tubes or scalæ on either side of the membranous cochlea are perilymph spaces. The upper tube, when followed down to the base of the cochlea, is found to open freely into the cavity of the vestibule; hence its name of *scala*

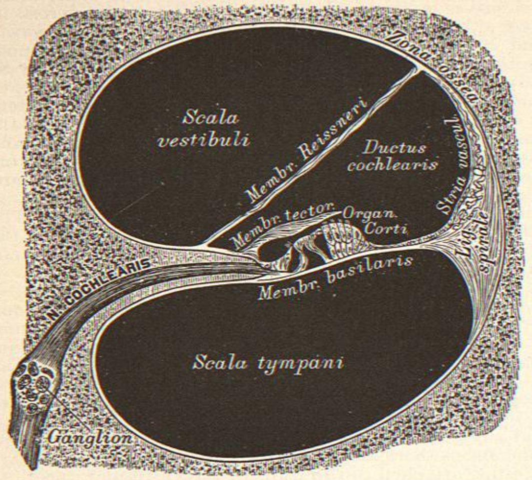

FIG. 408.—Semidiagrammatic Section of a Cochlear Whorl. (After Heitzmann.)

vestibuli. The lower tube ends blindly at the base of the cochlea, but, where this part bulges into the tympanum as the "promontory" of its inner wall, it is perforated by the aperture known as the *fenestra rotunda* whose proper membrane alone prevents the perilymph from escaping into the middle ear. This tube is therefore called the *scala tympani*. From its central position the membranous cochlear canal is sometimes known as the *scala media*.

As the spiral staircase formed by the osseous lamina spiralis and the membranous basilar membrane winds round the modiolus from the base to the apex or *cupola* of the cochlea, the radial width of the basilar membrane increases while that of the bony lamina decreases. In the basal whorl of the cochlea the width of the two is about equal, but near the cupola the lamina spiralis is nearly wanting. The radial width of the basilar membrane is said to vary from .36 mm. at the top of the cochlea to about .21 mm. near the bottom. The scala vestibuli and the scala tympani have no communication except through a small aperture under the cupola of the cochlea known as the *helicotrema*; this is bounded by the hook-like termination, the *hamulus* (Fig. 404), of the bony lamina spiralis, which forms the greater part of a ring completed by the pointed, blind extremity of the canalis cochlearis fastened above the hamulus to the cupola.

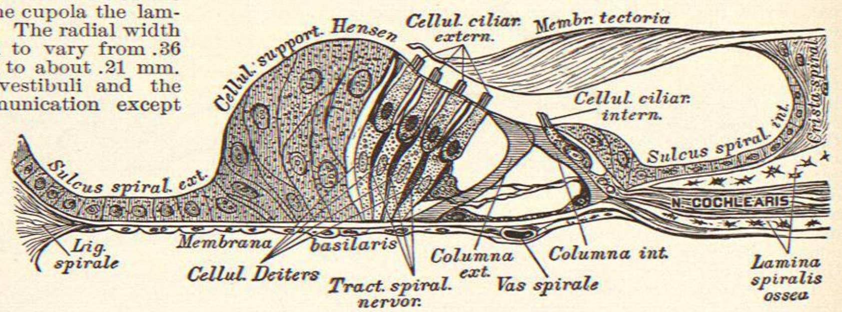

FIG. 409.—Semidiagrammatic Section of the Organ of Corti. (After Retzius, from Heitzmann's "Anatomie des Menschen.")

Transmission of Vibrations through the Labyrinth.—We have seen above (p. 613) that composite air waves differ from the single pendular vibrations of which they are made up by their form. That is, while in a single pendular vibration the motion of an oscillating air particle is similar, and its acceleration or retardation is uniform on each side of the point of rest, in the composite wave this is not so. The tympanic membrane must respond to all the variations in the sound pulses entering the meatus and transmit them with exactness, though with diminished amplitude and increased force, to the foot of the stapes. The end of the long process of the incus rises somewhat in its inward excursion, so that the head of the stapes is slightly raised at each impulse. The motion of the stapes in the fenestra ovalis is, therefore, not so much that of a piston in a cylinder as a *wobble* about an axis that runs parallel and near to the lower edge of the footplate.* As the maximum excursion of the incus-stapes articulation is only about $\frac{1}{14}$ mm., that of the foot of the stapes must be still further reduced and increased in power.

