II. *The Cochlea of the* Ornithorhynchus platypus *compared with that of ordinary Mammals and of Birds.*

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[Plates 45, 46.]

In the course of my researches into the structure of the cochleæ of various Mammals and Birds, I have been frequently struck with the marked dissimilarities displayed in these two forms of the organ. For this reason I naturally became anxious to examine it in a Monotreme, and to find, if possible, some links in structure between these two cochleæ.

I therefore made inquiries for specimens of the *Ornithorhynchus platypus* among my Australian friends, and, after a year or two's patience, succeeded in obtaining several skulls of that animal in an excellent state of preservation. These have enabled me to make some researches into the morphological and microscopical structure of this cochlea, the results of which I trust will be deemed worthy of the consideration of the Royal Society.

Morphology.

That part of the bony labyrinth which constitutes the cochlea of this animal consists of a somewhat curved tube, about $\frac{1}{4}$ inch (6·3 millims.) in length and $\frac{1}{20}$ inch (1·26 millim.) in diameter, projecting from the cavity of the vestibule and embedded in the substance of the petrous bone near its anterior extremity (see Plate 45, fig. 1).

This tube is directed almost horizontally forwards and is slightly curved outwards, its apex forming a little projection on the outer border of the petrous bone close to its pointed end.

In section this tube is of an oblong form at its commencement, vestibular end, with its greatest measurement ($\frac{1}{13}$ inch or 2 millims.) from top to bottom (see Plate 45, fig. 3). A little further forwards it becomes triangular, but soon it assumes its general oval-shape with its greatest diameter ($\frac{1}{22}$ inch or 1·15 millim.) from side to side (see Plate 45, fig. 2). The tube terminates in a slightly enlarged rounded extremity, which, however, is not spherical but flattened from top to bottom. Its greatest diameter (from side to side) is $\frac{1}{17}$ inch or 1·7 millim. This enlargement is due to the partial

coiling up of the anterior extremity of the membranous labyrinth, showing the tendency to assume the spiral form: thus, the ductus cochleæ of the *Ornithorhynchus* may be likened to that of a typical Mammal which has been unwound except at its extreme apex.

The general form of the Duckbill's cochlea contrasted with that of the typical Mammal and Bird.†*

On comparing the general form of these three cochleæ it is at once evident that there is much more resemblance between those of the Duckbill and Bird than between either of these and that of the typical Mammal. Thus the cochleæ of both Duckbill and Bird consist of curved tubes enlarged at their anterior extremities, with not much difference in diameter throughout except at their apex.

These two differ, however, in that the Duckbill's is more curved; that it is curved *outwards*, whereas the Bird's is curved *inwards* (towards the median line of the body); and in that the enlargement at the apex in the latter is more oval in shape instead of being rounded.

The differences between the general form of this Monotreme's cochlea and that of other Mammals will be found to be very marked. Whereas the former is merely a curved tube of nearly equal diameter throughout, the latter is made up of a coiled tube which tapers from commencement to apex so as to assume the form of the inside of a Snail's shell.

The length of the tube is much greater in typical cochleæ; thus in the smaller Mammals, such as the Cat, Dog, and Rabbit, it measures about $\frac{3}{4}$ inch (19 millims.) against $\frac{1}{4}$ inch (6·3 millims.) in the Duckbill. Lastly, the axis of the spiral cochlea is horizontal, whereas that of the curved tube is vertical.

The internal arrangement and minute structure of the Duckbill's cochlea.

It may be well to premise that on examining the interior of this cochlea the resemblance between it and that of the Bird is almost entirely lost, and its true Mammalian type becomes at once apparent.

The interior of the tube is divided horizontally into two unequal parts by means of a lamina, the upper division being larger than the lower. The outer and larger portion of this horizontal lamina is bony, the inner portion membranous. A very

* For description of Mammalian cochlea see Quain's 'Elements of Anatomy,' 8th ed., vol. ii., and Stricker's 'Histology,' vol. iii.

† For description of the Bird's cochlea see—

Paul Meyer, 'Labyrinthe Membraneux du Limaçon chez les Reptiles et les Oiseaux.'

Hasse, Die Schnecke der Vögel in v. Siebold's und Kölliker's Archiv. für Wissensch. Zoologie Bd. xvii., p. 381, 1867.

Hasse, Nachträge zur Anat. der Vögelschnecke, ibid., p. 461.

Deiters, Untersuch. ü. d. Schnecke d. Vögel Archiv. f. Anat. u. Phys., p. 409, 1860.

delicate membrane proceeds from the upper surface of the osseous lamina, near to its inner margin, to the inner wall of the cochlea tube; this membrane forms an acute angle with the inner portion of the horizontal lamina, and thus cuts off a third tube, which is triangular in section and very much smaller than the other two divisions of the cochlea tube.

The upper large tube is the scala vestibuli, and communicates posteriorly with the general cavity of the vestibule; the small triangular tube is the scala media or ductus cochleæ, and communicates with the saccule of the vestibule. The lower tube is the scala tympani, and communicates posteriorly with the tympanic cavity in the dried bone.

The scala vestibuli is largest at its vestibular end; here it is nearly square, being $\frac{1}{24}$ inch or 1·05 millim. high, by $\frac{1}{25}$ inch or 1 millim. broad. Further forwards it becomes smaller and alters its form until it becomes oval, with its greatest diameter $\frac{1}{22}$ inch or 1·15 millim. from side to side, and $\frac{1}{43}$ inch or ·58 millim. from top to bottom. Near the apex of the cochlea the scala vestibuli communicates with the scala tympani by means of an oval opening—helicotrema—formed by the absence of the bony lamina, which does not extend as far forward as the apex of the cochlea (see Plate 45, fig. 1).

The scala tympani is throughout much smaller than the scala vestibuli, and this is due to the fact that the osseous lamina encroaches much further inwards on its lower than on its upper side. The scala tympani is nearly circular in section, and varies very slightly in diameter, $\frac{1}{45}$ inch or ·56 millim. throughout its entire length. At its anterior extremity it unites with the scala vestibuli, as already stated.

