Paparella: Volume I: Basic Sciences and Related Principles

Section 1: Embryology and Anatomy

Part 1: Ear

Chapter 2: Anatomy of the Ear

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The peripheral auditory system functions to receive mechanical vibrations, to conduct these vibrations to the site of the primary receptor cells, and to transduce this energy into an encoded electrical form appropriate for conduction into and analysis by the CNS. The reception, conduction, and transduction processes are strictly determined by the structural characteristics of this special receptor. Corresponding in part to these functions, the ear can be divided into three regions, each of which has distinct structural and functional characteristics. The external ear, whose function is to receive sound waves, consists of the auricle and a short tube, the external acoustic meatus. The external meatus is closed medially by the tympanic membrane. The middle ear is an air-containing space in the petrous portion of the temporal bone containing the auditory ossicles. The main function of the middle ear is to conduct sound waves received by the external ear to the receptor cells with little energy loss. To do this, the middle ear must act as an impedance matcher. The inner ear, consisting of the osseous and membranous labyrinths, serves a dual function as the primary receptor site for both hearing and balance.

External Ear

Auricle (Fig. 1). The auricle is a flexible appendage of thin elastic cartilage covered by perichondrium and skin. Anteriorly, the skin is firmly attached, while posteriorly the skin is separated from the cartilaginous surface by a distinct subcutaneous layer. The tight adherence of the skin to the cartilage results in ridges and concavities of the auricle (Fig. 1a) corresponding to the ridges and concavities of the auricular cartilage (Fig. 1b). The absence of a subcutaneous layer between skin and cartilage anteriorly makes the auricle susceptible to frostbite despite a rich supply of superficial vessels.

The auricle is connected to the skull and scalp by three extrinsic muscles: the anterior, superior, and posterior auricular muscles (Fig. 1c and d).

Arterial supply to the auricle originates from the *superficial temporal* and *posterior auricular arteries;* venous drainage is supplied by the corresponding veins and the mastoid emissary vein. Lymphatic drainage is to the anterior, posterior, and inferior auricular nodes.

Branches of the *fifth* and *tenth* cranial nerves and the *third* cervical nerve provide *sensory innervation to the auricle.* The *great auricular nerve*, a branch of the third cervical nerve, innervates the medial side of the auricle; the upper portion is innervated by the *lesser occipital* *nerve.* The lateral side of the auricle is innervated by twigs of the great auricular nerve coursing over the helix and by a branch of the fifth cranial nerve, the *auriculotemporal nerve.* The auricular branch of the tenth cranial nerve innervates a small portion of the auricle and the meatal floor. Motor nerves to the extrinsic muscles extend from the temporal and posterior auricular branches of the facial nerve.

External Acoustic Meatus (Figs. 2 and 3). Between the auricle and the tympanic membrane, the external acoustic meatus assumes a medial and inferior S form. The shorter posterosuperior wall is 25 mm long, while the longer anteroinferior wall is 31 mm in length. The difference is caused by the oblique placement of the tympanic membrane. The size and shape of the canal vary. It is elliptical in cross-section, with the greater diameter of the ellipse being vertical at the auricular end and nearly horizontal at the tympanic end. Two prominences limit visibility of the tympanic membrane. The floor of the bony canal has an upward convexity at about its midpoint, while the anterior wall of the canal has a posterior convexity at its midpoint. Visibility of the drum membrane may be enhanced by pulling the auricle posteriorly, superiorly, and laterally. These irregularities in the external auditory meatus also predispose the canal to foreign body entrapment anteroinferiorly at the medial end of the bony canal. This region of the canal is known as the sulcus.

Slightly more than the medial half of the external acoustic meatus is bony, and the remaining lateral portion is a fibrocartilaginous tube that is incomplete superiorly. The skin of the meatus is relatively thick in the cartilaginous portion, but gradually becomes very thin in the body portion, especially anteriorly and inferiorly. It is firmly attached to perichondrium and periosteum, respectively. This skin of the cartilaginous meatus contains numerous fine hairs, which continue only posteriorly and superiorly in the bony meatus. Sebaceous glands are exceptionally large in the cartilaginous portion, although present only on the posterosuperior wall of the bony meatus. Two horizontal clefts, the incisures of Santorini, are usually present in the anterior cartilaginous wall. Although these allow increased flexibility of the meatus, they also allow extension of parotid abscesses into the meatus.

The blood supply to the external acoustic meatus is provided by the posterior auricular and superficial temporal arteries as well as by the deep auricular artery, which also supplies the tympanic membrane. Venous blood drains by way of the maxillary and external jugular veins and the pterygoid venous plexus. Lymphatic drainage is to the anterior, posterior, and inferior auricular nodes. Sensory innervation is supplied to the inferior and posterior portions of the meatus by the auricular branch (Arnold's) of the vagus nerve and to the anterior and superior portions of the meatus by the auriculotemporal branch of the mandibular nerve.

