the periotic spaces develop is derived from the condensed mesenchyme that establishes itself as an encapsulating mass around the otic vesicle in embryos between 4 mm. and 10 mm. long. This condensed mesenchyme is subsequently differentiated into the cartilagenous capsule that completely invests the epithelial labyrinth excepting for the three openings that persist in the adult as the internal auditory meatus, the aqueductus cochleae and the aqueductus vestibuli, which openings are present in the very earliest stages.

Originally the cartilagenous capsule abuts directly against the epithelial wall of the labyrinth. In embryos about 14 mm. long, however, the cartilage-forming tissue in the immediate neighborhood of the epithelium undergoes a dedifferentiation, so that an area is established all around the membranous labyrinth, and conforming to it in shape, that is less like cartilage and more like embryonic connective tissue. It is this that constitutes the foundation for the open-meshed periotic reticulum which in embryos 30 mm. long everywhere bridges the space existing between the membranous labyrinth and the surrounding

cartilage. The membrana propria that supports the epithelial part of the labyrinth and the perichondrium lining the cartilage are both derived from this periotic reticulum. It is also a modification of the meshes of this same reticulum that results in the formation of the perioticular spaces in a manner that will now be outlined.

Unmodified periotic reticulum is characterized by a rather uniform narrow mesh. The essential change which it undergoes in the process of space formation consists in the disappearance of some of the trabeculae of the mesh followed by the coalescence of the corresponding adjacent spaces. The trabeculae consist of the protoplasmic processes of the constituent cells of the reticulum and their disappearance is probably to be explained, not by a dissolution or liquefaction of these cell-processes but by an alteration in their form. It apparently is the result of an active motility of the cell protoplasm involving the successive detachment and retraction of the trabeculae. When a trabecula becomes detached it gradually retracts and adapts itself to the formation of a larger space, reshaping itself either as a smooth border or as a constituent part of another trabecula. As spaces become larger they require longer trabeculae, and as trabeculae become longer they also tend to become thicker.

The differentiation of the margin of the periotic spaces constitutes the final feature in their maturation. During the period in which the enlargement of an individual space is actively going on, the margins of the main cavity consist of smooth delicate strands of nucleated protoplasm that resemble the trabeculae between the large reticular spaces. These linear margins are interrupted here and there by openings into adjacent spaces. They tend, however, to form a continuous line that definitely marks off the space from the adjacent reticulum. As the space becomes more mature, the membrane-like border becomes thicker until it reaches a state that will probably not admit of any further opening-up for the coalescence of additional spaces. Any further growth is thereafter limited to simple distention of the wall of the space with the consequent adjust-

ment of its constituent cells. In its final form the margin of the space roughly resembles an endothelial membrane. Immediately lining the space is a thin membrane with flattened nuclei which is supported underneath by a thin coat of nucleated protoplasm that has the form of fibrous connective tissue. The former, judging only from its final appearance, could be designated as endothelium, thus making a distinction between it and the underlying tissue. In its histogenesis, however, it differs in no way from the rest of the wall and the difference that exists later seems to be merely the result of its adaptation to the existing physical conditions. Its early behavior is entirely different from that of vascular endothelium. Therefore if one uses the term endothelium for its designation this must be done with a considerable amount of reservation.

These phenomena can be particularly well studied in the scalae while they are in the process of spreading and enlarging. As we shall see, the scalae are more mature in their proximal portions and are progressively less mature as one approaches the apex of the cochlea. Thus any one specimen shows several stages in the development. Typical views showing some of the steps in this process are represented in figures 1 to 3. Figure 1 represents a section through the second turn of the cochlea in a human fetus 130 mm. CR length (Carnegie Collection, No. 1018). It shows the topography of the cochlear duct and the general character of the periotic spaces that are developing along its inner margins. The upper one or scala vestibuli is in a more mature condition. The lower one or scala tympani is less mature and along its peripheral (right) margin, it is in the act of spreading so as to underlie, as it eventually will do, the future basilar membrane. The scala tympani finally reaches the peripheral margin of the cochlear duct, and it does this by the coalescence of the enlarging reticular spaces which become incorporated with the main cavity of the scala.