The fluid of the labyrinth being incompressible, any considerable inward movement of the stapes must be attended by provision for the outlet of the displaced fluid. Such a safety valve is found in the fenestra rotunda. Perilymph pressed away from the oval window may find a free vent by passing through the scala vestibuli toward the apex of the cochlea, through the helicotrema, backward by way of the scala tympani, at the basal end of which it finds the fenestra rotunda, and may cause its covering membrane to bulge into the tympanum. That such a transference of fluid in the direction from the oval to the round window can take place was demonstrated by Politzer, who inserted a glass tube in the fenestra rotunda and found that fluid in the tube took a higher level when strong air pressure was brought to bear on the outside of the tympanic membrane. It is hardly conceivable, however, that actual molar motion of perilymph through the helicotrema occurs with each oscillation of the foot of the stapes. The effect upon the membrane of the round window of a continuous musical note, for example, is probably to give it a fixed position midway between that resulting from the maximum and that resulting from the minimum displacement at the oval window. This action may be illustrated by a device sometimes used for the determination of the mean arterial blood pressure of an animal; the mercury manometer is constricted at one point to a narrow orifice which blocks the rapid oscillations of the heavy mercury, so that the difference in level of the fluid in the two limbs of the instrument is constant and represents the mean between the varying pressures. That the actual transfer of fluid from the scala vestibuli to the scala tympani is not necessary for the irritation of the nervous mechanism of the cochlea is indicated by audition through bone conduction, in which it seems that molecular vibrations may arouse the sense of sound by direct transmission through the osseous cochlea. We may look upon the action of the stapes as that of a hammer which applies sharp taps to the perilymph.

As the terminations of the auditory nerve are all within the closed and complex membranous labyrinth, vibrations of the perilymph, to have sensory effect, must be taken up by the wall of that structure. The sensory epithe-

* Henke, quoted by Hensen: Hermann's Hdb. der Physiologie, Bd. iii., Th. 2, S. 36.

lium of the saccule, utricle, and semicircular canals would seem to be impressed by vibrations proceeding directly from the oval window. Considering the minuteness of the canalis reuniens, it is not probable that irritation of the cochlear nerve depends upon vibrations reaching them through the endolymph of the saccule, but that it is achieved through motion imparted by the broad way of the scala vestibuli, the diminishing calibre of which toward the apex of the cochlea would seem adapted to the concentration of energy of vibration toward that point. The indirect tubular communication between the various chambers of the membranous labyrinth and with the cranial cavity through the *ductus endolymphaticus* and its dilated extremity afford evident provision for the equalization of pressure throughout the endolymph.

The Membranous Cochlea and the Organ of Corti.—The *ductus cochlearis* is somewhat triangular in cross section, its floor being composed, in the lower whorls of the cochlea, of the *basilar membrane* and the edge of the lamina spiralis (Fig. 408); but the latter component decreases as the apex is reached, so that both the relative and the absolute width of the basilar membrane increases as the cupola is approached (p. 622). The delicate *membrane of Reissner*, stretched from a line on the lamina spiralis somewhat back from its edge to the wall of the bony cochlea, separates the canalis cochlearis from the scala vestibuli, as the basilar membrane does from the scala tympani.

From the physiological standpoint interest is chiefly centred in the basilar membrane and the structures supported by it. The *basilar membrane* is a sheet of complex tissue tightly stretched between the edge of the lamina spiralis and the outer wall of the cochlea. The membrane is fibrillated and splits readily in a radial direction, and has been supposed to represent essentially a series of stiff elastic fibres more or less coherent in a cement substance (Fig. 409). Seated on the inner part of the basilar membrane is the peculiar structure known as the *organ of Corti* (Figs. 408, 409).