These two scalæ are lined with endothelium and contain epilymph. In one of my specimens the scala tympani is almost completely filled, especially its posterior portion, with a substance resembling organising lymph, the true nature of which I am at present unable to explain.

Before passing on to the description of the scala media it will be more convenient to describe the lamina ossea, or outer* portion of the horizontal lamina which divides the general tube. This corresponds both in position and structure to the lamina spiralis ossea of the typical Mammal.

It is a wedge-shaped mass attached by a very broad base to the outer wall and floor of the cochlea tube, thus encroaching much more on the lower than the upper half of this tube, as already stated.

The upper surface of the lamina, except near its attachment to the wall, is almost horizontal; but just before its free margin it is raised up into a rounded eminence—the limbus—and this terminates in a sharp edge the upper lip of the marginal sulcus.

* In describing the position of the parts in the spiral cochlea it is usual to consider the modiolus or axis as the centre; but in describing the curved cochlea of the Duckbill the median line of the body is taken as the centre. As a result of this difference, the relative meaning of inner and outer is reversed; thus the outer part of the spiral cochlea corresponds to the inner of the Duckbill's.

The lower surface of the lamina slopes upwards and inwards from the floor of the tube, curving round so as to become almost parallel to the upper surface. It also terminates in a sharp edge the lower lip of the marginal sulcus; this lower lip projects much further inwards than the upper.

The free margin of the lamina is deeply grooved, forming the sulcus just alluded to.

The lamina ossea does not extend to the apex of the cochlea, but terminates beforehand in a curved border, which forms part of the boundary of the oval communication between the scala vestibuli and tympani. As the lamina approaches its anterior termination it gradually loses its wedge-shape and ceases to be attached to the outer wall of the tube; so that at last it simply consists of a plate springing from the floor and curving round so as to become horizontal at the limbus.

The substance of this lamina ossea is modified bone, like the lamina spiralis ossea of typical Mammals. It is not so dense as ordinary bone, and chiefly consists of what may be called ossified stellate fibrous tissue. It is well supplied with blood vessels, which have a tendency to become tortuous. The substance of the limbus is again modified, being more homogeneous in structure and not unlike the matrix of hyaline cartilage; moreover, its surface is deeply grooved transversely, giving it a dentate appearance, the free edges of the teeth forming the sharp upper lip of the marginal sulcus.

Through the lamina, close to its lower surface, run the bundles of nerve fibres on their way to the organ of Corti; these will be described further on.

From this brief description it will be seen that the lamina ossea agrees entirely in structure and position with the lamina spiralis ossea of the ordinary Mammal.

The Scala Media or Ductus Cochleæ.—This constitutes the membranous labyrinth of the cochlea. Taken as a whole it is a triangular tube rather more than $\frac{1}{4}$ inch in length which is coiled round at the apex of the cochlea, and is connected posteriorly with the saccule of the vestibule by means of a circular tube with very delicate membranous walls, in a manner that I have not completely made out. As already mentioned, it is triangular in section. The floor or base of the triangle is formed by the limbus of the osseous lamina and by the membrana basilaris, which stretches from the lower lip of the marginal sulcus to the ligament of the cochlea. This ligament is a large cushion of connective tissue adherent to the inner wall of the cochlea, and forms the inner boundary of the scala media. The third and upper side of the triangle is formed by the delicate membrane of Reissner, which stretches from the upper part of the ligament to the upper surface of the osseous lamina, being attached just where the elevation of the limbus commences.

The whole of the inner surface of the scala is lined with epithelium, which is variously modified according to its position,—that part of this epithelium which lies on the central portion of the floor being developed into that complex form of nerve epithelium known as the organ of Corti.

The membrana basilaris is a strong membrane made up of three layers. The lower

consists of fibres running lengthways, in the direction of the scala; these fibres have spindle-shaped nuclei, which present a rounded appearance like the nuclei of epithelium when seen in transverse sections of the cochlea. The next layer, the thickest, is more homogeneous in appearance, its component fibres run transversely from the lower lip of the marginal sulcus to the ligamentum cochleæ with which they blend. The upper layer is simply composed of one layer of fine fibres covering the inner part of the second layer; these are continuous with the rods of CORTI, to be described later.

The ligamentum cochleæ is a large cushion of connective tissue, somewhat triangular in section; its inner surface is closely adherent to the wall of the cochlea, and its outer one is raised up into two horizontal ridges one above the other. The lower is pointed and situated opposite the lower lip of the sulcus; to this ridge the membrana basilaris is attached: the upper is rounded off, corresponds and is opposite to the upper lip of the sulcus. The grove between may be called the secondary sulcus.

The connective tissue of the ligament is made up chiefly of fine interlacing fibres, but those composing the lower ridge are much coarser and transparent, they radiate from the point of attachment of the membrana basilaris. The whole substance of the ligament is very vascular.

The membrane of REISSNER is composed of a very delicate basement membrane, which is exceedingly difficult to demonstrate, and a layer of cells on each side—those on the outer or upper side being the endothelial cells of the scala vestibuli, and those on the inner or under side the epithelial cells lining the scala media. These epithelial cells are hexagonal in form and arranged in a single layer; they are much thicker than the endothelial cells, and have larger nuclei.

Here and there on the upper surface of the membrane of REISSNER are found blood-vessels, which pass across from the lamina to the ligament, and in certain spots a blood-vessel becomes convoluted so as to form an elevated knot (see Plate 46, fig. 7).

The epithelium lining the Scala Media.—That portion which lines the membrane of REISSNER has just been described, and if the cells of this layer be traced downwards on to the limbus they will be seen to become more rounded in form. At first they cover the surface of the limbus, but presently they are seen dipping down into the grooves between the teeth of the limbus, getting deeper and deeper, and thus entering the marginal sulcus without covering the teeth at all. The cells lining the sulcus and outer part of its lower lip are still rounded, but before arriving at the point of the lower lip the cells become entirely altered so as to form the organ of CORTI, which will be described later. On the other side of the organ of CORTI the epithelium is cuboid, and in this form it lines the inner part of the membrana basilaris and the surface of the ligamentum cochleæ to a little beyond the upper ridge. From this point to the attachment of the membrane of REISSNER the epithelium is peculiarly modified, and is traversed by numerous blood-vessels which chiefly run longitudinally (to the cochlea); this is the stria vascularis.

