The Cochlea of the Dolphin, *Tursiops truncatus*: General Morphology*

(organ of Corti/ear/light microscopy)

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ABSTRACT  The anatomy of the cochlea of the dolphin *Tursiops truncatus* was studied in a number of specimens after fixation by vital perfusion, colloidin embedding, and serial sectioning. The results reveal the general structural relations and cellular detail up to the limits of light microscopy. A description is given of the variations of structure along the course of the cochlea, in which there are many departures from the typical mammalian form, especially in the compact quality of the tissues and the sturdiness of its elements. Apparently these features represent an adaptation of the cetacean ear to the reception of high-frequency sounds.

Though many have studied the gross anatomy of the cetacean ear (1), the detailed structure of the cochlea has received little attention. Boenninghaus (2) examined several specimens of *Phocaena communis*, and observed the general form of the membranous labyrinth. Kolmer (3) studied a young specimen of *Phocaena* obtained a few hours after death, and was able to make out many of the cellular structures. He identified the kinds of epithelial cells, the supporting elements of the organ of Corti, and the hair cells, and pointed out especially the great size of the cells of Claudius, which he characterized as the largest epithelial cells known in mammals. Two other reports are mentioned in the references § (4¶).

METHOD

Our study was performed on specimens of the bottlenosed dolphin, *Tursiops truncatus* Montagu, that had been used in an electrophysiological investigation of sound conduction (5). At the end of the tests on these ears, the anesthetized animals were perfused for histological examination. The blood was flushed out through a cannula in the dorsal aorta with about 40 liters of physiological saline, and then the tissues were fixed with 120 liters or more of a mixture of potassium dichromate, sodium sulfate, formaldehyde, and (sometimes) mercuric chloride. The ears were removed, further fixed by immersion for 10 days, then held in 10% formol for final processing.

The dolphin ear is a formidable object for histology, as Kolmer remarked earlier (3). We used several specimens and more than a year for the necessary adaptations of our usual methods. In our final procedure, we decalcified the tissues in 0.5% nitric acid in 10% formol, changed the solution 60 times over a period of 3 months, dehydrated the tissues in a series of alcohols ranging from 20 to 100%, in 10% steps, over a period of 1 month, embedded the tissues in celloidin in four steps from 4 to 16% over a period of 6 months, and finally hardened them in chloroform and 80% alcohol.

We determined the proper orientation for sectioning by preparing skulls with the ear bones in place, and in two preparations the petrous bone was carefully ground away to expose the cochlear turns. Sections were cut at 30 µm, usually in a plane parallel to the cochlear axis, either approximately vertical to the head, as shown in Fig. 1, or at right angles to this position. One specimen was sectioned in a plane perpendicular to the cochlear axis.

All sections through the ear were stained and mounted. For some of the series, we used Pollak's trichrome stain and for others a combination of hematoxylin, azocarmine, and orange G.

* This is the first of a series of articles on the cochlea of the dolphin, *Tursiops truncatus*.
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§ Bloome, K., The delphinid auditory apparatus, Parts I and II. Unpublished; seen in manuscript. An electron microscope study of tissues from freshly killed dolphins. Special attention is given to the microvilli on many of the sensory cells.
¶ In Russian, translated by Joint Publications Research Service. The description of cochlear structures is brief and indicates close similarities to terrestrial mammals.

FIG. 1. A posterior view of a skull of *Tursiops truncatus*, showing the vertical planes for right and left cochleas.
Of 25 ears treated in the preliminary and final procedures, good to excellent results were obtained in 7, and in 6 others the series were useful for such purposes as observations of the width of the basilar membrane and the distribution of ganglion cells.

The first step in the study of these ears was the graphic reconstruction of the cochlear spiral by Guild's method (6). The junctions between the inner and outer pillar cells were located for every cochlear turn cut tangentially, and these points were laid out on a graph along a chosen axis. Semicircles were drawn from centers on the axis to connect the appropriate points, yielding a good approximation to a spiral except for the two end portions. The end points were located and measurements were made between them and cochlear turns already outlined, from which the extensions were drawn in. The result is an orthogonal projection to scale of the cochlear spiral, as represented for a particular ear in Fig. 2. Section numbers are shown on the left.