The *organ of Corti* has as its supporting framework a series of modified cuticular epithelial cells known as the *rods of Corti* (*Columnæ ext.* and *int.*, Fig. 409), which are arranged along the inner edge of the membrane in two rows, an inner and an outer. The feet of Corti's rods are separated at some distance on the basilar membrane, but the rods are inclined toward each other and are united at the top, leaving between them and the basilar membrane the *tunnel of Corti*. The inner rods are more numerous than the outer, so that the latter are fastened rather between than to the ends of the former. Leaning against the inner or median side of the inner row of rods is a single row of hair cells (Fig. 409), much like those described as seated on the maculæ and cristæ of the labyrinth, to which filaments of the auditory nerve are applied. On the inner face of these hair cells are several rows of columnar epithelial cells supported by a base of nuclei. External to the outer row of rods, and separated from it by a space, are four parallel rows of hair cells known as the *cells of Corti*. The hair cells do not rest upon the basilar membrane, but are upheld by four rows of specialized bodies, the *cells of Deiters*, inserted between and outside them and supported below by the basilar membrane. Outside these structures are several rows of columnar epithelial cells. The rods of Corti are peculiarly shaped at the top, the upper extremity of each being bent at an angle so as to project externally and parallel with the basilar membrane; these projections are the *phalangar processes* of the rods. These processes form the points of attachment, or the beginning, of the *reticulate membrane* (*membrana reticulata*), a peculiar network-like structure formed of cuticular rings and cross bars (not shown in the figure). The reticulate membrane stretches across the outer rows of hair cells, the body of each of which is enclosed and is held at the top within a ring of the network. The inner or median face of each cell of Deiters is modified into a cuticular thread which is fused below to the basilar membrane and above to a ring of the reticulate membrane.

A sheet of radially fibrillated tissue is attached to the vestibular lip of the *limbus*, a promontory composed of connective tissue resting upon and fringing the edge of the *lamina spiralis*. This sheet is known as the *tectorial membrane* (*membrana tectoria*) and reaches out over the organ of Corti as far as the outermost row of hair cells (Fig. 409). It is said, when in place, to lie in actual contact with the rods of Corti and the free ends of the hair cells, and it has been presumed to serve as a damper for the vibrations imparted to the organ of Corti. Howard Ayers* differs, in essential particulars, in his interpretation of some of the structures of the sensory organ of the cochlea from the current views which have been presented above. Thus Ayers asserts "that the so-called membrana tectoria is nothing more than the matted mass of hairs which spring from the tops of the hair cells and form a waving plume on the crest of the ridge of the organ of Corti."

He also holds the *membrana reticulata*, and several other structures described by different authors, to be nothing more than artifacts produced by the methods of preserving and manipulating the specimens.

Turning now to the connection of the sensory organ with the central nervous system, it is found that the cochlear division of the auditory nerve, together with the nutrient blood-vessels, penetrates the modiolus at its base and runs up through the spongy interior of the bony pillar (Fig. 408). As the nerve ascends through the modiolus its fibres are gradually given off to run in a radial direction between the bony plates of the lamina spiralis. A collection of nerve cells forming the *ganglion spirale* is interposed in the course of the auditory fibres at the base of the spiral lamina. The fibrils produced by splitting up of the auditory nerve fibres are generally believed to terminate in clusters about the bodies of the hair cells.

Function of the Sensory Organ of the Cochlea and Its Mode of Action.—There is no doubt that the basilar membrane and the organ of Corti are devoted to translating the vibrations of physical sound into physiological nerve stimuli. More than this, there is little doubt that the cochlear sense organ is an instrument for the analysis of the composite air waves, however complex in their genesis, into the simple pendular vibrations of which they are made up. It is the apparatus through which the period, phase, amplitude, and rate of motion of air particles are translated into auditory impulses which give rise to conceptions of harmony and discord. It is the musical organ of the ear. When we inquire into the way in which the cochlear instrument does its work, we are reduced to the use of hypotheses founded on the action of artificial instruments. The complexity of the organ of Corti in the ear irresistibly demands for it an important function in the acoustic process. But in singing birds, that must be supposed to have an "ear" for music, the organ of Corti is not developed. The radial fibrillation of the basilar membrane early suggested that it represented essentially a series of wires stretched side by side and capable, like those of a piano, of being thrown into sympathetic vibration by impulses reaching them from without. Calculation shows that the fibres are sufficient in number and vary enough in length to more than account for the known powers of the ear in its discrimination of pitch. The fibres of the basilar membrane are cemented laterally by a substance apparently little adapted to transmit vibrations. It may be supposed then, as Helmholtz first pointed out, that composite vibrations traversing the labyrinthine fluids are analyzed by the fibres of the basilar membrane, each fibre responding most powerfully to its own fundamental tone, and that thereby selected groups of the host of nerve fibrils supplying the hair cells are stimulated each with a particular rate and intensity of irritation which, transmitted to the brain, there excites specific sound sensations; the mind again combining these simple sound sensations into complex harmonies having little resemblance to their composing elements.

* Ayers: "The Vertebrate Ear." Journ. of Morphology, May, 1892.