This area is a particularly good one for studying the histogenesis of these spaces. It is shown under higher magnification in figure 2, which is a detail of the same section. By comparing this figure with figure 1, the exact location can be readily made

out. That portion of the cochlear duct that is to form the organ of Corti can be recognized by the characteristic form and grouping of its cells. A portion of the main cavity of the scala tympani is indicated and to the right of this are a few enlarged reticular spaces that are uniting with each other subjacent to the organ of Corti and the basilar membrane. These will in the end become part of the main space. They are here just in the

Fig. 1 Section through the second turn of the cochlea in a human fetus 130 mm. CR length (Carnegie Collection, No. 1018). Enlarged 60 diameters. This section shows the topography of the cochlear duct and the general character of the periotic spaces that are developing along its inner margin. Details of this same section as seen under higher magnification are shown in figures 2 and 3.

process of coalescence, the histological features of which procedure are well illustrated in this figure. The trabeculae are stretched out in long strands and in many cases are detached and project into the spaces as free ends. The detached trabeculae are seen in different degrees of retraction as their constituent protoplasm reshapes itself in adaptation to the new boundaries. It is only at the margins of the larger spaces that the cell-processes exhibit the characteristic flattened appearance,

which is the first indication of the formation of the marginal membrane. The residual undifferentiated reticulum that does not enter into the direct formation of the larger spaces constitutes the tissue from which is derived the adventitial coat of the completed scala.

Fig. 2 Detail of the section shown in figure 1, enlarged 278 diameters. This figure shows the part of the cochlear duct that is to form the organ of Corti, and the adjacent tissue that becomes incorporated in the basilar membrane. Below this is the periotic reticulum whose spaces are in the process of enlarging. By repeated coalescence these spaces finally unite with the large space that constitutes the scala tympani. This figure shows the histological appearance of the reticulum where the formation of tissue spaces is in active operation.

The appearance of the marginal membrane as seen in a more mature space is shown in figure 3, being a detail of the margin of the same scala vestibuli that is shown in figure 1. Here we have a firm membrane that forms a complete barrier between

the periotic reticulum and the lumen of the scala. After reaching this degree of development there is no evidence of any further coalescence of the surrounding reticular spaces with the main cavity. The membrane itself as seen in cross section consists of rather compact nucleated strands of protoplasm, which cannot as yet be separated into the so-called endothelial coat and the supporting fibrous coat. However, a comparison of the coagulated elements of the fluid seen in the reticular spaces with those seen in the scala would indicate a difference between the two and therefore it is probable that the membrane is already partially impervious.

Fig. 3 Detail of the section shown in figure 1, enlarged 400 diameters. It shows the character of the margin of the scala vestibuli in a more mature condition. The scala vestibuli is inclosed by a membrane consisting of the cells that had previously constituted the reticulum occupying this area and which have been modified in form in adaptation to the formation of this large tissue space, closing it off from the surrounding tissue.

DEVELOPMENT OF THE PERIOTIC CISTERN OF THE VESTIBULE

Aside from the scala vestibuli and the scala tympani, the largest of the periotic spaces is the large reservoir situated between the tympanic wall of the bony vestibuli with its articulated stapes, and the vestibular chambers of the membranous labyrinth. This is the spatium perilymphaticum vestibuli (BNA) or the cysterna perilymphatica (Retzius). In order to eliminate the word lymphatic from the terminology it will be designated here as the Cisterna periotica vestibuli or less formally the peri-

otic cistern. In this manner the descriptive term introduced by Retzius is retained.

Before there is any trace of the scalae the initial steps in the formation of the cistern can be seen. This is well illustrated in an embryo 35 mm. long (Carnegie Collection, No. 199). This particular embryo is cut into a sagittal series and the sections on slides 53 and 54 show the periotic cistern in its most rudimentary form. It consists of an area of reticulum bounded by the utricle, saccule, ductus reuniens, the proximal end of the cochlear duct and the ampulla of the posterior canal. The reticulum here is of the type seen along the semicircular canals in considerably older embryos. Whereas the reticulum elsewhere in this 35 mm. embryo presents a uniformly narrow mesh that is interrupted only by the numerous capillaries branching through it, this particular field gives the appearance of spaces which are more open and which are irregular both in shape and in size. From the very first the increase in the size of the mesh seems to be attained by the detachment and retraction of its constituent protoplasmic bridges, thereby allowing adjacent spaces to unite in the formation of composite larger spaces. Thus in the above section a few irregular protoplasmic free-ends are seen still projecting into the newly enlarged spaces. The area of this rudimentary periotic cistern is as yet very small and merges indefinitely into the adjoining reticulum. It is not until we come to fetuses about 40 mm. long that it develops spaces of any considerable size, and it is not until we come to fetuses about 50 mm. long that we find a single large space with walls that are definitely outlined so that it can be satisfactorily modelled.