The shape of these epithelial cells is irregular, somewhat resembling transitional

epithelium but packed closer together. Numerous blood-vessels traverse the layer but never appear quite on the free surface. As the form of epithelium, which is modified so as to receive the terminations of special nerves, is called "nerve epithelium," that of the stria vascularis might, I think, be very appropriately called "vascular epithelium."

The epithelial lining has now been traced back to the membrane of REISSNER, and thus right round the tube, with the exception of the organ of CORTI, which has now to be described.

As the organ of CORTI of the *Ornithorynchus* (see Plate 46, fig. 6) closely resembles that of the ordinary Mammal, which I described in a paper read before this Society in 1876,* I propose to give merely a brief sketch of its structure, and later on to note how it differs from the typical Mammal.

The organ of CORTI consists of two rows of rods separated from each other below, and united at their upper extremities, thus forming with the membrana basilaris, on which they stand, a triangular tunnel.

Each of the rods have enlarged upper and lower extremities; the latter are similar in both rods, being simply enlarged feet. But the form of the upper extremity differs in the two rows; in the rods of the outer one it is oblong, with a delicate process projecting inwards from its upper part. The upper extremity of the inner rods is more rounded and fits into a shallow concavity of the head of the outer rod. From the upper part of these inner rods there is also a delicate process projecting inwards and lying below that of the outer rod. The shafts of both rows of rods are cylindrical and of equal size.

On each side of the rods are arranged rows of cells, there being a greater number on the inner side (the side next to the ligamentum cochleæ). The most important of these are the hair or bristle cells which are arranged in four rows ;† one row to the outer side of the outer rods, and three rows to the inner side of the inner rods. These bristle cells are elongated with flattened upper extremities and rounded lower ones; their outline is well defined, and they contain a well-marked rounded nucleus; from their summit projects a row of four or five bristles.

* 'Proc. Roy. Soc.,' vol. xxiv., p. 346. See also—

U. P., "Structure and Function of the Rods of the Cochlea," 'Monthly Micros. Journ.,' 1873.

U. P., "Development of the Organ of Corti," 'Journ. of Anat. and Phys.,' vol. xiii.

WALDEYER, "The Cochlea," STRICKER'S 'Histology,' vol. iii.

LAVDOWSKY, "Untersuch. ü. d. Akustichen Endapparat. d. Säugeth.," 'Archiv. Micros. Anat.,' p. 497, Bd. xiii., 1877.

BŒTTCHER, "Ueber Entwick. u. Bau des Gehörlaby. u. Untersuch. a. Säugeth.," Nova Acta, Leopold. Acad., Bd. xxxv.

GOTTSTEIN, "U. d. fein. Bau u. d. Entwick. d. Gehörschnecke d. Säugeth.," 'Archiv. f. Micros. Anat.,' Bd. viii., p. 145.

WINIWARTER, "Untersuch. ü. d. Gehörschn. d. Säugeth.," 'Wien. Akad. Sitzber.,' Bd. lxi., 1 Abth., p. 683, 1870.

† See postscript for the account of an additional row.

A reticulate membrane covers and is closely adherent to the upper surface of the rod heads, and extends outwards and inwards over the summits of the bristle cells—the bristles passing through rounded meshes of the membrane. This membrana reticularis is made up of one row of circular meshes (annulæ) to the outer side of the rods, and on the inner side three alternating rows of annulæ with elongated meshes (phalanges) between.

Passing downwards from the inner portion of the membrana reticularis to the membrana basilaris we find three or four rows of fibres (trabeculæ), which run almost parallel to the inner rods, and are attached to the latter membrane by enlarged feet very like those of the rods. Between these trabeculæ and below the level of the bristle cells are three or four rows of nuclear cells—that is to say, cells with well-marked nuclei, but apparently no cell-walls; these are the cells of DEITERS.

In each of the lower angles of the triangular tunnel is situated a row of nuclear cells similar to the cells of DEITERS, and to the outer side of the outer rods are a number of these nuclear cells lying on the under lip of the sulcus.

The inner and outer boundary of the organ is formed of irregular columnar cells (the supporting cells), which are the transitional link between the ordinary epithelial layer and the nerve epithelium proper.

The nerve filaments which come through a row of holes on the upper surface of the lower lip of the sulcus (habenula perforata), pass into the organ of CORTI, and no doubt terminate in the nuclear cells and bristle cells; but this point I have not been able to demonstrate in the *Ornithorhynchus*.

To complete the description of the ductus cochleæ there only remain its commencement and termination to be considered. The former I have not yet been able to trace out, but with the latter I have been more fortunate.

The organ of CORTI and the rest of the lamina membranacea is not continued further forwards than the end of the lamina ossea; but the ductus does not terminate here, for it is continued round the circumference of the spheroidal extremity of the bony tube, and ends in an enlarged cul-de-sac close to the base of the lamina ossea. Thus the ductus makes a turn of about three-quarters of a complete circle at the apex of the cochlea tube. This will be better understood by referring to the drawing (Plate 45, fig. 1), where it will be seen that the ductus almost completely surrounds the oval communication (helicotrema) between the scalæ tympani and vestibuli.

At the end of the lamina ossea, where the ductus commences to curve round, a complete change takes place in the shape and walls of the membranous labyrinth. It first becomes contracted into a circular tube, and after passing the extreme apex of the cochlea it enlarges again into an ovoid chamber—the lagena (see Plates 45, 46, figs. 4, 5). The walls of this chamber are formed by a thick layer of dense connective tissue, lined internally by a single layer of epithelium. The cells of this epithelial layer are for the most part cuboid, but near the further end of the lagena a patch of nerve

epithelium is found; this patch extends round the chamber, but is broader on its inner wall.