The possibility of giving a satisfactory explanation of the function of the organ of Corti must be abandoned at the outset. The rods of Corti apparently serve as a supporting mechanism for the sensory epithelium. It has been supposed that they serve to pick up and magnify vibrations of the basilar fibres, and, through the medium of the reticulate membrane, transmit such irritations to the hairs of Corti's cells. There is no doubt that the ciliated "cells of Corti" are the special, and probably the only, peripheral sense organs of the auditory nerve. The cilia springing from their free ends are usually regarded as the sensory structures upon which the vibrations immediately act. If Ayers is correct in his opinion that the *membrana tectoria*, instead of being a damper for the vibrations for the organ of Corti, is really a mass of cilia or hairs torn off from the ends of the hair cells, great strength would be given to that view according to which the hairs themselves are the structures set into sympathetic vibration by the waves of the endolymph, not that their stimulation depends upon movements indirectly transmitted from the basilar membrane. In considering this view, it is significant that the scala vestibuli, the vibrations of whose perilymph it would seem should be more powerful than those within the scala tympani, adjoins the canalis cochlearis on the side next the free ends of the hair cells and away from the basilar membrane. Finally, Rutherford * has proposed the theory that the auditory nerve filaments simply transmit to the brain without analysis vibrations applied to them, much as a motor nerve carries to its muscle the impulses generated by induction currents. The basilar membrane, according to this view, vibrates as a whole, and has somewhat the relation to the nerve that a telephone plate has to the conducting wire of the instrument.

Functions of the Vestibular Sacs and of the Semicircular Canals.—Experiments upon the lower animals and the results of aural disease in man have rendered it extremely probable that the semicircular canals are peripheral organs for the complex *sense of equilibrium*, and that they give rise to perception of the movements of the head. There is reason for believing that the sensory cells of the *saccule* and *utricle* also serve as equilibrating organs, giving rise to sensations determined not so much by movements of rotation as by those in a straight line, and to some extent determining the position of the head while at rest. It is thought that the *otoliths* resting upon the hairs of the sensory cells, by their weight and inertia, aid or arouse the excitement of these cells according to the position of the head (see article on *Equilibrium*).

In the ears of fishes the cochlea is wanting, but the vestibular sacs, and especially the masses of otoliths in them, are well developed. But fishes respond to vibrations which may be supposed to arouse auditory sensation just as well when the labyrinth is removed as when it is present, probably through some cutaneous sense.† Such considerations indicate that sounds excite in these creatures other sensations than those of audition as we understand it. It is worth observing that the vestibular branch of the auditory nerve, that supplying the cristæ and maculæ, differs in its characters, in its development, and in its central connections from the cochlear branch of the same nerve. Some have supposed that the sensory cells of the maculæ are excited by the heterogeneous vibrations which we recognize as noises, while musical sounds need the cochlear organ for their interpretation.

Comparison of Visual and Auditory Sensations.—No definite relation can be shown to exist between visual and auditory sensations as such, because they are different in quality. A man born blind may describe the blare of a trumpet as having the color scarlet, but such a statement is evidently only a metaphor expressing the relations of the psychical effect of the trumpet's note and the blind man's inference as to the associations suggested by the color. It is an interesting fact that the language of visual sensation is continually employed in illustrating peculiarities of sound, as in indicating the *quality* as the *color* of the note. In the same way other sensory impressions are used to illustrate visual description, as "warm" and "cold" colors. The intimate association of sound with color in certain persons is an interesting fact of psychology.

Both the auditory and the visual sensory cells are brought into functional activity by physical vibrations, in the one case of ether and in the other of labyrinthine fluid. That continuous sensation shall be aroused these vibrations must be repeated at a definite rate. We have found (p. 612) that the lowest rate which is recognized as sound represents a vibration rate of 16 to 24 per second, while the highest note which is still audible varies in different individuals from 16,000 to 40,000 per second. In musical execution and in the ordinary uses of life the auditory range embraces about seven octaves, though the extreme range of hearing may be eleven octaves. Visual impressions, as those from alternating black and white sections of a rotating disc, fuse together when the different sensations succeed one another at an interval varying from one-tenth to one-fiftieth of a second, the interval being shorter with stronger illumination. But the ear is able to distinguish apart vibrations recurring as "beats" at the rate of 132 per second. The rate of succession of air waves falling upon the ear is marked in consciousness as a particular pitch. When separate luminous impressions, as those of a series of electric sparks, succeed one another with sufficient rapidity, the effect is that of a steady light; there is nothing analogous to musical pitch produced by increasing the rate of stimulation. Ether waves must represent a certain rate of vibration in order to excite visual sensation. The fastest vibration represented in the visible spectrum is less than twice the rate of the slowest; so that the range of vibration in the visual spectrum is included within a single octave. Difference of vibration rate, or of the factor usually considered the *wave length*, in ether, produces that peculiar variety of visual sensation known as color.