In a fetus 43 mm. long (Carnegie Collection, No. 886), the spaces forming the rudimentary cistern stand out much more definitely than is the case in the 35 mm. embryo that has just been referred to. There is now just opposite the stapes one space which is much larger than the adjoining spaces. On part of its margin the protoplasmic bridges are stretched along so as to form a smoothly curved continuous boundary. This boundary is defective in some portions and at such places the space merges

with the adjoining secondary spaces. Within the space are some faintly refractive branching threads of coagulated plasma. The scala vestibuli is not yet laid down and the scala tympani is only represented by a moderate widening of the meshes of the reticulum in the neighborhood of the fenestra cochleae (rotundum), along the basal border of the first turn of the cochlear duct.

In fetuses 50 mm. long the outlines of the cistern become very distinct due to the marked increase in the size of its main cavity and to the more definite membrane at its junction with the rest of the reticulum. Its form and relations are shown in figures 4 and 5. They represent a median and a lateral view of a waxplate reconstruction of this region in a human fetus 50 mm. long (Carnegie Collection, No. 84). Only the main cavity is shown in the model. At certain places around its borders the meshes of the reticulum are uniting into larger spaces and these in turn are taken up by the main cavity as it advances into the new territory. These smaller incomplete spaces were omitted in constructing the plates of the model.

It will be seen then from figure 4 and 5 that the periotic cistern in 50 mm. embryos consists of a flattened rounded bursa-like cavity that intervenes between the stapes and the lateral surface of the saccule and adjoining utricle. It extends forward to the ampulla of the lateral canal and upward to the beginning of the crus commune. Posteriorly it crowds backward against the ductus reuniens filling in the space between the utricle, saccule and the proximal end of the cochlear duct. Both on its median and lateral surfaces there is no further opportunity for expansion except as the vestibule itself enlarges. The delicate membrane-like wall of the cistern hugs closely against the parts of the membranous labyrinth on the one side and the tympanic wall of the cartilagenous vestibule on the other, being separated from them only by a thin layer of the original reticulum. Along the dorsal margin of the cistern, however, there is room for expansion and the reticulum in this region shows enlarging spaces in the process of uniting with the main cavity. On its ventral margin near the cochlea and extending along the apical surface of the

latter there is a definite row of reticular spaces actively coalescing and constituting the beginning of the scala vestibuli. The scala tympani is already well started at this time, but its development is quite independent of the cistern. Within the

Fig. 4 The figures 4 to 9 represent a series of median and lateral views of wax-plate reconstructions of the membranous labyrinth and the surrounding periotic tissue spaces, illustrating under the same scale of enlargement three typical stages in the development of these spaces. This figure shows a lateral view of a model reconstructed from a human fetus 50 mm. CR length (Carnegie Collection, No. 84). The scala vestibuli is in the first stage of its development and consists of a row of large reticular spaces which extend from the ventral margin of the cistern downward along the apical surface of the cochlear duct. The scala tympani is more advanced and shows more complete coalescence of its constituent spaces. Enlarged 9 diameters.

Fig. 5 Median view of the same model shown in figure 4. This view shows the topography of the scala tympani. Its large proximal end lies opposite the fenestra cochleae and corresponds to the focus at which its development originates. Distally it tapers off rapidly, where the spaces are smaller and their coalescence less complete. Enlarged 9 diameters.

cistern can be seen scattered clumps of faintly refractive granular threads of what seems to be a coagulated constituent of the plasma.

The subsequent growth of the cistern is shown in figures 6 to 9. Figures 6 and 7 show respectively a median and lateral view of a wax-plate reconstruction of the membranous labyrinth and its periotic spaces in a human fetus 85 mm. long (Car-

negie Collection, No. 1400-30). The growth of the cistern here has kept pace with the increase in size of the labyrinth and maintains the same general relations as regards the stapes and the parts of the membranous labyrinth. The view of the cistern in figure 6 is an oblique one which would tend to mislead one as to its width. In reality it is relatively a little wider.