Tympanic Membrane. The tympanic membrane is a membranous partition separating the external acoustic meatus from the tympanic cavity. It is semitransparent and elliptical - 9-10 mm vertically and 8 to 9 mm horizontally. Its external aspect is concave, the most depressed point being the umbo, which corresponds to the tip of the manubrium of the malleus. The manubrium itself extends from the umbo to the malleal prominence formed by the lateral process of the malleus. From the malleal prominence, the anterior and posterior malleal folds extend to the edges of the tympanic notch (notch of Rivinus) and separates pars flaccida (Shrapnell's membrane) above from pars tensa below. The average thickness of the tympanic membrane is 0.074 mm; it is thickest (0.09 mm) near the annulus inferiorly and anterosuperiorly, and thinnest (0.055 mm) in the middle of the posterosuperior quadrant.

The pars tens and the pars flaccida of the tympanic membrane are composed of three layers. The lateral layer is continuous with the skin lining the external auditory meatus. Medial to this is a fibrous layer, or lamina propria. More medial is the mucosal layer continuous with the tympanic cavity. The connective tissue fibers of the lamina propria are organized in two basic layers. This is also true of pars flaccida, which appears thinner than pars tensa. A radial layer of fibers originates from the handle of the malleus and inserts on the annular ring. Circular fibers originate more medially from the short process of the malleus. Transverse and parabolic fibers intertwine between these two layers. The chemical composition of the fibers is unknown. Epithelial migration of the tympanic membrane has been vividly demonstrated by Litton (1963), who showed that it moved centrifugally from the umbo at about 0.05 mm per day.

The blood supply is provided by vessels from the epidermal mucosal surfaces that communicate within the lamina propria. The arterial supply laterally is from the *tympanic branch of the deep auricular artery* and medially from the *anterior tympanic branch of the internal maxillary artery* and the *stylomastoid branch of the posterior auricular artery.* The venous drainage corresponds to that of the external meatus and the tympanic cavity. Innervation is via the *auricular branch of the vagus,* the *tympanic branch of the glossopharyngeus (of Jacobson),* and the *auriculotemporal branch of the mandibular.*

Middle Ear

The tympanic cavity or middle ear is a mucous membrane-lined space between the tympanic membrane and the osseous labyrinth. The cavity is flattened, with vertical and anteroposterior diameters of 15 mm and a mediolateral depth ranging from 6 mm superiorly to 2 mm at the umbo. The cavity can be divided into the tympanic cavity proper, medial to the tympanic membrane; the epitympanic recess, cephalad to the upper border of the tympanic membrane; the tympanic antrum with the mastoid air cells; and the hypotympanic recess, caudad to the tympanic membrane.

Auditory Ossicles. The three auditory ossicles responsible for the conduction of sound waves from the external ear to the inner ear are suspended within the tympanic cavity. The ossicles include the malleus, the incus, and the stapes. These bones are suspended as a chain that bridges the middle ear space from the tympanic membrane to the functional entrance of the inner ear, the vestibular fenestra, or oval window. The longest ossicle is the malleus. Its two major components are its head and manubrium. The head occupies a part of the epitympanic space and articulates with the body of the incus. The length of this bone is 8 to 9 mm. The incus has a slightly greater mass than the malleus and consists of a body, a short process (5 mm), and a long process (7 mm). The stapes is the smallest bone in the body. It consists of a footplate and two legs, the anterior and posterior crura. The two crura are joined superiorly at the head. Its overall height is approximately 3.3 mm; its footplate measures about 3 mm by 1.4 mm.

Primary attachment of the malleus to the tympanic membrane is made via the manubrium, with the tip of the manubrium terminating at the umbo. The concave shape of the tympanic membrane is a result of the manner of suspension of the ossicles within the middle ear. The tip of the manubrium tends to retract the tympanic membrane into the middle ear cavity. Articular ligaments join the head of the malleus to the body of the incus and the lenticular process of the incus to the head of the stapes. The annular ligament suspends the footplate of the stapes in the vestibular fenestra. Aside from the annular ligament of the stapes and drum membrane attachment of the malleus, five other ligaments suspend this ossicular chain in the middle ear. The superior, anterior, and lateral ligaments suspend the head of the malleus from the walls of the upper tympanum. The superior incudal ligament attaches to the body of the incus, while the short process is attached to the fossa incudis by the posterior ligament. Additional support for the system is provided by two muscles, one attached to the malleus (the tensor tympani) and the other to the stapes (the stapedius). These muscles can restrain the movement of the system and play a role in the protection of the inner ear structure from intense sounds.