This nerve epithelium is very similar to that of the maculæ acusticæ of the saccule and utricle*; thus it consists of a deep layer of small rounded cells connected with a superficial layer of ciliated ones—thorn cells and bristle cells. These are covered by a perforated cuticular membrane, through which the bristles and thorns pass; the whole is surmounted by a loose mucoid mass, into which the thorns and bristles project, and which no doubt contain otoliths in the fresh state.†

The last bundles of the cochlear nerve pass forwards to supply this acoustic spot, and terminate in the nerve epithelium in the same manner as in the saccule and utricle of the vestibule.

The course of the cochlear branch of the auditory nerve.—This passes through the substance of the bone a little to the outer side of the cochlea tube, and just above the level of the floor. As it proceeds forwards it gives off lateral bundles of fibres to the lamina ossea, its terminal bundles going to the lagena in the manner just described.

Tracing these lateral bundles they soon enter and pass out of a ganglion, which consists of bi-polar nerve-cells, and is situated in the broad base of the osseous lamina at its commencement, but further and further inwards as it is traced forwards to its anterior end. The fibres from the ganglion collect again into bundles which divide and subdivide, uniting and reuniting so as to form a plexus; in this manner they pass through the lower portion of the lamina until the lower lip of the sulcus is reached. This is pierced with a single row of holes (habenula perforata), so that the nerve filaments may pass into the organ of CORTI. At this point the fibres lose their myeloid sheaths, the axis cylinder alone entering the nerve epithelium.

Comparison of interior of the cochlea of the Duckbill with that of the typical Mammal.

As regards the scalæ vestibuli and tympani the following differences are to be noted. In the ordinary Mammal there is not so much difference in size between the scala vestibuli and scala tympani, except at the base of the cochlea, where the latter is the larger. Again, the size of both scalæ diminishes from base to apex of the cochlea in conformity with the general diminishing spiral.

In the Duckbill the scala vestibuli is throughout larger than the scala tympani; and whereas the former diminishes its size, and alters its shape from the commencement to the end of the cochlea, the latter is throughout of the same size and shape.

The Scala Media.—The scala media or ductus cochleæ in the typical Mammal is a triangular tube, almost equilateral at its commencement at the base of the cochlea.

* 'Quarterly Journal of Microscopical Science,' p. 397, 1876.

† In my specimens the acid decalcifying fluid has dissolved out the otoliths.

But on proceeding up the spiral, the floor becomes broader and the height lessened, so that the acute angle formed by the membrane of REISSNER and the lamina spiralis becomes more and more acute. These changes in form are not nearly so marked in the *Ornithorhynchus;* the membrana basilaris does get broader and broader, but not nearly in the same degree as in the typical Mammal. As regards the peculiar changes in the organ of CORTI, such as the lengthening of the rods, &c., which are so marked in the spiral cochlea, they are the same, but less marked in the *Ornithorhynchus* so far as I have been able to trace them out.

In the membrane of REISSNER of this Monotreme the epithelial cells are thicker than in the typical cochlea; but the great feature of difference is the presence of blood-vessels running across the membrane from lamina to ligament, forming here and there convoluted knots. These I have never found in any other Mammal, nor have they been described in this situation as far as I am aware.

The ligamentum cochleæ of the Duckbill, both as regards its shape and structure, scarcely differs at all from that of the typical Mammal; and the same may be said of the stria vascularis and its other epithelial lining.

The lamina spiralis ossea, with its limbus and sulcus, present no special points of difference. The same may be said of the membrana basilaris, with this slight exception—that whereas in the ordinary Mammal one large blood-vessel (the vas spirale) runs through its lower stratum just below the rods of CORTI, in the Duckbill two small vessels are generally to be found (see Plate 46, fig. 6)—one in the usual position, and the other a little further inwards (towards the ligament).

The organ of CORTI itself differs very slightly from that of the ordinary cochlea. There are the same number of rows of bristle cells as are found in the lower Mammals,* namely, one on the outer side of the rods and three on the inner. The trabeculæ are thicker, and their feet larger than usual; so much so, that the lower part of the first trabeculum may be easily mistaken for the foot of the inner rod.

The rods of CORTI are somewhat different; they stand more upright, so that the tunnel is not so wide; the extremities are not so well developed, the feet being smaller and the heads not so broad. I have not been able to make even an approximate calculation of the number of rods or bristle cells, but there must be a much fewer number of these in the Duckbill's cochlea than in that of the ordinary Mammal.

The course taken by the cochlear nerve and its branches differ in no essential points from those of the typical Mammal. There is in the former a ganglion very similar in relative position and component cells to the ganglion spirale. The only differences are that, whereas in the spiral cochlea the nerve trunk necessarily runs at right angles to the lamina spiralis, in this cochlea it runs parallel to the corresponding lamina; and that in the Duckbill the terminal branches pass to supply a lagena, an organ not found in the ordinary Mammal.

* In the primates there are five and six rows of bristle cells in the upper part of the spiral, as pointed out in my paper above cited.

The last and most important difference is the presence of this lagena at the end of the membranous labyrinth (ductus) of the Monotreme's cochlea. Nothing approaching it has ever been found in the spiral Mammalian cochlea, although a very similar condition is found at the apex of the Bird's, as will be described later on. This little addition in the Duckbill forms another of the many links between the Mammal and Bird found in this peculiar animal.

*A brief sketch of the Bird's cochlea** will now be necessary before any satisfactory comparison can be made, and it must be borne in mind that the cochlea of the Amphibia and Reptilia is similar in type, though less highly developed, to that of the Bird.

As already stated, the bony labyrinth of the Bird's cochlea is a slightly curved tube with an enlarged anterior extremity; within this is contained another more or less complete framework of dense connective tissue, cartilaginous in consistence, and very similar in structure to the so-called cartilage of the eyelid.

At the vestibular extremity of the tube this cartilaginous framework consists of two pieces, one on each side of the tube, named, from their shape, the quadrilateral and triangular cartilages (see Plate 46, fig. 8).

Stretching across the cochlea and joining these two is a strong membrane (membrana basilaris), and thus the tube is divided into two, which for convenience of description and clearness of comparison may be called the scala tympani and the ductus cochleæ.

These are not of equal size in any part of the cochlea tube; the upper or ductus cochleæ being the larger even at the commencement, and the lower or scala tympani becoming smaller and smaller until it quite disappears by ending in a cul-de-sac before the enlarged anterior extremity, the lagena, is reached.