This ear contains a little over two cochlear turns, and the length of the basilar membrane, found by stepping off the distances from the basal end as shown, is 38.5 mm. The concentricity of the constructed spiral indicates the accuracy of orienting the block of tissue in sectioning.

RESULTS

All the suitable specimens were thoroughly studied, and all enter into our conceptions of the anatomical relations. For simplicity of presentation, however, we mainly picture a single specimen, the one whose spiral is given in Fig. 2.

General orientation

A mid-modiolar section of the cochlea is shown at low power in Fig. 3, in which the cochlear spiral is cut through at four places. Reference to Fig. 2 at the level of Section 158 will show that this number of cuts must occur, and will show also that these cuts are nearly transverse, i.e., are nearly perpendicular to the course of the basilar membrane.

As we follow the four cochlear regions of Fig. 3 from lower-left upward and to the right, we encounter in order the lower basal, lower apical, upper apical, and upper basal half-turns. The same order is seen in the spiral diagram in going from left to right at the level of Section 158.

The large cochlear nerve is seen as it sends its bundles into the ganglionic masses in the different turns. The ganglia are only partially enclosed in the bone of the modiolus in basal and lower apical regions, and in the upper apical region the ganglion lies almost free in the scala tympani.

This picture indicates also the varying size of the cochlear structures from lower basal to upper apical regions. We see in this progression a decrease in the cross-sectional area of the scala tympani, an increase in the area of the scala vestibuli, the greatly diminishing mass of the external spiral ligament, a considerable increase in the width of the basilar membrane, and a moderate increase in the size of the tectorial membrane.

Cochlear structure

The features just mentioned, along with others, are better seen in enlarged views of the different regions. Five such views are given by the drawings and photomicrographs of Figs. 4-8, which include two positions in the lower basal and one each in the other three half-turns. The locations along the cochlea of all five figures are indicated by the numbered circles of Fig. 2.

(a) In the basal region there is no clear distinction between external sulcus cells and Claudius cells. These tall columnar cells extend as a continuous row from the edge of the basilar membrane along the shallow sulcus to the thickest portion of the spiral ligament. In the apical region, a distinction might be made: the Claudius cells may be taken as those over the basilar membrane and the external sulcus cells as the ones turning upward along the spiral ligament.

From the basal-end upward these cells undergo a progressive change in size, from a maximum height in the basal region around 145 µm to about 7 µm in the upper apical region. At the same time the epithelial strip greatly changes its form.

Kolmer described these large cells in Phocaena as showing a series of infoldings along their sides, a feature that he considered usual in mammals. No such feature is seen in our better specimens. Something similar appears in our poorer specimens, which we consider to be an artifact.

(b) Boettcher cells are found in most mammals only in the basal part of the cochlea as a compact group of low-lying cells on the outer edge of the basilar membrane, overlaid by the Claudius cells. These cells in Tursiops are few at the basal region.
end and increase steadily in numbers to the upper basal half-turn (Fig. 6), where about 12 may be seen in two levels. The two-level arrangement continues into the lower apical region (Fig. 7) with a slight increase in the numbers of cells. Beyond, in the upper apical region, these cells can no longer be identified.

(c) Internal sulcus cells almost fill the bay between basilar membrane and limbus in the lower basal region. A regular feature here is a roof-like structure formed by one or two of these cells that extend from the inner hair cell to the lower edge of the limbus, and appear to provide support for the inner hair cell and the head of the inner pillar. This feature is still present in the upper basal half-turn (Fig. 6), and a tenuous connection persists at the beginning of the lower apical turn (27 mm position). Thereafter in the apical turn (Fig. 8) this connection is absent.

(d) The organ of Corti contains the usual elements: arch of Corti, Hensen cells, Deiters cells, and hair cells, all overlaid by the tectorial membrane.

(i) The two pillars of Corti's arch are unusually thick and sturdy, especially in the basal region. Even toward the apex these elements are thick in comparison with those of other mammals.