Walls of the Cavity. The tympanic cavity has six walls that are approximately paired. The roof or tegmen tympani separates the tympanic cavity from the middle cranial fossa. The floor of the hypotympanic recess is narrow transversely and is covered with tympanic cells. It is thin centrally and may be dehiscent, exposing the dome of the jugular bulb. The floor separates the hypotympanic recess from the internal carotid artery anteroinferiorly and the dome of the jugular bulb posteroinferiorly.

The posterior tympanic wall is open above (aditus ad antrum) and contains a recess (fossa incudis) for the short process of incus. On this wall at the level of the stapes is a prominence, the pyramidal eminence, through which the stapedius tendon travels from the stapedius muscle to the neck of the stapes. The chorda tympani nerve enters the tympanic cavity through a foramen lateral to the pyramid eminence. Between the pyramidal eminence and the chorda tympani nerve is the suprapyramidal recess, often referred to as the facial recess. Medial to the pyramidal eminence is a cavity, the sinus tympani, which usually extends medial to the stapedius muscle and which may extend medial to the vertical course of the facial nerve or even medial to its horizontal course. The anterior wall of the tympanum funnels into the tympanic orifice of the auditory tube, above which is the semicanal of the tensor tympani muscle, and posteroinferior to which is the internal carotid artery as it changes from its vertical to horizontal course through the temporal bone.

The lateral wall of the tympanic cavity proper is formed by the tympanic membrane and the lateral wall of the epitympanic recess, the scutum (of Leidy). The epitympanic space is defined by the tegmen tympani superiorly, the prominence of the facial canal and horizontal semicircular canal medially, the scutum laterally, and the fossa incudis posteriorly. The major feature of the medial wall is the promontory produced by the bulging basal turn of the cochlea. Coursing almost vertically over the promontory is a groove for the tympanic branch (Jacobson's) of the glossopharyngeal nerve. Posterior to the promontory the wall is divided into three depressions by two bony structures, the subiculum and the ponticulus, when they are present. *The subiculum is a ridge formed by the posterior prolongation of the cephalad border of the fossula of the cochlear fenestra. The ponticulus is a fine bony bridge passing from the area of the pyramidal eminence to the promontory.* It is nearly parallel to the stapedius tendon. The lowest of these three depressions, caudad to the subiculum, is the fossula of the cochlear fenestra containing the secondary tympanic membrane. The central depression between the subiculum and the ponticulus is the anterior portion of the sinus tympani, and above the ponticulus is the fossula of the vestibular fenestra containing the stapes.

The prominence of the facial canal is above the fossula of the vestibular fenestra. The anterior extent of the facial canal prominence is marked by the cochleariform process through which the tensor tympani changes its route and courses laterally to the malleus. The tensor is a relatively large muscle, 22 mm long, forming part of the roof of the eustachian tube and part of the medial wall of the tympanum. It arises from the cartilaginous part of the tube, the great wing of the sphenoid, and the wall of its own semicanal, attaching to the manubrium of the malleus near its neck.

Tympanic Mucous Membrane. The tympanic cavity is lined with mucous membrane, which covers its walls and all exposed contents. This lining is continuous anteriorly with the mucosa of the auditory tube and posteriorly with that of the tympanic antrum and mastoid cells. Recent studies have shown that part of the mucosa is covered with cilia, which are supported in some areas by columnar pseudostratified cells and in other areas by low columnar epithelium. The cilia form distinct and consistent tracts over the anterior tympanic cavity, the hypotympanum, the epitympanum, the epitympanum, and part of the promontory. These ciliary tracts appear related to the clearance function of the middle ear.

Tympanic Spaces. Prussak's pouch is a space that is triangular in vertical section. It is limited by the pars flaccida, caudally by the short process of the malleus, and superiorly by the lateral mallear fold, which passes from the neck of the malleus to the tympanic scutum. Attic retraction pockets and, occasionally, cholesteatomas are found in Prussak's pouch.

Two other recesses, the pouches of von Troltsch, are formed from reflections of the anterior and posterior mallear folds - between the tympanic membrane, the ossicles, and their ligaments.

Tympanic Antrum. The tympanic antrum is located posteriorly and slightly lateral to the upper half of the tympanic cavity, with which it communicates via the aditus ad antrum. The antrum is lined with mucous membrane, which continues from the epitympanum through the antrum to the numerous cells in the mastoid and petrous apex. Of particular interest to the surgeon is the relationship of the tympanic antrum to the surface landmarks of the temporal bone. The major guide for the surgeon is Macewen's triangle. This is a triangle formed by the posterior prolongation of the upper border of the posterior root of zygoma (the temporal line), the posterior wall of the external auditory meatus, and a line connecting the two that is perpendicular to the temporal line. The tympanic antrum is medial to the triangle.