Fig. 6 Lateral view of reconstruction of the left membranous labyrinth and the periotic spaces in a human fetus 85 mm. CR length (Carnegie Collection, No. 1400-30) enlarged 9 diameters. Although the greater part of the cistern abuts against the stapes it will be noted that it also is beginning to spread over the dorsal surface of the utricle and along the inner border of the lateral canal. The scala vestibuli communicates freely with the cistern and extends downward along the apical surface of the cochlear duct throughout nearly two turns, showing the characteristic sacculated appearance near its tip where the coalescence of the spaces is less complete.

Fig. 7 Median view of same model shown in figure 6. The oval indentation in the proximal end of the scala tympani corresponds to the fenestra cochleae. This space extends along the cochlear duct about the same distance as the scala vestibuli; the two however do not communicate with each other as yet. The peripheral border of the scala tympani is characterized by sacculations corresponding to spaces that are coalescing with the main space. This indicates the direction of the growth of the scala at this time.

It has also extended upward on the dorsal surface of the utricle and is beginning to creep along the inner side of the posterior end of the lateral canal. Ventrally it communicates freely with the scala vestibuli which now extends well down along the cochlear duct.

The oldest stage studied is shown in figures 8 and 9. These show two views of a wax-plate reconstruction of these structures in a human fetus 130 mm. long (Carnegie Collection, No. 1018). At this time the periotic cistern has spread over the vestibular part of the membranous labyrinth, covering it nearly everywhere excepting at the macular portions where the nerves terminate. In figure 9 it can be seen that the mesial surface of the saccule is not covered; this lies closely against the wall of the cartilaginous vestibule. The uppermost division of the cistern situated between the crus commune and the ampulla of the posterior canal does not yet open into the general cavity. It has formed separately and owing to the position in which it lies its coalescence with the other parts of the cistern is retarded. Otherwise free communication exists between all divisions of the cistern.

DEVELOPMENT OF THE SCALA TYMPANI AND SCALA VESTIBULI

The scala vestibuli may be regarded as an extension downward of the cistern into the region of the cochlea and as such its growth starts from a focus opposite the fenestra vestibuli (ovale). The scala tympani in a similar way makes its first appearance opposite the fenestra cochleae. From these two foci the scalae extend gradually downward along the cochlear duct as two separate spaces which do not communicate with each other until they reach the tip of the duct, where there is finally developed a free opening between them known as the helicotrema.

In their formation they go through a series of histogenetic changes in essentially the same manner that has been followed in the case of the formation of the cistern. This as we shall see consists of the enlargement of the spaces of the periotic reticulum that originally occupies this region, the enlargement being a result of the disappearance of the protoplasmic bridges of the

reticulum whereby adjacent spaces unite in the formation of composite larger spaces. This process continues until there is a single continuous space extending down along the cochlear duct representing each scala and at the margins of each of them there is developed a membranous arrangement of the reticular cells which completely walls off the space from the surrounding tissue. In these alterations in the reticular mesh and in the formation of the surrounding membrane there is an active change

Fig. 8 Lateral view of a wax-plate reconstruction of the left membranous labyrinth and the periotic spaces in a human fetus, 130 mm. CR length (Carnegie Collection, No. 1018) enlarged 9 diameters. The cartilagenous stapes was removed from this model and the oval impression that it makes on the cistern can be plainly seen. The cistern has spread over the top of the utricle and along the lateral canal. The scala vestibuli extends to the tip of the cochlear duct where it communicates with the scala tympani, thus forming the helicotrema.

Fig. 9 Median view of the same model shown in figure 8. The oval impression on the proximal end of the scala tympani corresponds to the fenestra cochleae. As yet there is no communication at this point between the scala tympani and the subarachnoid spaces corresponding to the aquaeductus cochleae. The spaces making up the cistern cover almost the whole of the utricle and saccule excepting the places at which the nerves enter and a small part of the medial surface near the attachment of the appendage.

in the form of the reticular cells which repeatedly adapt themselves to the new conditions. There is no evidence to indicate that any other cells take part in the formation of the scalae.