On tracing the two cartilages forwards their triangular and quadrilateral forms become, first, more marked and then they increase in size. Not only do they enlarge generally, but their upper and lower margins extend further and further round the circumference of the tube until they meet both above and below; thus forming a complete cartilaginous tube, which is somewhat loosely adherent to the bony wall by means of connective tissue.

As this cartilaginous tube is being completed, the scala tympani is gradually encroached upon, until it is entirely filled up by the cartilage, which at length also displaces the membrana basilaris; thus there is only a single scala at the anterior end of the cochlea. Before the disappearance of the scala tympani the quadrilateral and triangular plates begin to diminish in thickness and gradually lose their characteristic forms, until in the lagena the cartilaginous tube becomes of equal thickness all round.

The roof of the ductus is membranous; and this membranous roof is not a simple arch, but is re-duplicated into a number of longitudinal (to the tube) folds of some thickness, which in many Birds fill up the greater part of the interior of the ductus

* This description has been taken from my own observations, which confirm most of the statements of Hasse and Meyer.

(see Plate 46, fig. 8). This is called the tegmentum; it is a very vascular membrane, lined with large, rounded, granular, pigmented, epithelial cells, intermixed with some very transparent ones.

Tracing the epithelial layer down to the triangular cartilage on one side, and the quadrilateral cartilage on the other, the cells change their character. Those lining the upper surface of the triangular cartilage and the adjacent portion of the membrana basilaris become transitional or cuboid in shape, with well marked nuclei. Those covering the upper surface of the quadrilateral cartilage are columnar, and of these there are two kinds. The contents of those nearer to the tegmentum are peculiar, resembling in appearance the matrix of ordinary cartilage, and this is readily coloured by staining agents. Further onwards, where the surface of the cartilage curves downwards to come to the level of the membrana basilaris, these cells are replaced by other columnar cells, the contents of which are very transparent. These are again succeeded by the mass of nerve epithelium, which may be termed the organ of CORTI.

The organ of CORTI is a broad band of nerve epithelium, resting partly on the upper surface of the quadrilateral cartilage and partly on the adjacent portion of the membrana basilaris.

This organ of CORTI consists chiefly of two layers of cells. One set is composed of nuclear cells (as described in the Mammalian organ of CORTI) which lie on the membrana basilaris and surface of the quadrilateral cartilage. The other layer is situated at the surface of the organ; the cells of this layer have distinct outlines, are rounded or elongated, have distinct nuclei, and they each bear on their summit a short thorn. These thorns are formed of several short bristles united together, and they project through holes in a membrane which limits the organ, and which is very similar to the membrana reticularis of the maculæ acusticæ and serving the same purpose.

From this membrana reticularis pass down numerous fibres or trabeculæ to the membrana basilaris, binding the two membranes together.

Covering the whole organ and also some of the columnar cells of the quadrilateral cartilage is a thick mucoid layer into which the thorns project; this mucoid layer is the membrana tectoria.

The cochlear branch of the auditory nerve runs along the tube, first in the scala tympani and then in the substance of the quadrilateral cartilage. It gives off fibres all the way up, which immediately enter ganglionic cells, and then pass upwards towards that part of the upper surface of the cartilage on which the organ of CORTI lies.

Here the fibres pierce and enter the organ, not by a single row of perforations but by numerous apertures throughout the whole width of this portion of the quadrilateral cartilage. From these perforations nerve filaments pass in a radiating manner to the upper row of cells (hair cells), and possibly also to the lower cells, but their exact distribution has not been made out.

At the enlarged extremity (lagena) of the cochlea tube, which is entirely occupied by the membranous labyrinth, the lining is considerably modified, and a large patch of nerve epithelium is found, quite distinct in character and separate from the organ of CORTI. This nerve epithelium is made up of cells exactly like those found in the macula acustica of the vestibule of Mammals* and Birds, *i.e.*, with the alternating long bristles and thorns which project from the surface into a mucoid mass containing otoliths. The terminal branches of the cochlear nerve pass forwards to this patch of nerve epithelium, and terminate in the same manner as in the macula acustica of the vestibule.

The interior of the cochlea of the Ornithorhynchus *compared with that of the Bird.*

The differences between these two are so great that it will be well first to notice the homologous and analogous parts in each, and then to consider the similarities and dissimilarities.

In examining the drawings Nos. 2 and 8, it will be at once evident that the lamina ossea of the *Ornithorhynchus* (and other Mammals) corresponds to the quadrilateral cartilage of the Bird, and that the Mammalian ligamentum cochleæ is represented in the Bird by the triangular cartilage. Also, that whereas the lower division or scala tympani of each corresponds, the ductus cochleæ of the Bird occupies the whole of the upper division, and therefore corresponds to the scala vestibuli and scala media (or ductus cochleæ) of the Mammal. On more minute examination, the peculiar folded tegmentum of the Bird will be found to take the place of the stria vascularis and membrane of REISSNER of the Mammal; and by carrying the examination into the fœtal condition, the peculiar hyaline columnar cells of the quadrilateral cartilage will be found homologous with the teeth of the Mammalian limbus, which is represented in the early fœtus by very similar cells.

Dissimilarities in the Bird's cochlea:—

The absence of the scala vestibuli and membrane of REISSNER.

The gradual tapering and final termination in a cul-de-sac of the scala tympani.

The cartilaginous condition of the structure corresponding to the Mammalian ligament.

The cartilaginous condition of the structure which corresponds to the lamina ossea.

The cartilaginous tubular formation towards the apex of the cochlea.

The tegmentum, with its folds and peculiar pigmento-granular cells.

The absence of the marginal sulcus.

The absence of the rods of CORTI.

The large number of rows of hair cells.

The matting together of the hairs into a sort of spine.

The numerous perforations for the passage of nerve filaments into the organ of CORTI.

* 'Quarterly Journal of Microscopical Society,' October, 1876.

Lastly, the ductus cochleæ is almost straight in the Bird, whereas in the typical Mammal it is spiral, and even in the *Ornithorhynchus* it is coiled round at the apex.