Auditory Tube. The auditory tube descends downward medially and anteriorly from the anterior wall of the tympanum to the nasopharynx. It is about 37 mm long and is shaped somewhat like an hourglass flattened anteroposteriorly. The tympanic one third of the tube is osseous and the pharyngeal two thirds are cartilaginous. A constriction at the junction of its lateral bony wall and medial cartilaginous portion, the isthmus, may be as small as 1.0 by 1.5 mm.

The cartilage of the tube is elastic except at the isthmus, where it becomes hyaline, losing its elastic fibers. In the bony part of the tube the mucous membrane of low columnar ciliated epithelium is firmly bound to periosteum. The lining of the cartilaginous tube, on the other hand, is of pseudostratified columnar cells, many of which are ciliated. Near the pharyngeal orifice are found goblet cells and tubuloacinar glands that secrete mucus into the tubal lumen. Surrounding the pharyngeal orifice is a ring of lymphoid tissue known as the tubal tonsil of Gerlach.

Vessels and Nerves. The arteries of the tympanic cavity derive from both the *internal and external carotid arteries.* The *anterior tympanic artery* branches from the internal maxillary artery and distributes to the anterior part of the cavity, including the tympanic membrane, malleus, and incus. The *stylomastoid artery* originates from the posterior auricular artery and proceeds to the posterior tympanic cavity and mastoid air cell region. The *superficial petrosal artery* originates from the middle meningeal artery and provides a major blood supply to the facial nerve. The vascular plexus that supplies the incudostapedial joint region is derived from the superficial petrosal artery and its anastomosis with the stylomastoid artery. The *inferior tympanic artery,* from the ascending pharyngeal, provides the blood supply to the mucosa of the promontory and hypotympanum. In addition, the *caroticotympanic branch,* from the internal carotid, supplies the anterior wall. The veins correspond roughly to the arteries and empty into the superior petrosal sinus and pterygoid plexus.

The lymphatics begin as a network in the mucous membrane and end chiefly in the *retropharyngeal* and *parotid lymph nodes.*

The nerves of the mucosa are principally represented by the *tympanic plexus,* formed by the *tympanic branch of the glossopharyngeus (Jacobson's).* Additional innervation is provided by the *inferior and superior caroticotympanic nerves,* from the internal carotid plexus of the sympathetic system, and from the *lesser petrosal nerve.* The chorda tympani crosses through the tympanic cavity from the posterior to the anterior wall. Sensory fibers within the nerve provide *taste sensation to the anterior two thirds of the tongue,* while *secretory fibers innervate the submandibular and sublingual glands.* The tensor tympani muscle is innervated by a branch of the mandibular nerve from the otic ganglion; the stapedius muscle is innervated by the facial nerve.

Facial Nerve

The facial nerve originates in the pons. Within the internal auditory canal, it is superior to the cochlear nerve and anterior to the superior vestibular nerve. As the nerve leaves the internal auditory canal and enters the labyrinthine segment, it passes above the transverse crest and anterior to a vertical crest of bone known as Bill's bar. From here it passes anteriorly between the basal turn of the cochlea and the vestibule. At the geniculate ganglion, it expands and then proceeds in a posterior direction, defining the external genu. At the external genu, the greater petrosal nerve leaves the geniculate ganglion. From the external genu, the tympanic segment of the nerve passes along the medial wall of the tympanic cavity superior to the oval window. As the nerve curves around the stapes niche, it begins its vertical, or mastoid, segment. The chorda tympani originates along the vertical segment of the facial nerve, either as it passes within the posterior wall of the tympanum or after it has exited from the skull at the stylomastoid foramen.

Inner Ear

Osseous Labyrinth. The osseous labyrinth housing the sense organ of hearing and balance is located in the petrous temporal bone. It consists of several parts: the vestibule housing the saccule and utricle, the cochlea with its organ of Corti, the three semicircular canals, and the vestibular and cochlear aqueducts.

The vestibule is an irregular ovoid cavity approximately 4 mm in diameter. It is located medial to the tympanic cavity, with which it communicates through the fossula of the cochlear fenestra and the fossula of the vestibular fenestra. The three semicircular canals arise from recesses in the posterior wall of the vestibule and return to it - each forming about two thirds of a circle. Each canal lies at the right angles to the other two. The ampullae of the superior and lateral semicircular canals are located at the anterosuperior aspect of the vestibule. The superior canal courses cranially, medially, and posteriorly and joins the nonampullated end of the posterior canal, forming the crus commune, which then enters the posterior aspect of the vestibule. The course of the lateral semicircular canal, the shortest of the canals, is in a posteroinferior plane, returning to the posterior aspect of the vestibule. The lateral semicircular canal is intimately associated with the facial canal along its horizontal aspect. From the posterior portion of the vestibule, the posterior semicircular canal courses in a posteromedial plane.

