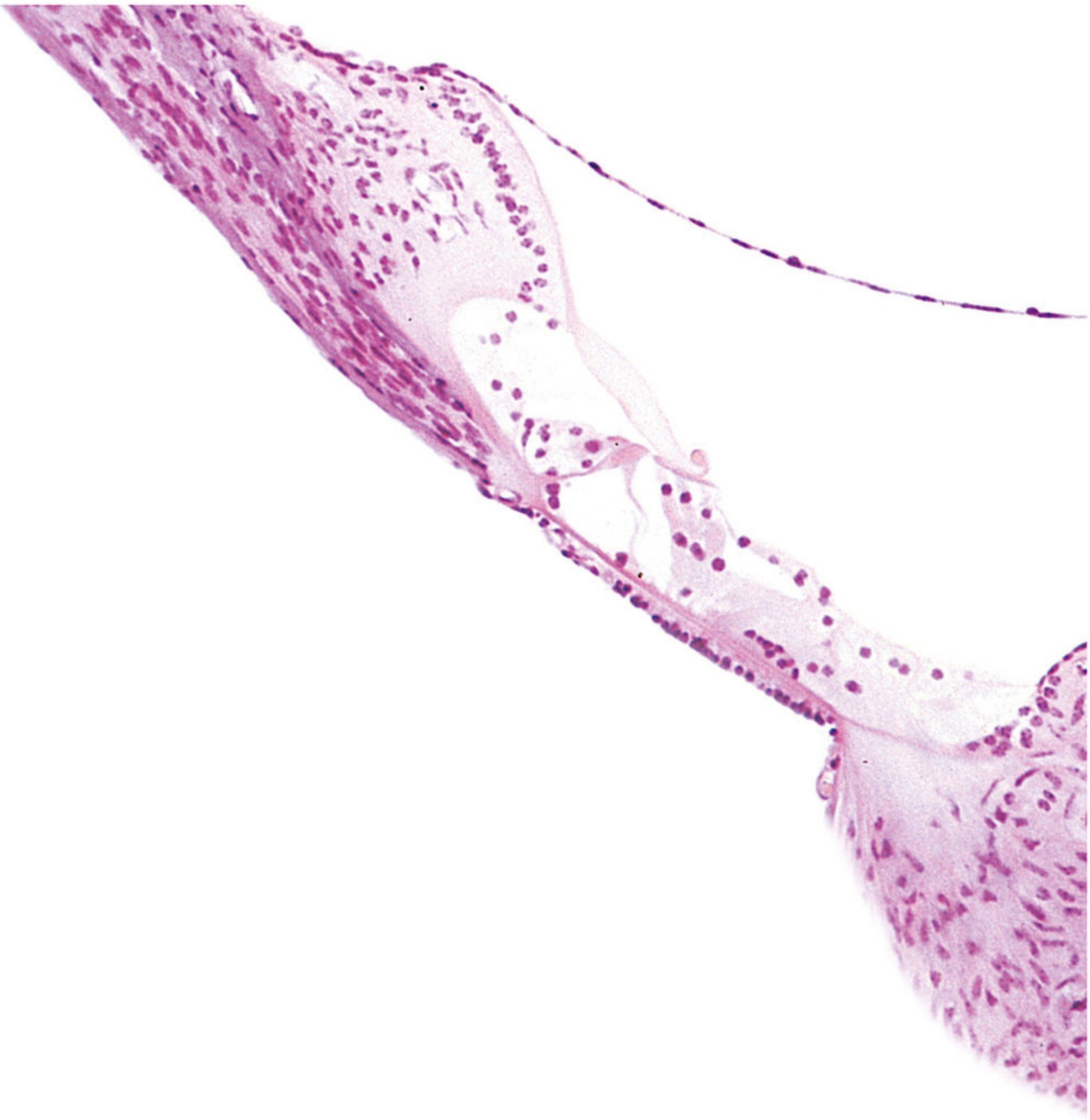


25

EAR

■ OVERVIEW OF THE EAR

The **ear** is a three-chambered sensory organ that functions as an **auditory system** for sound perception and as a **vestibular system** for balance. Each of the three divisions of the ear—the **external ear**, **middle ear**, and **internal ear**—is an essential part of both systems (Fig. 25.1). The external and middle ears collect and conduct acoustic energy to the internal ear, where auditory sensory receptors convert that energy into electrical impulses. The sensory receptors of the vestibular system respond to gravity and movement of the head. They are responsible for the sense of balance and equilibrium and help coordinate movements of the head and eyes.