The first evidence of the formation of scalae is found in fetuses about 40 mm. long, which is a little later than the first appearance of the cistern. In a fetus 43 mm. CR length (Carnegie Collection, No. 886) along the proximal part of the cochlear duct on its basal surface, there is a distinct widening of the meshes of the periotic reticulum. This is the beginning of the scala tympani. On the opposite side of the cochlear duct where one would look for the scala vestibuli the periotic reticulum retains its primitive appearance characterized by a narrow and rather uniform mesh. Thus the scala tympani makes its appearance slightly in advance of the scala vestibuli, that is, if we regard the latter as distinct from the cistern.

In fetuses 50 mm. long both the scala tympani and the scala vestibuli can be plainly identified, although they are still very incomplete. A wax-plate reconstruction of them representing their form and their relation to the membranous labyrinth in a human fetus 50 mm. CR length (Carnegie Collection, No. 84) is shown in figures 4 and 5, being a median and a lateral view respectively. It will be seen that the scala tympani is larger and more advanced in its development than the scala vestibuli. The latter is in its earliest stage and consists of hardly more than a row of enlarged reticular spaces that extend downward from the cistern along the dorsal and apical surface of the cochlear duct.

The scala tympani consists of an elongated oval space lying along the basal surface of the proximal part of the cochlear duct, about corresponding to the proximal half of the first turn of the duct. In the main part it is a single space with a distinct margin separating it from the general periotic reticulum. In the more apical portion it tapers off into multiple incompletely united smaller spaces which actively coalesce as the process advances into the new territory along the duct. It is of interest to note that the most mature and the largest part of this scala, representing the focus at which it first appeared, is opposite

the fenestra cochleae (rotundum), just as the cistern forms opposite the stapes and the fenestra vestibuli. The scala tympani always begins at the same place and extends downward along the cochlear duct, at first a little in advance of the scala vestibuli, but subsequently the latter catches up with it and the two reach the tip of the duct at about the same time.

It is well known that the proximal portions of the cochlear duct mature sooner than the distal portions. One might expect that the accompanying periotic spaces would correspond in their development to the maturity of the duct and therefore the proximal parts of the scalae would differentiate first. In other words the maturation of the cochlea proceeds as a wave from the proximal end to its tip involving all of its constituent structures as it passes along, including mesenchymal parts as well as epithelial. This conception might explain the direction of development of the scalae but it can hardly be applied to the cistern, the vestibular representative of the scala vestibuli. One cannot say that those portions of the membranous labyrinth lying opposite the focus of development of the cistern, that is, the lateral walls of the saccule and utricle mature in advance of the rest of the labyrinth. There is no indication that a wave of differentiation passes through the epithelial elements of the labyrinth in the same direction and synchronously with the extension of the cistern as it advances from its primary focus up on the roof of the utricle and over on its median surface. In the case of the cistern it seems much more likely that the point at which it first appears is determined by the position of the stapes, which is doubtless an expression of the physical relation that subsequently exists between the two. By analogy this would yield additional significance to the relation existing between the fenestra cochleae and the point of beginning development of the scala tympani.

The form and relations of the scalae in fetuses between twelve and thirteen weeks old are shown in figures 6 and 7. These figures show median and lateral views of a wax-plate reconstruction of the membranous labyrinth and the surrounding periotic spaces in a human fetus 85 mm. CR length (Carnegie Col-

lection, No. 1400-30). Attention has already been directed to these figures in the description previously given of the cistern. The scala vestibuli can be seen in figure 6. Above, it opens freely into the cistern and extends downward along the apical side of the duct as a single main space, possessing a rather uniform diameter. It extends along the first two turns of the duct, gradually tapering off and showing a less mature character in its distal portions. Along the second turn of the duct the spaces are incompletely fused and the contour becomes correspondingly irregular. As a rule the peripheral margin of the scala seems less mature and more irregular than the central margin. The scala vestibuli does not connect with the scala tympani at any point as yet. The two are separated in the first place by the cochlear duct and then more centrally by a framework of connective tissue in which are the radiating bundles of the cochlear nerve with the nodes of ganglion cells that form the spiral ganglion. These latter structures are not shown in the model, they occupy however the V-shaped groove seen between the two scalae.