Three recesses are formed in the posterior wall of the vestibule. The spherical recess, housing the saccule, is located anteroinferiorly. The elliptical recess, which contains the utricle, is located posterosuperiorly. The cochlear recess is located posteroinferiorly on the medial wall of the vestibule. The cochlear recess contains the basal hook region of the cochlear duct. The vestibular crest separates the spherical recess from the elliptical recess and divides into two limbs, which bound the cochlear recess. The opening of the vestibular aqueduct passes from the area of the elliptical recess to the posterior surface of the temporal bone. Through it the endolymphatic duct passes to the saccus endolymphaticus.

Anteroinferior to the vestibule is the bony cochlea, which is shaped like a flattened cone whose base is 9 mm in diameter and whose height is 5 mm. The cochlea makes two and one half turns around a central axis known as the modiolus, through which cochlear vessels and the cochlear division of the eight cranial nerve pass to the cochlea. The cochlear canal is divided into the scala tympani and scala vestibuli by the osseous spiral lamina, which spirals around the modiolus. The two compartments join at the apex of the cochlea, the helicotrema.

Blood Supply of the Labyrinth. The labyrinth is supplied by the *internal auditory artery*, which originates as a branch of either the basilar, anteroinferior cerebellar, or occasionally the vertebral arteries. The internal auditory artery (or labyrinthine artery) subdivides into the anterior vestibular artery and the common cochlear artery. The anterior vestibular artery supplies parts of the saccule, utricle, and semicircular ducts. The common cochlear artery, in turn, divides into the vestibulocochlear artery and the main cochlear artery. The vestibulocochlear artery supplies one half to two thirds of the basal coil of the cochlea, the greater part of the saccule, the body of the utricle, the posterior semicircular duct, and parts of the lateral and superior semicircular ducts. The main cochlear artery supplies the remaining parts of the cochlea. Occasionally, the main cochlear artery may be missing; it is then replaced by the cochlear branch of the vestibulocochlear artery.

The labyrinthine venous drainage is via the vein of the cochlear aqueduct. The apical and basal spiral modiolar veins drain appropriate parts of the cochlea. There may be additional drainage routes of the cochlea formed by connections with vessels in the surrounding bone and with veins of the internal auditory meatus (the internal auditory veins). The venous supply of the semicircular ducts and vestibule is provided by the anterior and posterior vestibular veins, which, in turn, drain into the vein of the cochlear aqueduct.

Membranous Labyrinth. The membranous labyrinth is a system of epithelium-formed spaces and tubes containing endolymph. It is surrounded by the perilymph-filled periotic labyrinth, which, in turn, is enclosed in the bony labyrinth of the otic capsule.

The membranous labyrinth consists of the endolymphatic duct and sac, the saccule, the utricle, the semicircular canals, and the cochlear duct. These are interconnected by small canals: the utricular duct, the saccular duct, and the ductus reuniens.

Endolymphatic Duct and Sac. The endolymphatic sac usually lies partly within the vestibular aqueduct and partly on the posterior surface of the petrous portion of the temporal bone between the layers of the cranial dura mater. The sac is connected to the endolymphatic system via the endolymphatic, utricular, and saccular ducts. There is much variation in size, shape, and position of the external aperture of the vestibular aqueduct, as well as in the amount of expansion of the aqueduct immediately inside the external aperture. The location of the sac and the proportion of it within or outside the temporal bone are correspondingly variable. The sac itself varies considerably in size, shape, and position. Its lumen is frequently quite rugose. The cells within the middle or intermediate part of the sac are specialized for pinocytic activity. Its outer wall is surrounded by vascular connective tissue.

The endolymphatic sac can usually be reached through the temporal bone by removing the cells between the posterior semicircular canal and sigmoid portion of the transverse sinus. In this location, its cephalad border is most frequently found at or at varying distances below a line through the lateral semicircular canal.

The Utricle and Saccule. The utricle is an oblong, slightly flattened sac with a rounded end (Fig. 17). It occupies the elliptical recess in the posterosuperior portion of the vestibule. The saccule is a spherical organ, smaller than the utricle, located in the anteroinferior portion of the vestibule in the spherical recess.

The utricle connects posteriorly with the semicircular canals and anteriorly via the utricular duct with the endolymphatic and saccular ducts. Communication between the utricle and utricular duct may be limited by the utricular fold or valve (of Bast). The saccule communicates inferiorly via the ductus reuniens with the cochlear duct. It is at the junction of the utricular and saccular ducts that the endolymphatic duct arises.