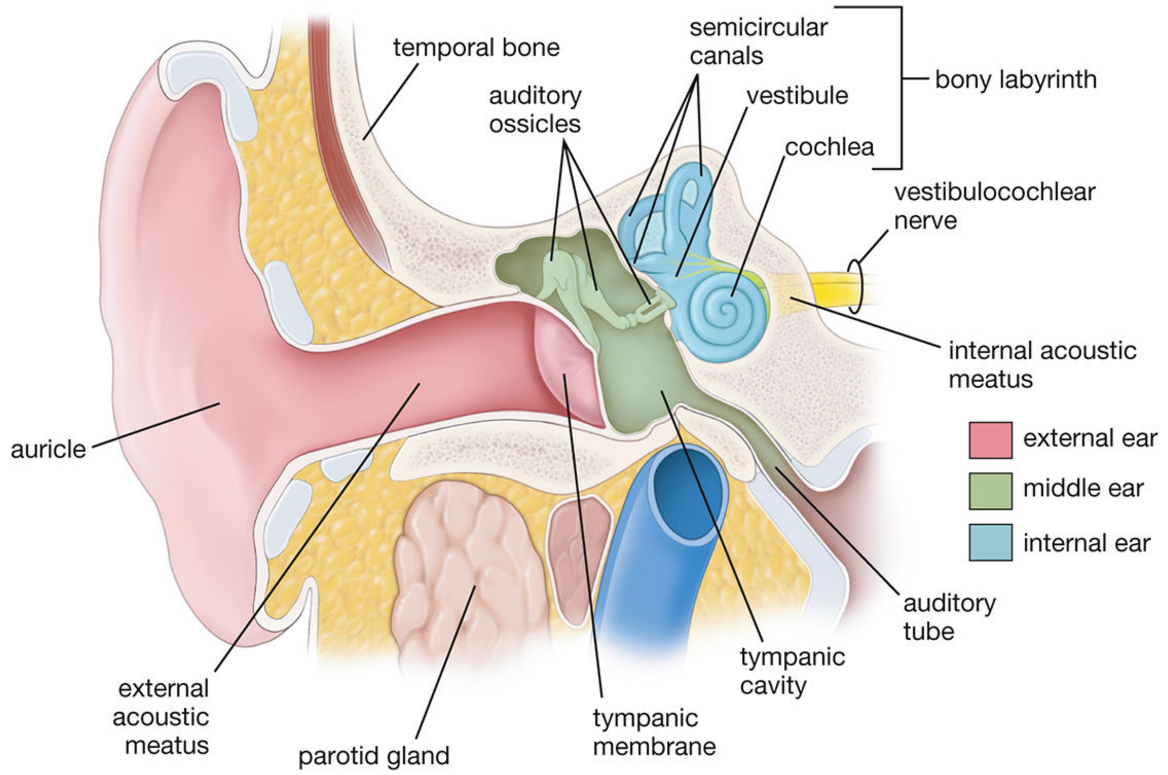


FIGURE 25.1. Three divisions of the ear. The three divisions of the ear are represented by different colors and consist of the external ear (auricle and external acoustic meatus; *pink*), the middle ear (tympanic cavity, auditory ossicles, tympanic membrane, and auditory tube; *green*), and the internal ear containing the bony labyrinth (semicircular canals, vestibule, and cochlea; *blue*) and the membranous labyrinth (not visible).

The ear develops from surface ectoderm and components of the first and second pharyngeal arches.

The internal ear is the first of the three ear divisions to begin development. At the end of the third week, a thickening of **surface ectoderm** that appears on each side of the myelencephalon develops into the **otic placode**. Early in the fourth week, the otic placode invaginates and then pinches off to form the **otic vesicle (otocyst)**, which sinks deep to the surface ectoderm into the underlying mesenchyme (Fig. 25.2). The otic vesicle serves as a primordium for the development of the epithelia that line the membranous labyrinth of the internal ear. Later, development of the first and part of the second pharyngeal arch provides structures that augment hearing. The endodermal component of the **first pouch** gives rise to the **tubotympanic recess**, which ultimately develops into the **auditory tube (Eustachian tube)** and the **middle ear** and its epithelial lining. The corresponding ectodermal outgrowth of the **first pharyngeal groove** gives rise to the **external acoustic meatus** and its epithelial lining (see Fig.

25.2). The connective tissue part of the pharyngeal arches produces the ossicles ("ear bones"). The **malleus** and **incus** develop from the first pharyngeal arch and the **stapes** from the second pharyngeal arch. The sensory epithelia of the membranous labyrinth that originates from the otic vesicle link with cranial nerve VIII, which is an outgrowth of the central nervous system. The auricle of the external ear develops from six **auricular hillocks** located at the dorsal ends of the first and second pharyngeal arches surrounding the first pharyngeal cleft. The cartilaginous, bony, and muscular structures of the ear develop from the mesenchyme surrounding these early epithelia.