(ii) The Hensen cells are difficult to identify in our material. Kolmer used two criteria to distinguish them from Claudius cells: a low position for the nucleus of the Hensen cell, as opposed to a position at the top end in the Claudius cell, and the presence of a diplosome near the nucleus of the Claudius cell. These criteria have not proved useful for our material. No diplosome could be found, and the nuclei had somewhat variable positions for both types of cells. Therefore, the Hensen cells could only be distinguished by position. They lie just outside the outermost hair cells, and seem to serve two functions, as a buttress for the outer edge of the reticular membrane and (sometimes) as a support for the line of outermost Deiters cells. The buttress cells are usually small but the supporting cells are usually large.

At the extreme basal end are only two cells that can clearly be identified as Hensen cells. One serves the buttress

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**Fig. 4.** Drawing of a section of the right ear of a specimen from *truncatus*, showing the lower basal region (Section 242, representing a position 7.9 mm from the basal end). This and the next four figures are from the same ear, and the figure numbers are shown in the circles along the spiral of Fig. 2. (×200)

**Fig. 5.** Drawing of the same specimen as in Fig. 4, showing the lower basal half-turn at a point 12 mm from the basal end of the cochlea. (×95)
function by an attachment to the reticular membrane, and also extends downward to the basilar membrane as a supporting element. The other cell, that is considerably thicker, fills the space between the first cell and the Deiters cell.

In the middle of the lower basal half-turn (Fig. 4) the buttress structure is better developed, and consists of three or four cells forming a lateral column that extends from the edge of the reticular membrane. A long, thick supporting cell with its foot on the basilar membrane runs along the outermost Deiters cell.

Farther apically, the number of small surface cells grows and the lateral extent of the buttress increases, and at the same time the number of space-filling cells grows. With this proliferation in the apical region (Figs. 7, 8) it becomes difficult to determine where Hensen cells stop and Claudius cells begin.

(iii) The Deiters cells arise from expanded feet on the basilar membrane as long columns that support the outer hair cells. In the extreme basal region they are thick and sturdy, and are inclined about 60° to the basilar membrane in line with their hair cells. Their upper ends contain deep depressions in which the base of the hair cell snugly rests.

Farther apically in the lower basal region (Fig. 5 and Fig. 9(a) the Deiters cells are longer and more slender, and their inclination increases to about 45°. From here on they cease to be perfectly aligned with their hair cells (Fig. 9b). Farther up the cochlea, the Deiters cell becomes still more oblique in its lower portion, and its upper portion curves around to make

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**Fig. 6.** Photomicrograph of the same specimen as in Fig. 5, showing the upper basal half-turn at a point 21.5 mm from the basal end of the cochlea. (×180)

**Fig. 7.** Photomicrograph of the same specimen as in Fig. 6, showing the lower apical half-turn at a point 29.8 mm from the basal end of the cochlea. (×180)

**Fig. 8.** Drawing of the same specimen as in Fig. 7, showing the upper apical half-turn at a point 36.4 mm from the basal end. (×200)
the junction with the hair cell (Fig. 9c). In the apical turn, the misalignment between the main course of the Deiters cell and its hair cell becomes of the order of 120°.

(ii) Outer hair cells occur mostly in three rows, as in many mammals, but beginning in the lower apical half-turn there is a somewhat irregular occurrence of four rows that continues in the upper apical region. These hair cells are relatively short, of the order of 8 μm in the lower basal region and increasing to about 17 μm in the apical region.

The inner hair cells are larger, flask-shaped, and lie in a single row medial to the arch of Corti. They rest on the inner supporting cells and are bounded laterally by the internal sulcus cells.

In summary, the organ of Corti in the dolphin is distinguished by a sturdy structure, with relatively large, closely packed supporting cells. The usual lymph spaces are much reduced. The inner sulcus at the basal end is entirely filled and elsewhere shows only a small opening. The structure gives an appearance of great strength and rigidity, and seems well adapted to the reception of high-frequency tones.

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