The sensory receptors and supporting structures responsive to positional changes of the body from the maculae of the utricle and saccule. The macula of the utricle is a spade-shaped, thickened area situated anteriorly and laterally in the horizontal plane within the utricle. The macula of the saccule is a 2-mm by 3-mm sensory structure located on the medial wall of the saccule. The macula of the saccule lies in approximately a vertical plane, perpendicular to the utricular macula. These maculae are innervated by the utricular and saccular branches of the vestibular nerve.

Both maculae are structured similarly. The primary receptor cells are hair cells, which are of two types (Fig. 18): Type I tends to have an expanded base (flasklike) and is surrounded by chalice-type afferent nerve endings. The type II cells are more tubular in shape and are supplied by smaller afferent and efferent nerve endings. The upper surface of these cells is cuticular, in which nonmotile stereocilia and a single peripheral kinocilium are embedded. The location of the kinocilium determines cell polarity. Each of the hair cells is surrounded and held firmly by a matrix of supporting cells. The kinocilia and stereocilia hairs of these cells project into an otolithic membrane, which lies atop each macula (Fig. 19). Many crystals of calcium carbonate, the otoconia, are found within the otolithic membrane.

Each macula can be divided into two parts by a narrow zone or striola, which extends down the middle. The hair cells are spatially organized according to the kinocilium position relative to the striola. The hair cells of the utricular macula are aligned with the kinocilium toward the striola. The opposite is true in the macula of the saccule. Observations suggest that this organization is of some functional significance. Thus, bending the hairs in the direction of the kinocilium results in a depolarization and excitation of the cell, whereas bending the hairs in the opposite direction results in a hyperpolarization of the cell. The increase in mass of the otolithic membrane provided by the presence of the otoconia plays a major role in determining the adequate stimulus for excitation of these hair cells.

Semicircular Ducts. The membranous labyrinth of the semicircular canals is tubular in form. At one end of each canal is an enlargement termed the ampulla. These ducts occupy only about one quarter of the diameter of the respective bony canals and open into the utricle through five orifices. Each canal opens directly at its ampullar end, but the posterior and superior ducts open through a common crus at their posterior end. The ampulla of each canal is an expanded area containing a transverse ridge of sensorineuroepithelium and supporting structures, the crista ampullaris (Figs. 20 to 22). Although grossly of a different form, microscopically the crista ampullaris is very similar to the maculae of the saccule and utricle. Type I and type II hair cells are found in this structure.

From their apical surfaces projects a tuft of stereocilia and a single kinocilium. Cellular orientation is again determined by the location of the kinocilium - this time relative to the utricle. In the crista of the lateral semicircular canal, the kinocilium is located on the utricular side of the cell. In the superior and posterior canal crista, the kinocilium is oriented away from the utricle. The cilia of these cells insert into a gelatinous cupula, which caps this ridge of sensorineuroepithelium. The cupula ampullaris extends from the surface of the crista to the roof of the ampulla. Movement of the endolymphatic fluid within the semicircular duct moves the cupula relative to the surface of the crista, thus providing the adequate stimulus for bending these hairs. Concomitant excitation or inhibition of the hair cells is believed to depend on cupular deviation and thus the kinocilium deflection either toward or away from the utricle. The posterior, superior, and lateral ampullary nerves of the vestibular portion of the eighth cranial nerve provide the afferent innervation for these sensory receptors.

Cochlear Duct. This portion of the membranous labyrinth follows the spiral canal of the bony cochlea through its length of two and one half turns. The duct extends from the cochlear recess of the vestibule to end as a blind pouch, the cupular cecum, at the level of the apex of the cochlea. At its basal extent, the small ductus reuniens allows communication of the endolymph of the cochlear duct with that of the saccule.

In transverse section the cochlear duct is somewhat triangular in form (Fig. 23). The floor of the duct is formed by the osseous spiral lamina and the basilar membrane, which inserts laterally along the tough spiral ligament. Overlying the spiral ligament, and forming the lateral wall of the cochlear duct, is the highly vascular stria vascularis. At the upper limit of the stria, the thin bicellular-layered vestibular membrane (Reissner's) extends from the spiral ligament to the limbus overlying the osseous spiral lamina, thus forming the third wall of the cochlear duct.

The basilar and Reissner's membranes divide the cochlear labyrinth into three canals. The closed central canal is, of course, the endolymph-filled cochlear duct, or scala media. Adjacent to Reissner's membrane is the scala vestibuli. Adjacent to the basilar membrane is the scala tympani. Both the scalae vestibuli and tympani are perilymph filled. The fluid of these two scalae is in communication beyond the apical closed end of the cochlear duct through the helicotrema.