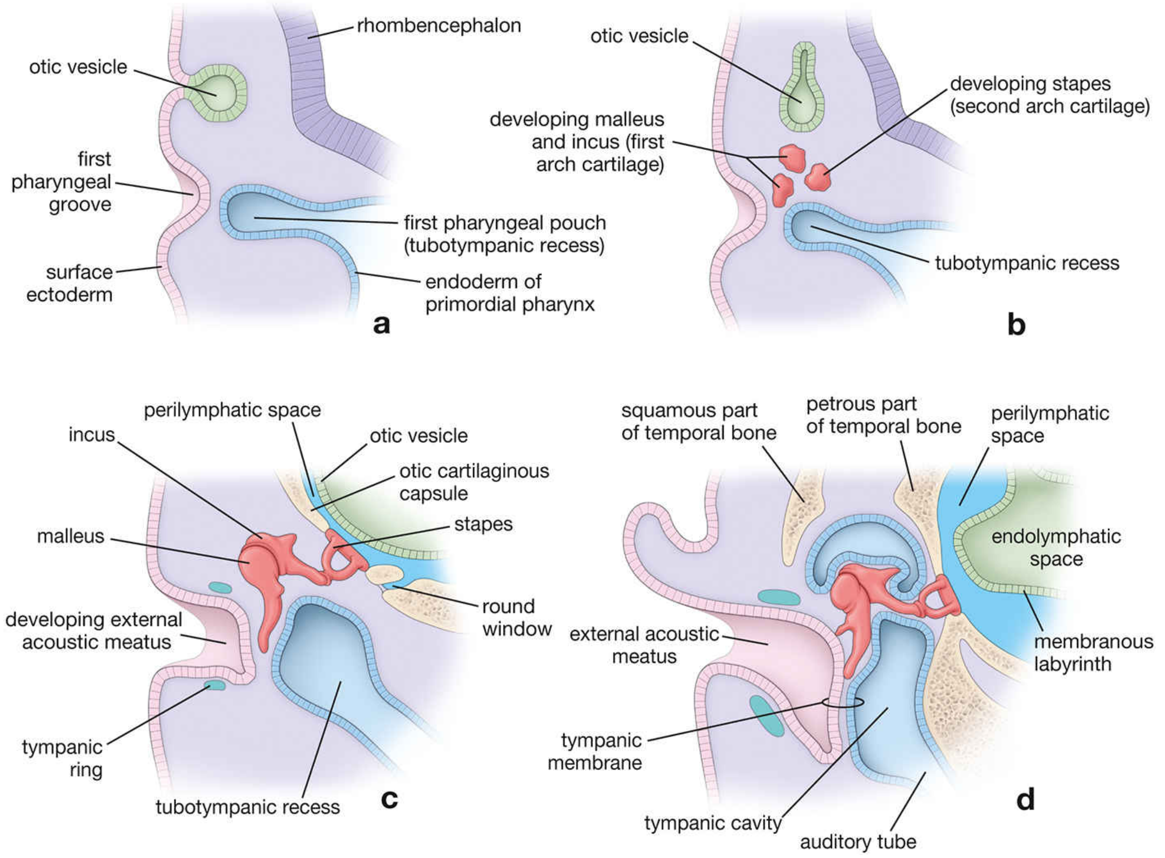


FIGURE 25.2. Schematic drawings showing development of the ear. a. This drawing shows the relationship of the surface ectoderm–derived otic vesicle to the first pharyngeal arch during the fourth week of development. **b.** The otic vesicle sinks deep into the mesenchymal tissue and develops into the membranous labyrinth. Note the development of the tubotympanic recess lined by endoderm into the future middle ear cavity and auditory tube. In addition, accumulation of mesenchyme from the first and second pharyngeal arches gives rise to the auditory ossicles. **c.** At this later stage of development, the first pharyngeal groove grows toward the developing tubotympanic recess. The auditory ossicles assume a location inside the tympanic cavity. **d.** This final stage of development shows how the tympanic

membrane develops from all three germ layers: surface ectoderm, mesoderm, and endoderm. Note that the wall of the otic vesicle develops into the membranous labyrinth.

■ EXTERNAL EAR

The auricle is the external component of the ear that collects and amplifies sound.

The **auricle (pinna)** is the oval appendage that projects from the lateral surface of the head. The characteristic shape of the auricle is determined by an internal supporting structure of elastic cartilage. Thin skin with hair follicles, sweat glands, and sebaceous glands cover the auricle. The auricle is considered a nearly vestigial structure in humans, compared with its development and function in other animals. Nevertheless, it is essential in collecting the sound and directing it into the external acoustic meatus.

The external acoustic meatus conducts and amplifies sounds on the way to the tympanic membrane.