The scala tympani, as can be seen in figure 7, extends downward on the basal side of the cochlear duct along its first two turns. This corresponds to about the same linear dimension as that of the scala vestibuli. In its proximal portion it shows a greater area in cross section than the latter, but further toward the apical region it is about the same size and in some places it is even smaller. The peripheral margin of the scala tympani is distinctly more irregular than the central margin. This irregularity is due to spaces along the margin that are actively coalescing with the main space, but in which the fusion is not yet complete. The irregularity of this margin is thus an indication of the direction of the expansion of the scala. As the diameter of the whole cochlear mass increases it is evident that the main growth of the scala must radiate outward in a peripheral direction. This is accomplished by the continual assimilation of new reticular spaces along this margin. At the proximal end of the scala tympani can be seen an oval depression which

corresponds to the fenestra cochleae (rotundum) and with which it stands in intimate relation.

In fetuses about sixteen weeks old the form and relations of the scalae have nearly attained the adult conditions and this represents the oldest stage studied in connection with the present paper. The conditions found at that time are shown in figures 8 and 9 which present median and lateral views of a wax-plate model of a human fetus 130 mm. CR length (Carnegie Collection, No. 1018). On comparing the scala tympani and scala vestibuli as seen in these figures with those in figures 6 and 7 it will be seen that they are larger in cross section and more nearly cover in the cochlear duct. Furthermore they now extend to the extreme tip of the duct and communicate with each other across its central margin thus forming a helicotrema. It will be noted that now even as far as the tip of the cochlea each of the scalae consists of a continuous principal space. They are however more mature and larger in their proximal portions. Along the first turn of the cochlear duct they are walled off by a smooth membranous margin which separates them from the adjacent reticular tissue. The spaces of the latter do not seem to be taking any further part in the process of enlargement of the scalae. Along the second turn of the cochlear duct, a section of which was shown in figure 1, the coalescence of reticular spaces with each other and with the scalae is still in active operation. This produces a greater irregularity of the scalae than is shown in the model. The subsidiary spaces are shown as a solid mass, the slender clefts separating them are not represented. The nearer we approach the tip of the duct the more immature are the scalae until the condition is reached where the membrane-like margin is quite incomplete and the spaces merge irregularly with the surrounding reticulum. Thus a single specimen if studied in its different parts shows several stages in this interesting process of the formation and growth of the scalae.

PERIOTIC SPACES OF THE SEMICIRCULAR CANALS

From the descriptions given of the adult the reticulum along the canals never develops a single continuous wide periotic space like that of the cistern and the two scalae. There always remain a few trabeculae such as are seen in the cistern and scalae in their earlier stages, and these constitute partitions which subdivide the space and give it the appearance of a series of separate spaces extending along the inner margins of the canals. Although these spaces along the canals are incomplete as compared with the cistern and scalae, they are however entirely analogous with them in their formation.

The space along the lateral canal is the largest. Its posterior end exists as a continuation of the cistern. This can be seen in the lateral view of the model shown in figure 8 where the cistern extends for a considerable distance along the inner border of the lateral canal. Along the other two canals of the same specimen (130 mm., CR length) the reticulum has commenced the process of space-formation, but complete channels are not yet established.

COMMUNICATION OF THE PERIOTICULAR SPACES WITH THE ARACHNOID SPACES

The relation of the scala tympani and scala vestibuli to the subarachnoid spaces surrounding the hind-brain is of considerable interest both on account of the possibility of their functional relationship and on account of the similarity that exists in their development. For a satisfactory investigation of the establishment and the character of the communications that are formed between these two allied systems of tissue-spaces one should resort to other methods than those used in the present study, and furthermore one should examine older fetuses than those described here. Certain observations, however, were made in the course of the above investigation that bear a relation to these matters, and they will be briefly outlined here. In the first place the histological picture of the periotic reticulum is essentially the same as the early stages of the pia-arachnoidal tissue,

that invests the central nervous system. The enlargement of the meshes of the latter and the formation of the subarachnoid spaces and the arachnoid cistern, as has been recently described by Weed,³ correspond exactly with the appearances seen in the histogenesis of the perioticular spaces in the ear. The perioticular spaces are not however extensions of the arachnoid spaces that have invaded the cavity of the cartilagenous labyrinth. If this were so we should find them first appearing among the rootlets of the vestibular and cochlear nerves along which the subarachnoid space extends for some little distance. Instead, they begin at points where there can be no connection with the arachnoid tissue and their direction of growth is quite independent of it. The perioticular spaces may be analogous to the arachnoid spaces, but they are not identical with them, nor are they an extension of them.