The Organ of Corti. The sensory receptors and supporting structures responsive to acoustic energy are located on the basilar membrane. These structures, forming the organ of Corti, are best examined from two views - a transverse view and a horizontal view. In the former case the midmodiolar sections illustrate the relations of the organ of Corti to the other structures of the membranous and periotic labyrinths (Fig. 23). Extension of scanning electron microscopy studies of the organ of Corti has further contributed to our knowledge of this system and our ability to illustrate its organization (Fig. 24A to C). By combining these approaches, the cytoarchitecture of this complex three-dimensional structure can best be appreciated.

The spiral length of the basilar membrane is approximately 32 mm. Its width increases from 80 microm at the base to approximately 500 microm one half turn from the apex. In transverse section, one of the most prominent features of the organ of Corti is the tunnel of Corti formed by two pillar cells. The basilar membrane has been divided into two sections: the zona arcuata, which extends from the tympanic lip of the osseous spiral lamina to the base of the outer pillars; and the zona pectinata, which extends from the lateral pillar to the spiral ligament.

A single row of inner hair cells is found medial to the tunnel of Corti, and three rows of outer hair cells are found lateral to the tunnel (Fig. 24B). This pattern of hair cell representation is followed throughout the length of the organ of Corti. Near the apex, however, fourth and even fifth row outer hair cells may be found. These hair cells are the primary receptors sensitive to acoustic energy. Other structures of the organ of Corti serve as supporting elements, determining to a great extent the range of mechanical stimuli capable of eliciting a response from the hair cells.

The single row of inner hair cells includes approximately 3500 cells. There are over 20.000 outer hair cells in the organ of Corti. Figure 25A and B illustrates diagrammatically the major characteristics of these hair cells. Inner hair cells are flasklike in shape as opposed to the more "test-tube" shape of the outer hair cells. The upper surface of the hair cells is formed by a thickened cuticular plate. It is in this cuticular plate that the stereocilia hairs of these cells are embedded. Two straight rows of approximately 50 nonmotile stereocilia are found on the inner hair cell. On the outer hair cell the stereocilia are arranged in rows, forming a W pattern. The number of rows varies according to species. The guinea pig "W" consists of three rows; however, human outer hair cells may have five or six rows (Fig. 24B). The angle formed by the legs of the W extends from approximately 70 degrees on apically placed hair cells to approximately 120 to 130 degrees on basal turn hair cells.

A cuticular-free region is found on the surface of each hair cell lateral to the stereocilia. In this region, the basal body of the kinocilium may be observed. As noted in electron microscopic studies of the hair cells, a high concentration of Golgi apparatus and mitochondria is formed beneath this cuticular-free region. Based upon such observations, it has been suggested that this high metabolic region of the hair cell may be involved primarily in the transduction process by which mechanical energy is converted into an electrical form.

Each inner hair cell rests in a cuplike inner phalangeal cell (Fig. 25A). These cells send their phalangeal processes up to the apical zones of the inner hair cells. At the base of the outer hair cells outer phalangeal cells (Deiters') are found. Similar to the supporting cells at the base of the inner hair cells, Deiters' cells send phalangeal processes to the surface of the organ of Corti, where they are connected to the apical surfaces of the outer hair cells.

The inner and outer phalangeal cells and the pillar cells are responsible for supporting the organ of Corti. The pillar cells rest on the basilar membrane and are connected to each other at their heads to form the tunnel of Corti (Fig. 25A).

Medial to the tunnel of Corti, the inner pillar cells and inner row of phalangeal cells support the inner hair cells. Lateral to the tunnel of Corti, the outer pillar cells and the first row of outer phalangeal (Deiters') cells hold the apical ends of the first row of outer hair cells in place. More laterally, the second and third rows of outer hair cells are supported by the outer two rows of Deiters' cells.

The heads of the pillar cells, the phalangeal processes of the Deiters' cells, and the apical ends of the hair cells interdigitate to form a thick plate, the reticular lamina (Fig. 24C). The phalangeal processes of each Deiters' cell does not interdigitate with the apical surface of the hair cell it supports but extends three to four sensory cells farther toward the apex before contributing to the reticular lamina. The distribution of the cell processes forms a reticular pattern when observed from the surface of the organ of Corti and provides rigid three-dimensional support for the sensory cells.

The cells of Hensen are located beyond the most laterally placed phalangeal process (Fig. 23). These cells extend from the lateral border of the organ of Corti down to the tall columnar epithelial cells, the cells of Claudius, which rest upon the basilar membrane and extend laterally to the spiral ligament and stria vascularis.