The important visual phenomenon of fatigue finds its analogue in auditory sensation. For if a simple musical tone is sounded and immediately thereafter a composite note of which that tone is an upper partial, the note will be found to differ from its normal quality because it falls upon an ear disproportionately fatigued for one of its component tones.

Judgments of Direction and Distance. Ventriloquism.—The direction and distance from which sounds come to the ear are not perceived directly, but our estimate of them is a judgment based on the loudness and quality of the sound sensation, combined with a power of reasoning from past experience. Thus, in seeking to discover the direction whence a sound comes, it is usual for an observer to turn the head to the position in which the sound is heard loudest, and thus to form an opinion as to its source. Errors of judgment as to direction are frequent, owing to the sound reflected from some object appearing louder than that coming in a direct line from its source. It is said that when there is total deafness in one ear, every sound seems to have its origin on the side of the healthy ear.

When the eyes are closed and the head is unmoved, sounds produced anywhere in the median plane of the head are very imperfectly localized. There is a tendency to refer such sounds in a direction above and in front, no doubt because this is the space from which most sounds noticed come to us.

The quality as well as the loudness of a sound varies according to the distance of its source. Thus, the lower tones of a composite note die away earliest as a sound recedes, bringing the overtones into undue prominence. The art of the ventriloquist consists largely in altering the quality of the sounds he produces to imitate the quality they would naturally have if arising under the conditions which he would lead his hearers to believe to be their origin. A comparatively feeble sound near at

* Rutherford, W.: "A New Theory of Hearing." Journ. Anat. and Phys., xxi., 166. (Quoted in Hermann's Jahresbericht d. Physiologie, Bd. xv., S. 108.

† M. Foster: "Text-Book of Physiology," pt. iv., p. 1494, 1900.

hand may have the same quality as a very loud one heard at a distance; thus a frog croaking in an adjoining room was once mistaken by the writer for a large dog barking outside the building.

Acuteness of hearing differs greatly in normal individuals, and tests frequently show disparity in the sensitiveness of the two ears. The hearing ability of children is said to improve up to the age of twelve years. There is no functional relation between keenness of hearing and sensibility to pitch.*

Albino animals and also white cats and dogs with blue eyes are usually deaf. Rawitz † has found the cochlear sense organ degenerated in such cases.

It seems probable that congenital deafness, at least, is inheritable, and that Graham Bell's prediction as to the establishment of a race of deaf mutes from the intermarriage of such unfortunates may be verified.

(In the foregoing pages the author has made some use of his article on Hearing in the "American Text Book of Physiology.") *Henry Sewall.*

AUDITORY CANAL, ANATOMY AND PHYSIOLOGY OF.—The external auditory canal, or meatus auditorius externus, extends from the bottom of the concha to the tympanic membrane, and serves to convey sound vibrations to the middle ear.

It develops in the embryo from the persistent portion of the first outer visceral furrow, making its appearance during the fourth week of fetal development.

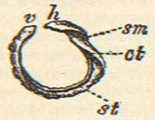

FIG. 410.—Annulus Tympanicus of the Left Side, as Seen from the Inside of the Tympanum. (After Gruber.) *h*, Anterior, *v*, posterior upper end; *sm*, sulcus malleolaris; *ct*, crista tympanica; *st*, sulcus tympanicus.

The centre of ossification shows itself during the third month in the lower wall of the membranous canal.

At birth this bone development has assumed the shape of an incomplete ring, *the annulus tympanicus*. This ring presents a slight groove along its concave border for the attachment of the tympanic membrane, the deficiency upward and backward forming the so-called Rivinian fissure or notch.

At birth the auditory canal is a partially collapsed tube, the roof and floor being in contact throughout a considerable portion of its extent and containing small masses of broken-down epithelial scales and vernix caseosa.