Similarities:—

The membrana basilaris and membrana tectoria are very much alike in both types of cochlea. Also the mode of distribution of the nerves, including the ganglionic mass.

But more important than these is the presence of a lagena with its vestibular-like nerve epithelium, which is found at the apex of the cochlea both in the *Ornithorhynchus* and the Bird, but not in that of the typical Mammal.

General résumé.

1. That although the general form of the cochlea tube of the *Ornithorhychus* is like that of the Bird (as it is almost straight and of equal size throughout, instead of being a tapering spiral), yet its internal arrangement and microscopical structure is unmistakably Mammalian in type.

2. That the acoustic apparatus of the organ of CORTI is not nearly so extensive as in typical Mammals, nor do the various minute structures forming it appear to be so well developed.

3. That the cochlea of the *Ornithorhynchus* possesses an addition (the lagena) to its membranous labyrinth which is also found in the Bird, but which is not found in the ordinary Mammal. And thus the presence of this lagena may be looked upon as another of the many links between the Bird* and Mammal which are found in this Monotreme.

Mode of preparation adopted in this research.

For obtaining thin sections of this cochlea I made use of the same mode of procedure as described in my paper on the organ of CORTI in Mammals, read before this Society in 1876, which is briefly as follows:—

The tissues were hardened in an alcoholic solution of chromic acid; the bone decalcified in a dilute ($\frac{3}{4}$ per cent.) solution of nitric acid aided by almost constant movement of the tissue, by means of an ordinary meat roasting-jack.

Saturated with gum-water, then dehydrated in alcohol, imbedded in parafin, cut by a razor in a STIRLING'S machine. Variously stained and mounted.

In order to obtain a correct idea of the relation of the parts, I mounted the sections of certain cochleæ in their proper order throughout; this I did with sections cut transversely and longitudinally, in the former case cutting the cochlea into about 120 sections, and in the latter making about 10 thicker ones. By this means, aided by

* But it must be borne in mind, as already stated, that the Bird's cochlea is similar to that of Reptiles and Amphibians; and therefore this lagena is really a link between the cochlea of the higher and lower vertebrates, and not merely between that of the Mammal and Bird.

unsoftened preparations filed down, I was able to get a very clear demonstration of the relative position of the parts.

But all these methods, and in fact the whole research, would have failed had it not been for the very prompt and careful manner in which the skulls were prepared and preserved before they were sent over to England, and for which kindness I desire here to offer to my Australian friends my sincere and heartfelt thanks.

Description of Plates.

Fig. 1. Longitudinal section through Duckbill's cochlea. × barely 20 diameters.

1. Opening into vestibule.
2. Apex, or anterior extremity of cochlea.
3. Helicotrema, the communication between the scalæ tympani and vestibuli.
4. Cavity of lagena; (⟵⋘) tube connecting it with ductus cochleæ.
5. Upper surface of lamina ossea.
6. Upper surface of organ of Corti, (α) membrane of Reissner covering organ of Corti, &c., (α') ditto turned back.
7. Ligamentum cochleæ cut through.

Fig. 2. Transverse section through Duckbill's cochlea (middle), from No. 27 of series. × 75 diameters.

1. Scala tympani.
2. Scala vestibuli.
3. Scala media or ductus cochleæ.
4. Lamina ossea, (α) nerve with ganglion.
5. Ligamentum cochleæ, (c) blood-vessels, (b) stria.
6. Membrane of Reissner.
7. Organ of Corti, (d) membrana tectoria, (e) membrana basilaris, (f) marginal sulcus.

Fig. 3. Transverse section through Duckbill's cochlea (vestibular end), from No. 38 of series. × 22 diameters.

1. Scala tympani.
2. Scala vestibuli.
3. Scala media or ductus cochleæ.
4. Lamina ossea.
5. Ligamentum cochleæ.
6. Membrane of Reissner.
7. Membrana basilaris.

Fig. 4. Transverse section through Duckbill's cochlea (apex), from No. 13 of series. × 22 diameters.

1. Scala tympani.
2. Scala vestibuli.
3. Scala media or ductus cochleæ.
4. Lamina ossea, (*a*) ganglion.
5. Ligamentum cochleæ, (*b*) stria vascularis.
6. Membrane of REISSNER.
7. Membrana basilaris.
8. Cavity of lagena.

Fig. 5. Transverse section through lagena of Duckbill's cochlea, from No. 13 of series. × 100 diameters.

1. Cavity of lagena.
2. Scala vestibuli.
3. Nerve epithelium.
4. Nerve fibres.
5. Mucoid mass.

Fig. 6. Transverse section of organ of CORTI of Duckbill, built up from several specimens. × 400 diameters.

1. Scala tympani.
2. Scala media or ductus cochleæ.
3. Lamina ossea, (*a*) nerve.
4. Membrana basilaris, (*b*) blood-vessels, corresponding to vas spirale.
5. Triangular tunnel.
6. Marginal sulcus.
7. Outer rod of CORTI.
8. Inner rod, (*c*) trabeculæ.
9. Inner hair cells.
10. Outer hair cell.
11. Cells of DEITERS.
12. Extra row of hair cells.

Fig. 7. Transverse section of lamina ossea (Duckbill) showing a blood-vessel passing up on to the membrane of REISSNER. × 150 diameters.

1. Limbus of lamina ossea.
2. Membrane of REISSNER.
3. Blood-vessel.
4. Blood-vessel forming a knot.

Fig. 8. Transverse section through middle of the Magpie's cochlea. × 75 diameters.

1. Scala tympani.
2. Ductus cochleæ.
3. Quadrilateral cartilage, (*a*) blood-vessels.

4. Triangular cartilage.
5. Nerve, (*b*) ganglionic cells, (*c*) fibres passing through cartilage.
6. Tegmentum, (*e*) folds.
7. Organ of CORTI, (*f*) membrana basilaris, (*g*) membrana tectoria, (*d*) bone.

POSTSCRIPT.