The **external acoustic meatus** is an air-filled tubular space that follows a slightly S-shaped course for about 25 mm to the **tympanic membrane (eardrum)**. Because of its length, the external acoustic meatus can amplify sounds with frequencies of 2,000–5,000 Hz. By passively conducting sounds at this frequency and acting as a **resonator**, the external acoustic meatus increases the sound pressure at the tympanic membrane by approximately a **factor of 2**.

The wall of the meatus is continuous externally with the auricle. The wall of the lateral one-third of the meatus is cartilaginous and is continuous with the elastic cartilage of the auricle. The medial two-thirds of the meatus are contained within the temporal bone. Both parts of the meatus are lined by skin, which is also continuous with that of the auricle.

The skin in the lateral part of the meatus contains hair follicles, sebaceous glands, and **ceruminous glands**, but no eccrine sweat glands. The coiled tubular ceruminous glands closely resemble the apocrine glands found in the axillary region. Their secretion mixes with that of the sebaceous glands and desquamated cells to form **cerumen**, or **earwax**. Because the external acoustic meatus is the only blind pouch of the skin in the body, the earwax provides the means to evacuate desquamating cells from the stratum corneum, thus preventing their accumulation in the meatus. The **cerumen** lubricates the skin and coats the meatal hairs to impede the entry of foreign particles into the ear. It also provides some antimicrobial protection from bacteria, fungi, and insects.

Excessive accumulation of cerumen (**impacted cerumen**) can plug the meatus, resulting in **conductive hearing loss**. The medial part of the meatus located within the temporal bone has thinner skin and fewer hairs and glands.

■ MIDDLE EAR

The middle ear is an air-filled space that contains three small bones, the ossicles.

The **middle ear** is located in an air-filled space, called the **tympanic cavity**, within the temporal bone (Fig. 25.3). It is spanned by three small bones, the **auditory ossicles**, which are connected by two movable joints. The middle ear also contains the **auditory tube (Eustachian tube)**, which opens to the nasopharynx as well as the muscles that attach to the ossicles.