According to the descriptions of the adult anatomy of the ear a communication becomes established between the scala tympani and the subarachnoid space near the fenestra cochleae, the so-called aquaeductus cochleae. Vague and conflicting statements are also made concerning a communication through the internal auditory meatus connecting the arachnoid spaces with the scalae. Such communications must be established quite late. In the oldest fetus examined, 130 mm. CR length, they do not yet exist. As to the latter communication it can be seen that the arachnoid spaces extend peripherally through the internal auditory meatus along the trunk of the acoustic nerve-complex and slender pockets and clefts from them extend along the larger bundles of the cochlear nerve; they terminate, however, before reaching the margins of the scalae, and there is no evidence at this stage that there is ever to be a communication between them and the scalae. As to the aquaeductus cochleae in the 130 mm. fetus it can be plainly seen that it is already forming as a derivative of the arachnoid spaces although the communication with the scala tympani is not yet established. The arachnoid spaces

³ Weed, L. H. The development of the cerebro-spinal spaces in pig and in man. Contributions to Embryology, vol. 5, No. 14, Publications of Carnegie Inst. of Wash., No. 225, 1917.

invest the glossopharyngeal nerve and extend down along its trunk and pass closely and directly posterior to the region of the fenestra cochleae (rotundum). A thin-walled tubular pouch projects from these spaces leaving the nerve trunk and extending obliquely toward the scala tympani in a direction that would meet it just distal to the fenestral impression on its basal surface. This fundament of the aquae ductus cochleae is present in fetuses 85 mm. CR length, but is longer in the 130 mm. fetus where it nearly reaches the scala tympani. The communication must be established soon after this.

SUMMARY

The earliest histological evidence of the formation of the perioticular spaces occurs near the stapes, in the reticulum lying between the sacculus and the fenestra vestibuli, where in embryos between 30 mm. and 40 mm. long it can be seen that its meshes are becoming irregular and its spaces are beginning to coalesce. This constitutes the rudiment of the vestibular cistern. It makes its appearance before there is any trace of the scalae, but it is not until the fetus becomes about 50 mm. long that the cistern is definitely outlined and clearly differentiated from the adjoining reticulum.

After the cistern, the scala tympani is the next space to become established. It can be recognized as a moderate widening of the meshes of the reticulum in the region of the fenestra cochleae in fetuses 43 mm. long, along the basal border of the first turn of the cochlear duct. The scala vestibuli, as can be seen in fetuses 50 mm. long, develops as an extension downward of the cistern along the apical border of the cochlear duct. Starting from these definite foci these three spaces spread into their destined territory absorbing as they go the enlarging reticular spaces of the invaded region by a process of space-coalescence. In fetuses 85 mm. long the two scalae extend downward along the cochlear duct to its last turn as two separate spaces which do not communicate with each other. When they reach the tip of the duct, which occurs in fetuses about 130 mm., crown-rump length,

a free opening is developed between them and this represents the helicotrema.

The perioticular spaces are analogous in their development to the pia-arachnoidal spaces; they are not however extensions of them that have invaded the cavity of the cartilagenous labyrinth. They begin at points where there can be no connection with the arachnoidal tissue and their direction of growth is quite independent of it. The communication that is found in the adult between the scala tympani and the subarachnoid space in the neighborhood of the fenestra cochleae, the so-called aquaeductus cochleae, is established quite late. In fetuses 85 mm. CR length it exists as a tubular pouch projecting from the subarachnoid spaces along the glossopharyngeal nerve toward the scala tympani. In the 130 mm. fetus, the oldest examined, this pouch is longer and nearly reaches the scala. The communication must be established soon after this.

Similar projections from the subarachnoid spaces at the internal auditory meatus extend as perineural clefts along the trunk and branches of the acoustic nerve. No actual communications were seen between these spaces and the two scalae.