As noted in Figure 23 (the transverse section of the cochlea), medial to the supporting cells of the inner hair cells may be found a series of cuboidal inner sulcus cells extending from the inner hair cells to the fibrous spiral limbus, which rests upon the osseous spiral lamina. It is from the superior surface of the spiral limbus that the tectorial membrane extends over the organ of Corti throughout the spiral extent of the cochlear duct. The exact relationship between the sensory cell stereocilia and the tectorial membrane in humans is unclear. The taller stereocilia of the outer hair cells are embedded in the tectorial membrane in some species.

The cross-sectional view of the cochlear duct (Fig. 24A) shows that beneath the tectorial membrane and within the organ of Corti, there exist a number of fluid-filled spaces. The largest is the tunnel of Corti. In addition to this, adjacent to the outer hair cells and between the outer pillar cells and the outer hair cells are the small spaces of Nuel. These regions are filled with cortilymph, a fluid considered to be similar in its ionic constituents to that of perilymph.

The submicroscopic structure of the organ of Corti suggests that the hair cells function as biologic transducers. The sensory cells are rigidly fixed by the supporting cells to the basilar membrane. On the other hand, the tectorial membrane, in which the sensory hairs of the outer hair cells are embedded, forms a loose attachment with the basilar membrane via the spiral limbus. As a result of this arrangement, movement of the basilar membrane results in a shearing movement between the tectorial membrane and the cuticular plates of the hair cells. This results in a bending of the stereocilia of the outer hair cells and thus initiates the transduction response of these sensory receptors. Similarly, a differential movement of the tectorial membrane relative to the reticular lamina causes a movement of the fluid in this space. This fluid movement affects the free-standing stereocilia of the inner hair cells. They are bent and transduction is initiated. This arrangement may account for the differential sensitivity of inner and outer hair cells; the outer hair cells are approximately 30 dB more sensitive that the inner hair cells. It probably also accounts for the greater sensitivity of outer hair cells to acoustic trauma.

Innervation. The cell bodies of the bipolar afferent neurons form the spiral ganglion in Rosenthal's canal. There are two types of neurons. Type I neurons are myelinated, constitute 95 per cent of the total population, and are distributed to the inner hair cells. Type II neurons are unmyelinated, constitute 5 per cent of the total, and are distributed to the outer hair cells. The fibers pass from the osseous spiral lamina to the organ of Corti via the habenula perforata, at which point they lose their myelin sheath. Fibers for the external hair cells cross Corti's tunnel along the basilar membrane and spiral in three groups between the Deiters' cells. The terminal branches originate in the spiral fibers and innervate multiple outer hair cells. In contrast, each inner hair cell is innervated by multiple type I fibers. All nerve endings are chalice shaped and nonvesiculated.

In addition to these afferent fibers with their agranular endings, a number of granulated endings have been observed to make contact with both the outer hair cells and the terminal endings of the afferent fibers. These granulated endings are efferent fibers originating from the brain stem in Rasmussen's olivocochlear bundle. The cell bodies are located in the superior-olivary complex. The fibers first travel from the brain stem with the inferior vestibular nerve but enter the cochlea as the vestibulocochlear anastomosis (bundle of Oort). From intraganglionic spiral bundles, the fibers are distributed by internal spiral bundles to the afferent fibers innervating the inner hair cells. Alternatively, the fibers go to the middle of the tunnel of Corti and are distributed to the bodies of the inner hair cells. The exact function of these fibers is unknown but they may be inhibitory.

Blood Supply. The blood supply to the organ of Corti and other structures of the cochlear duct is provided by the vessels within the stria vascularis, the spiral vessels underlying the basilar membrane, and the spiral limbus vessels. The main cochlear artery enters through the modiolus along with the eight nerve fibers. Arterioles divide at the level of the spiral lamina, with one group of vessels proceeding to a position underlying the basilar membrane. The second arteriole system travels within the periosteal lining across the wall of scala vestibuli to the region of the spiral ligament. At this point the arterioles break up to form three capillary networks along the lateral wall of the periotic labyrinth. The first group of vessels supplies the region of the spiral ligament immediately above the insertion of Reissner's membrane. The second group of vessels forms the highly anastomosed capillary bed of the stria vascularis. The third set of capillaries supplies the vessel of the spiral prominence. A significant proportion of the arterioles of the lateral wall form vessels that bypass these three capillary systems, connecting directly with the collecting venules of the scala tympani. The vessels of the lateral wall and spiral vessels underlying the basilar membrane drain into venules, which form the apical and basal spiral modiolar vein. These form the common modiolar vein in the basal turn of the cochlea, which finally empties into the vein of the cochlear aqueduct.

It may be noted that neither the structures of the organ of Corti nor the cortilymphatic space has blood vessels. The neuroepithelium of the organ of Corti must thus receive oxygen and nutrients indirectly from either the vessels of the lateral wall of the cochlear duct, the spiral vessels underlying the basilar membrane, or other nearby vessels, such as the spiral limbus vessels.