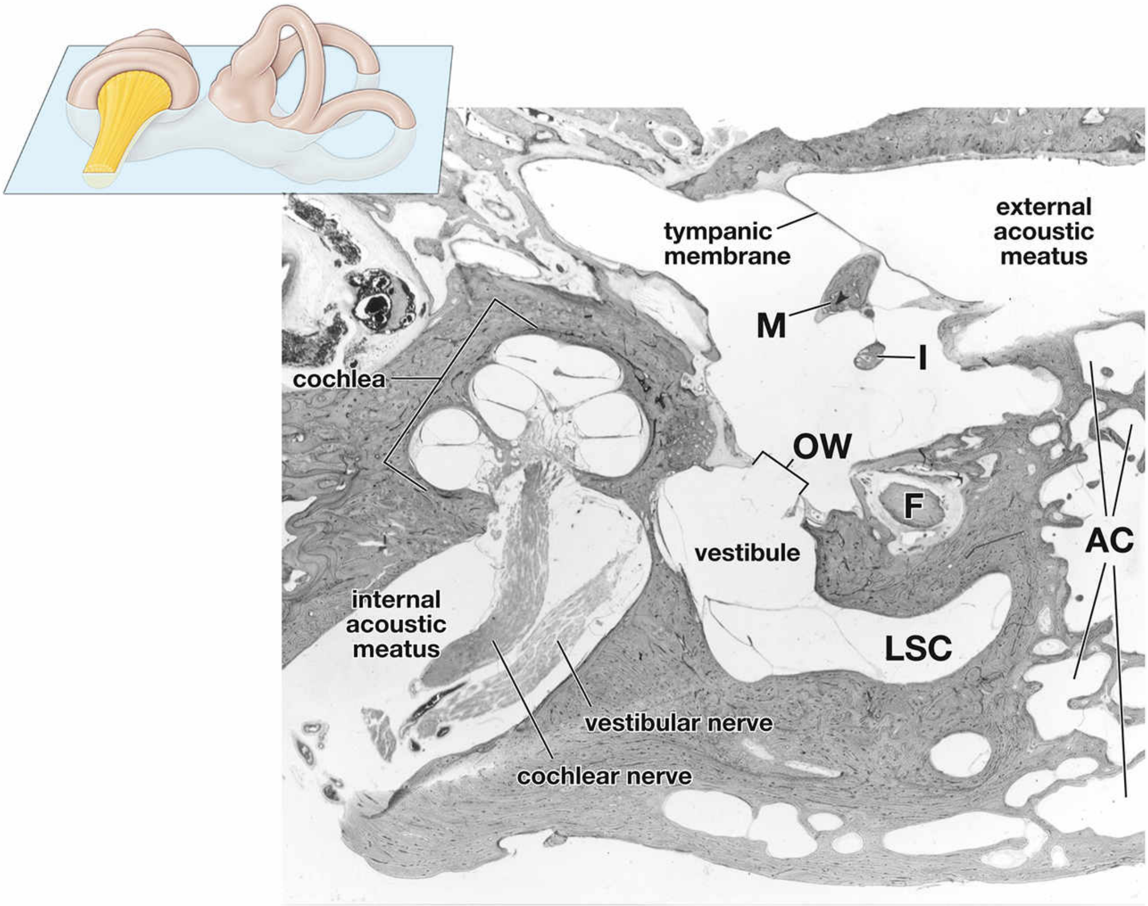


FIGURE 25.3. Horizontal section of a human temporal bone. The relationships of the three divisions of the ear within the petrous part of the temporal bone are shown. Note the orientation icon that shows the plane of section. The *tympanic membrane* separates the *external acoustic meatus* from the tympanic cavity. Within the tympanic cavity, sections of the malleus

(*M*) and incus (*I*) can be seen. The posterior wall of the tympanic cavity is associated with the mastoid air cells (*AC*). The lateral wall of the cavity is formed principally by the tympanic membrane. The opening to the internal ear or oval window (*OW*) is seen in the medial wall of the cavity (the stapes has been removed). The facial nerve (*F*) can be observed near the oval window. The *cochlea*, vestibule, and a portion of the lateral semicircular canal (*LSC*) of the bony labyrinth are identified. The *cochlear* and *vestibular nerves* are divisions of cranial nerve VIII and can also be observed within the *internal acoustic meatus*. *Inset* in the upper left of the photomicrograph shows the plane of the section through the bony labyrinth. ×65.

The tympanic cavity has a roof, floor, and four walls: anterior, posterior, lateral, and medial. The tympanic cavity contains an opening of the auditory tube and is bound anteriorly by a thin layer of bone that separates it from the internal carotid artery. The posterior wall of the tympanic cavity is formed by the spongy bone of the **mastoid process**, which contains the **mastoid antrum** and other, smaller, air-filled spaces called **mastoid air cells**. The middle ear is bound laterally by the **tympanic membrane** and medially by the bony wall of the internal ear. The floor and roof of the tympanic cavity are both formed by a thin layer of bone, which separates them from the internal jugular vein and middle cranial fossa, respectively.

The middle ear is a mechanical energy transformer. Its primary function is to convert sound waves (air vibrations) arriving from the external acoustic meatus into mechanical vibrations that are transmitted to the internal ear. Two openings in the medial wall of the middle ear, the **oval (vestibular) window** and the **round (cochlear) window**, are essential components in this conversion process.

The tympanic membrane separates the external acoustic meatus from the middle ear.

The intact **tympanic membrane** is a semitransparent, thin (about 0.1 mm) membrane approximately 1 cm in diameter that has an average surface area in humans of about 65 mm^2. It is shaped like an irregular flat cone, the apex of which is located at the **umbo** that corresponds to the tip of the manubrium of the malleus. The tympanic membrane at the end of the external acoustic meatus is tilted anteriorly and inferiorly. Thus, orientation of the tympanic membrane has been compared to the position of a miniature satellite dish tuned to receive signals coming from the ground in front of the body and to the side of the head. During otoscopic examination of a normal ear, the tympanic membrane is a semitransparent light gray color and has a visible concavity toward the external acoustic meatus. Owing to its concavity, light from the otoscope reflects off the tympanic membrane as a triangular **cone of light** (light reflex) that radiates anteriorly and inferiorly from the umbo (Fig. 25.4). The malleus is one of three small auditory ossicles residing in the middle ear and is the only one that attaches to the tympanic membrane (see Fig. 25.1).