During the first few years of life we find proportionately little difference in the length of the canal when compared with that of the adult, 20 mm. being about the average length at birth. The calibre of the canal is smaller and more oval in shape. The general direction is straighter, passing inward with a decided downward inclination, so that when examining the membrana tympani in the child the speculum can be used to more advantage if the external ear be pulled downward and outward.

The fully developed adult canal is made up of an inner bony portion and an outer cartilaginous and membranous portion. The bone formation extends from the annulus tympanicus outward in the membranous canal, forming the anterior, inferior, and a portion of the posterior bony wall of the perfected canal. The roof is formed by the horizontal plate of the squama and the root of the zygoma; the posterior wall by the annulus, squama, and mastoid prominence.

The outer portion of the canal is a continuation inward of the cartilage of the auricle, the cartilaginous elements being absent in the upper and posterior portion, this gap being filled in by fibrous membrane. The amount of cartilage making up the canal is found to lessen as it extends inward; at its commencement two-thirds of the circumference is composed of cartilage, at its attachment to the bony canal it represents less than one-third of the lower front wall. The cartilaginous portion is attached to the roughened edge of the tympanic ring—now developed into the bony external auditory canal—by fibrous tissue. The fibrous portions of the upper and back wall become merged into the periosteum of the mastoid and squamous portions of the bony canal.

The length, size, and shape of the canal varies according to age, race, and the form of cranial development.

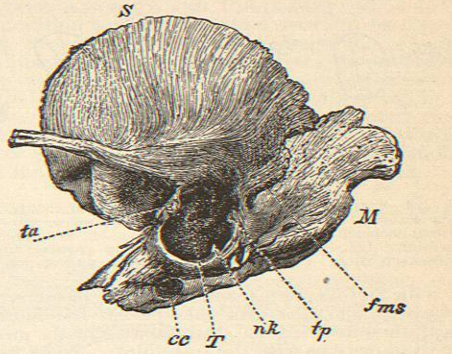

FIG. 411.—Temporal Bone of New-Born Infant. (After Gruber.) *S*, Upper part of squamous portion; *M*, mastoid portion; *Z*, zygomatic process; *T*, tympanic cavity; *fms*, fissura mastoides squamosa; *cc*, foramen caroticum; *ta*, *nk*, *tp*, bony processes representing the beginnings of growth outward on the part of the annulus tympanicus.

The length of the canal is stated variously by different authors, depending on the points from which the measurements are taken; the average length from the bottom of the concha being about 24 mm., of which 16 mm. are found to be bone and 8 mm. cartilage.

Von Troeltsch has given the most complete measurements of the different walls. Starting from a plane drawn from the posterior wall at right angles to the axis of the canal, he found the following measurements: Anterior wall, 27 mm.—9 mm. cartilage, 18 mm. bone; inferior wall, 26 mm.—10 mm. cartilage and 16 mm. bone; posterior wall, 22 mm.—7 mm. cartilage, 15 mm. bone; superior wall, 21 mm.—7 mm. cartilage, 14 mm. bone; the variations in the length of the different walls being due to the oblique position of the tympanic membrane at the inner end of the canal. The shape of the canal at the external orifice is somewhat oval, the long axis inclining slightly backward from the vertical.

Ostman, from a study of 2,302 skulls, found that with the dolichocephalic skull the canal was shorter and more circular, while in the brachycephalic skull the canal was longer and more oval. It is a clinical fact that in the negro race the canal is more circular and straighter, making it often unnecessary to resort to the speculum in order to view the tympanic membrane.

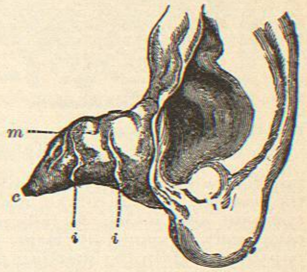

FIG. 412.—*m*, Cartilaginous meatus; *c*, inner extremity of the cartilaginous meatus; *ii*, fissuræ Santorini.

The smallest diameters of the canal are near the end of the cartilaginous portion, and in the bony canal close to the inner third. The following diagrams show the shape and size of the canal at different parts of its course, as found by Bezold from a study of casts of the cavity.

The direction of the canal is sigmoid. In its outer third it is inclined somewhat forward and ascends very

* Seashore: Studies in "Psychology," Bull. Univ., Iowa, vol. ii., 1899.

† Rawitz: Zoölogischer Jahresbericht, 1896, Arch. f. Anat. u. Physiol., 1897.