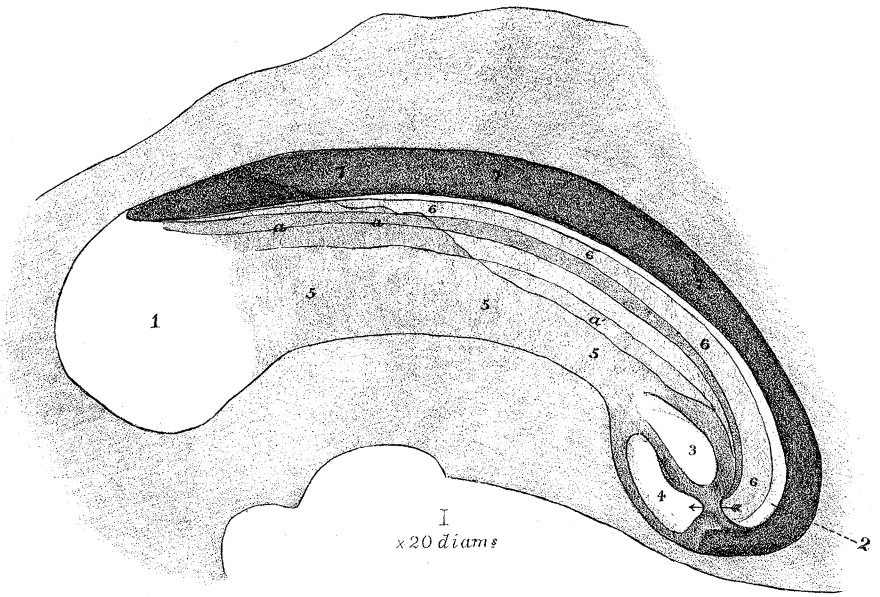
(Added January 26, 1881.)

To prevent misunderstanding, it may be as well to state that the object of this memoir being the description of the cochlea of the *Ornithorhynchus* and its comparison with that organ in the ordinary Mammal and Bird, I have purposely omitted the description of these last, except where necessary for such comparison.

Very complete descriptions of these will be found in QUAIN'S 'Elements of Anatomy,' 8th edition, vol. ii., for the Mammal; and in PAUL MEYER'S 'Labyrinthe Membraneux du Limaçon chez les Reptiles et les Oiseaux, 1876' (published by J. B. BAILLIÈRE et FILS, Paris), for the Bird and lower vertebrates.

Since presenting this memoir I have discovered a second row of hair cells to the outer side (corresponding to inner side of ordinary Mammals) of the rods of CORTI (see Plate 46, 12, fig. 6, 12).

This is the only animal in which I have seen an additional row of hair cells in this position; nor, indeed, am I aware of such a peculiarity having been noticed by other observers in any form of cochlea.



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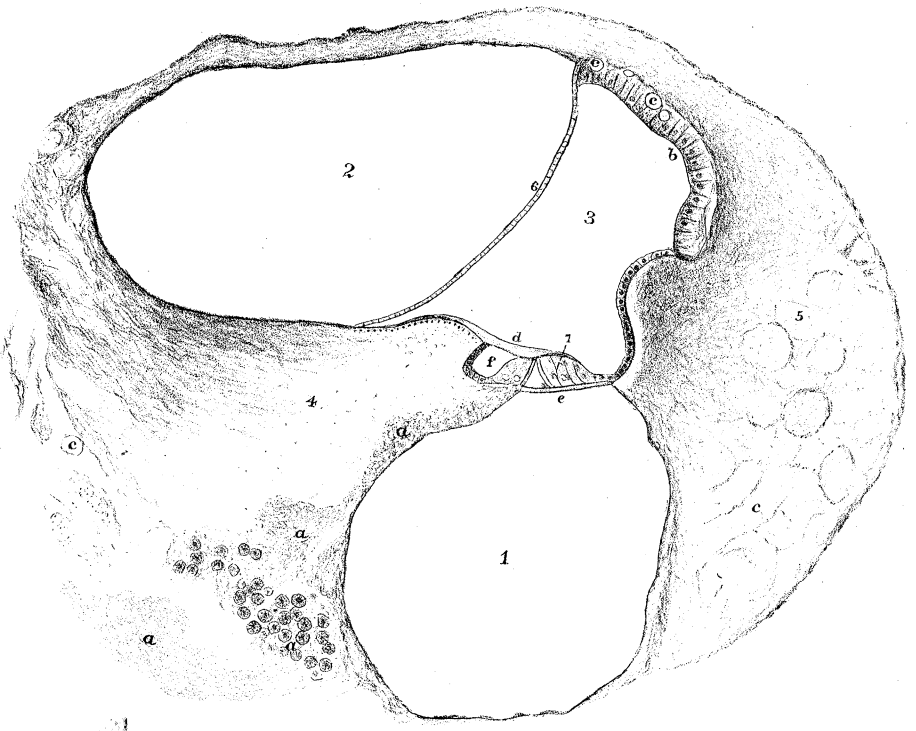

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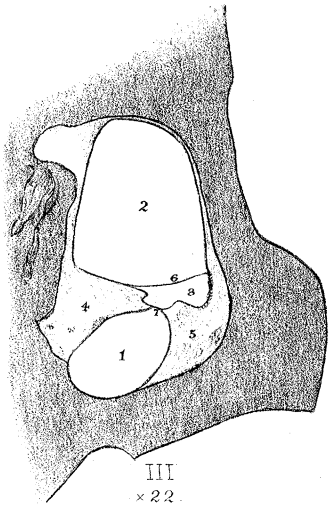
×75



III
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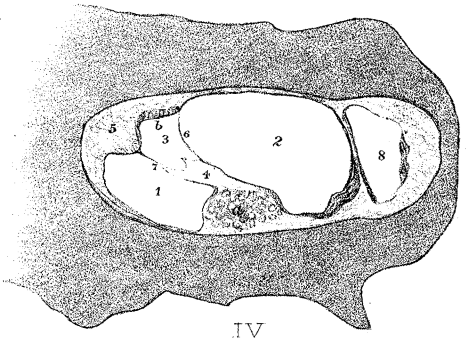
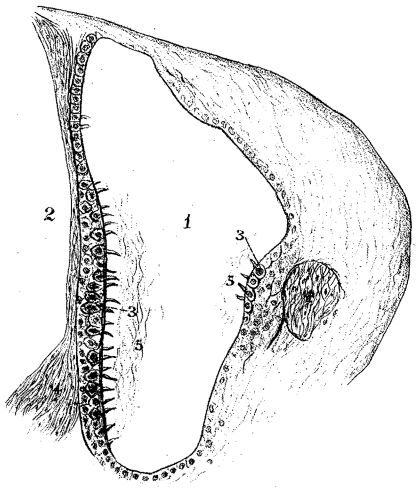