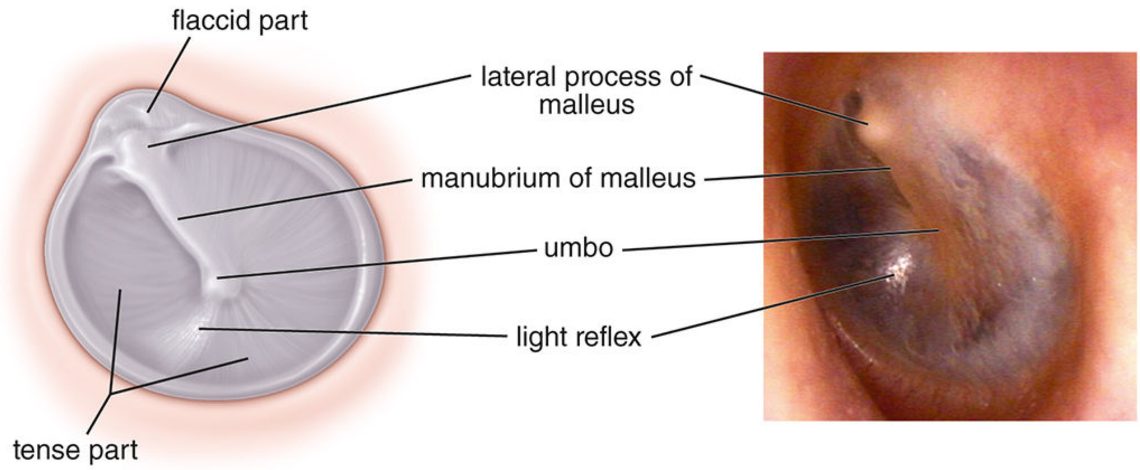


FIGURE 25.4. The tympanic membrane in otoscopic examination of the external ear. This diagram and photograph show the left tympanic membrane seen with an otoscope during examination of the external acoustic meatus. The landmarks of the tympanic membrane include the manubrium of the malleus with its visible attachment to the tense part of the membrane, umbo at the tip of the manubrium, and projecting lateral process of the malleus. A small, flaccid part of the tympanic membrane is located above the lateral process of the malleolus. Note the cone of light (light reflex) that is usually seen extending anteroinferiorly from the umbo of the tympanic membrane. (Courtesy of Dr. Eric J. Moore.)

The **tympanic membrane** forms the medial boundary of the external acoustic meatus and the lateral wall of the middle ear (Fig. 25.5). From outside to inside, the three layers of the tympanic membrane are

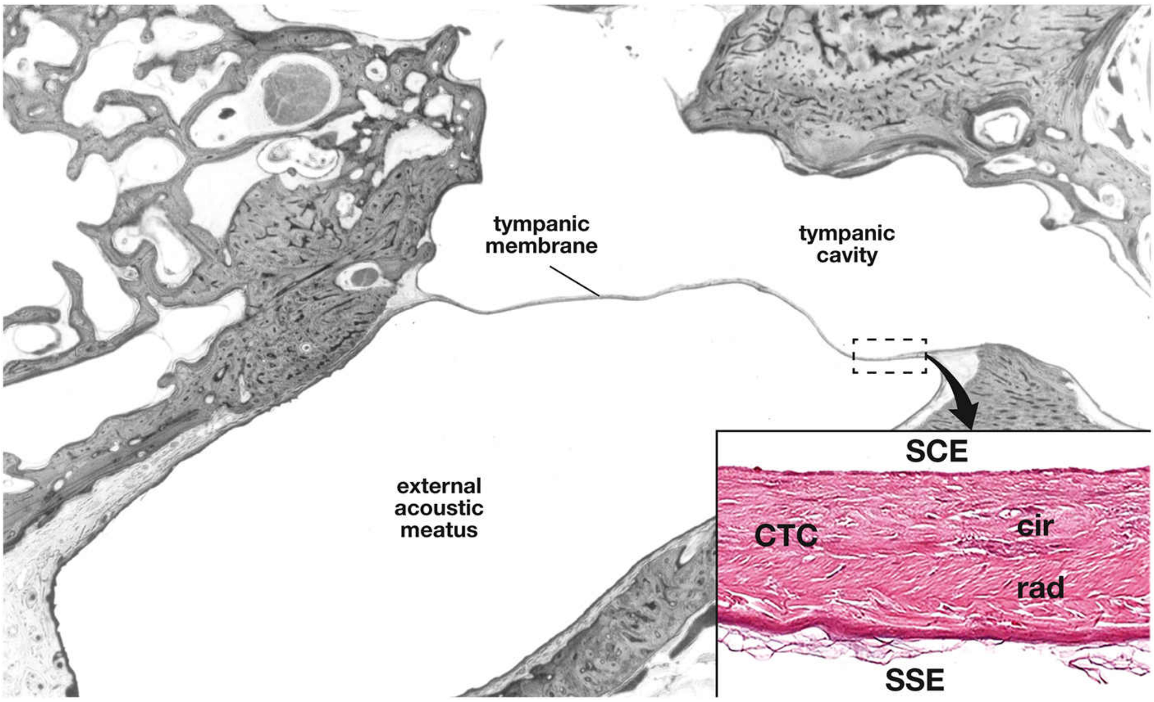


FIGURE 25.5. Cross section through a human tympanic membrane. This photomicrograph shows the *tympanic membrane*, *external acoustic meatus*, and *tympanic cavity*. ×9. **Inset.** Higher magnification of the tympanic membrane. The outer epithelial layer of the membrane consists of stratified squamous keratinized epithelium (*SSE*), and the inner epithelial layer of the mucous membrane consists of low simple cuboidal epithelium (*SCE*). A middle layer of connective tissue core (*CTC*) lies between the two epithelial layers. The dense irregular connective tissue core is formed by two layers: the outer layer in which fibers are radially arranged (*rad*) and the inner layer with circumferentially arranged fibers (*cir*). ×190.