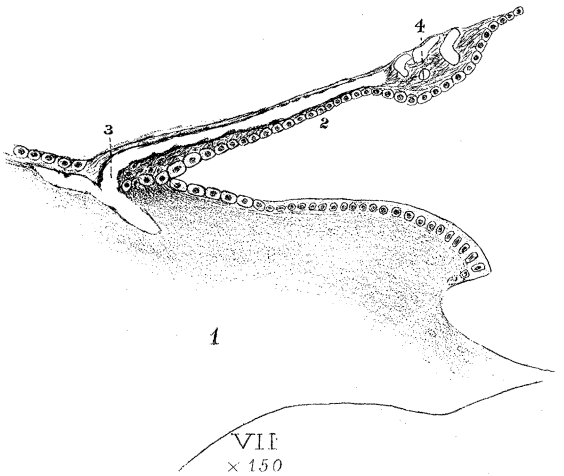
IV
×22

E. M. SPILLER, del.

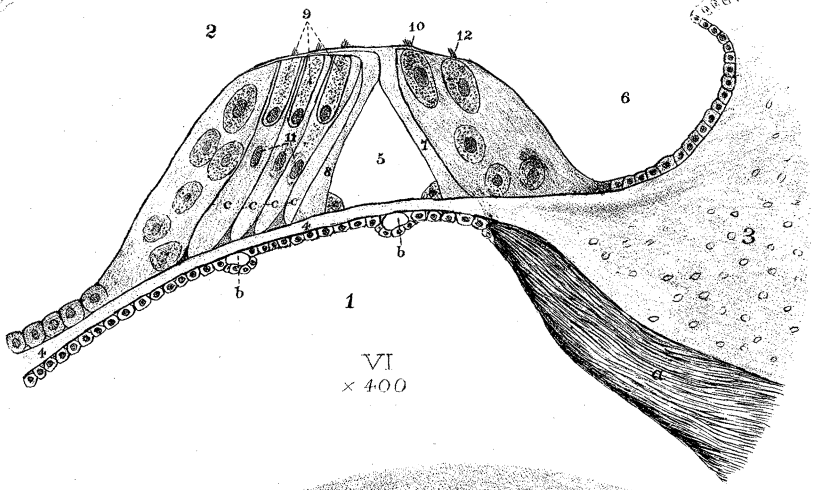
Lithographed etc. under the direction of E. Noble Smith.



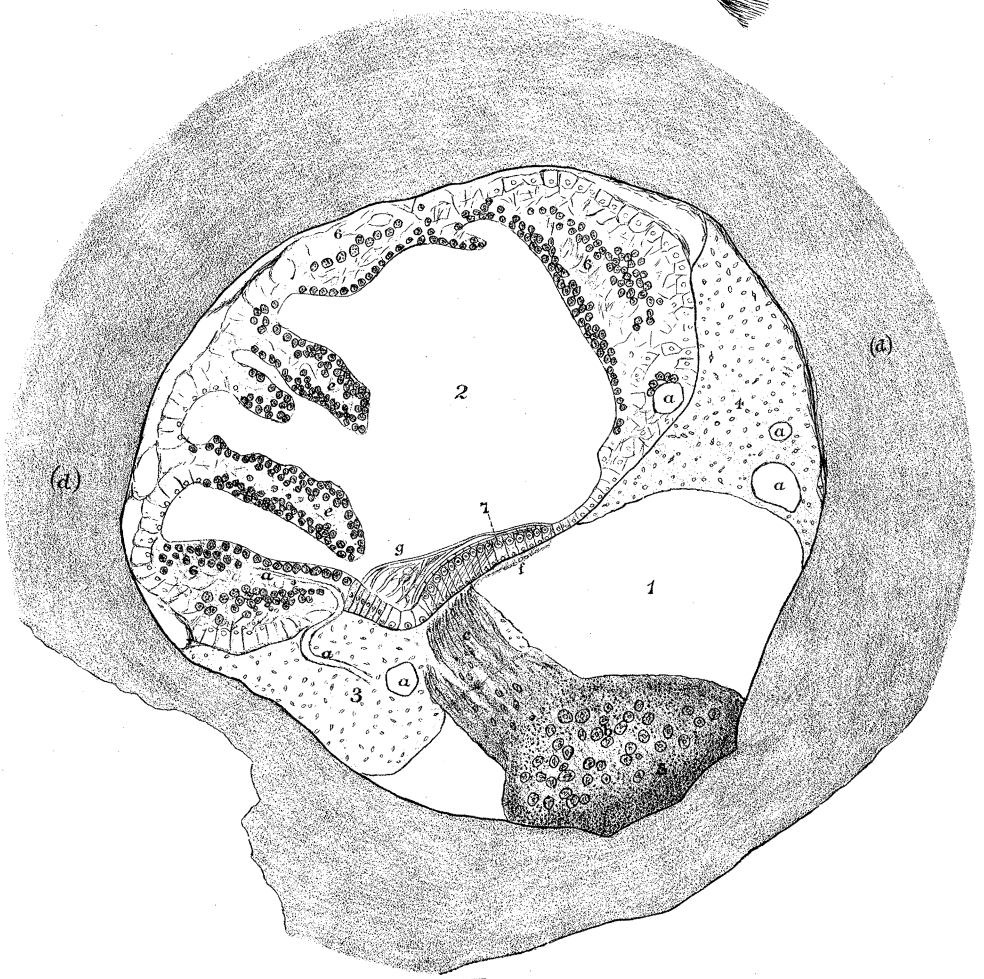
V
× 100



VII
× 150



VI
× 400



VIII
× 75

E.M.SPILLER, del.

Lithographed etc under the direction of E.Noble Smith.