- the skin of the external acoustic meatus (epidermis composed of stratified squamous keratinized epithelium)
- a core of connective tissue with an outer layer of radially and inner layer of circularly arranged collagen fibers, and
- the mucous membrane of the middle ear (composed of simple cuboidal epithelium).

The larger, lower part of the tympanic membrane (**tense part** or **pars tensa**) is tightly stretched and has a thick middle core that contains radial and circular collagen fibers and gives the membrane its shape and smooth appearance. The smaller, upper part of the tympanic membrane that lies superior to the lateral process of the malleolus is loose (**flaccid part** or **pars flaccida**) and lacks a prominent middle fibrous layer (see Fig. 25.4). Sound waves cause the tympanic membrane to vibrate, and these vibrations are transmitted through the ossicular chain of three small bones that link the external ear to the internal ear.

Tympanic membrane perforations are caused by a rupture in the tympanic membrane that creates a connection between the external auditory meatus and the middle ear. This rapture can be attributed to infections, mechanical injury, or rapid changes in pressure, leading to sudden ear pain (otalgia), ear discharge (otorrhea), ringing in the ears (tinnitus), and a sensation of feeling off-balance (vertigo). Most perforations resolve spontaneously without complications; however, some may cause transient or permanent **hearing impairment**.

The auditory ossicles connect the tympanic membrane to the oval window.

The **three auditory ossicles** or bones—the malleus, the incus, and the stapes—cross the space of the middle ear in series and connect the tympanic membrane to the oval window (Fig. 25.6). These bones work like a lever system that increases the force transmitted from the vibrating tympanic membrane to the stapes by decreasing the ratio of their oscillation amplitudes. The ossicles help convert sound waves to mechanical vibrations (hydraulic waves) in tissues and fluid-filled chambers. Movable synovial joints connect the bones, which are named according to their approximate shape:

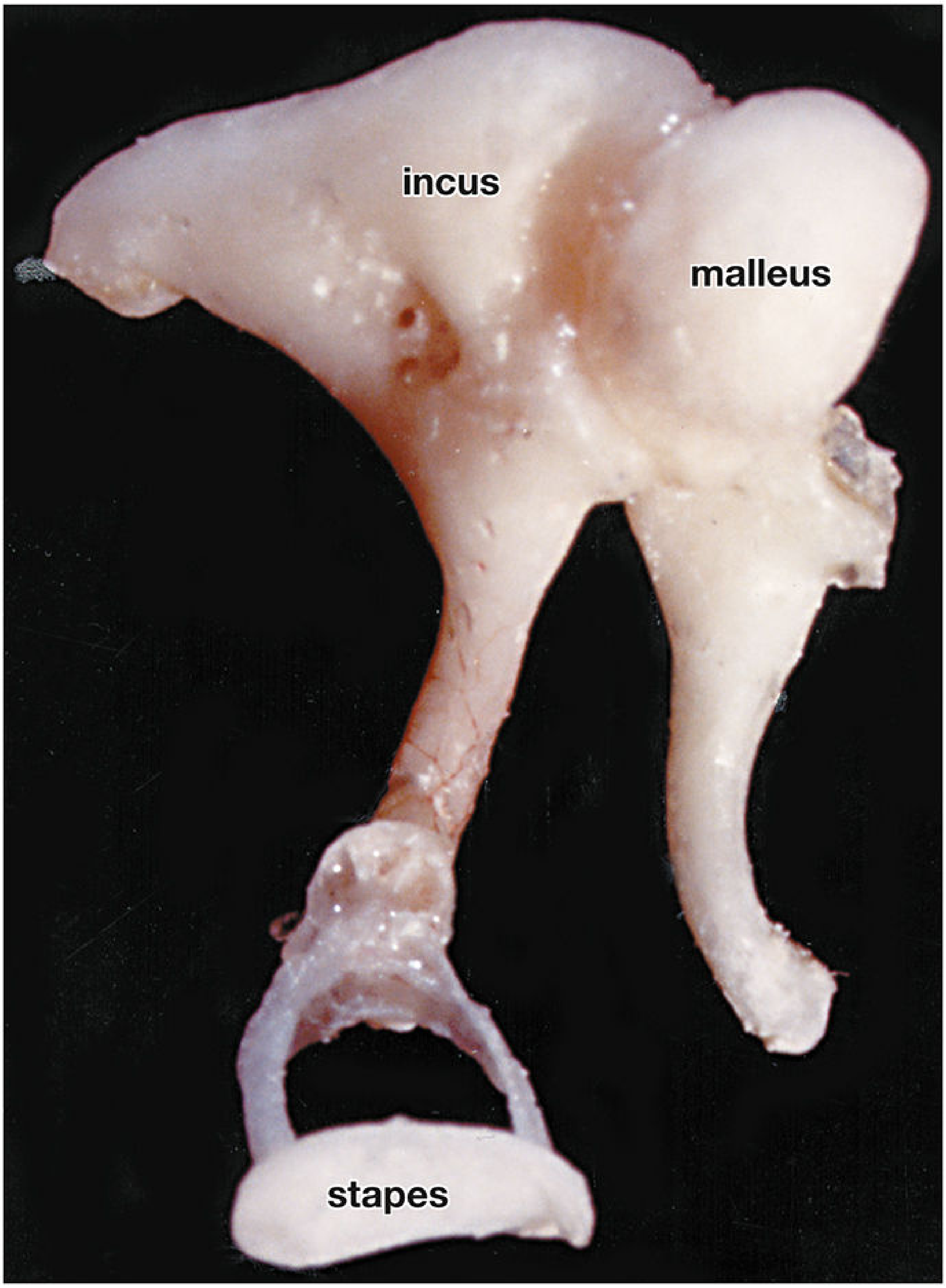


FIGURE 25.6. Photograph of the three articulated human auditory ossicles. The three ossicles are the malleus, the incus, and the stapes. ×30.

- The **malleus (hammer)** attaches to the tympanic membrane and articulates with the incus.

- The **incus (anvil)** is the largest of the ossicles and links the malleus to the stapes.
- The **stapes (stirrup)**, the footplate of which fits into the oval window. The footplate in the human stapes measures approximately 3 mm × 1 mm and has an average surface area of 3 mm^2. It acts like a small piston on the cochlear fluid, creating hydraulic waves to represent the air-pressure fluctuations of the sound wave.

Diseases that affect the external acoustic meatus, tympanic membrane, or ossicles are responsible for **conductive hearing loss** (see Folders 25.1 and 25.2).

FOLDER 25.1

CLINICAL CORRELATION: OTOSCLEROSIS

Otosclerosis is one of the most common causes of acquired hearing loss. It is reported that ~13% of the U.S. population has nonclinical otosclerosis (histologic otosclerosis); however, the incidence of clinical disease ranges from 0.5% to 1.0%. Individuals with clinical otosclerosis have progressive hearing loss. Symptoms usually become apparent between ages 20 and 45 years. Otosclerosis is characterized by the abnormal overgrowth of bone that uniquely affects the temporal bone and ossicles. Although the cause of bone overgrowth in otosclerosis is unknown, recent studies suggest an association with measles virus infection. In otosclerosis, mature bone in the area of the oval window on the medial wall of the tympanic cavity, which separates the middle ear from the internal ear, is removed by osteoclasts and replaced with much thicker immature (woven) bone. Because the footplate of the stapes normally resides and freely vibrates within the oval window to allow the transmission of sound into the internal ear, bone remodeling in this area results in fixation of the stapes into the surrounding bone. The "frozen" stapes cannot vibrate, which prevents sound waves from reaching the perilymphatic fluid space of the internal ear and causes conductive hearing loss. Treatment of otosclerosis includes several options: pharmacologic treatment to suppress bone remodeling with fluorides and bisphosphonates, amplification of sounds with hearing aids, and surgical removal of the stapes (**stapedectomy**) with subsequent implantation of a prosthesis between the incus and the oval window. Surgery is usually the most effective method of managing otosclerosis; >90% of patients experience a complete reversal of their hearing loss.

FOLDER 25.2

CLINICAL CORRELATION: HEARING LOSS—VESTIBULAR DYSFUNCTION

Several types of disorders can affect the auditory and vestibular system and result in deafness, dizziness (vertigo), or both. Auditory disorders are classified as either sensorineural or conductive. **Conductive hearing loss** results when sound waves are mechanically impeded from reaching the auditory sensory receptors within the internal ear. This type of hearing loss principally involves the external ear or structures of the middle ear. Conductive hearing loss is the second most common type of loss after sensorineural hearing loss, and it usually involves a reduction in sound level or the inability to hear faint sounds. Conductive hearing loss may be caused by otitis media (ear infection); in fact, this is the most common cause of temporary hearing loss in children. Fluid that collects in the tympanic cavity can also cause significant hearing problems in children. Other common causes of conductive hearing loss include excess wax or foreign bodies in the external acoustic meatus or diseases that affect the ossicles in the middle ear (otosclerosis; see also Folder 25.1). In many cases, conductive hearing loss can be treated either medically or surgically and may not be permanent.

Sensorineural hearing impairment may occur after injury to the auditory sensory hair cells within the internal ear, cochlear division of cranial nerve VIII, nerve pathways in the central nervous system (CNS), or auditory cortex. Sensorineural hearing loss accounts for about 90% of all hearing loss. It may be congenital or acquired. Causes of acquired sensorineural hearing loss include infections of the membranous labyrinth (e.g., meningitis, chronic otitis media), fractures of the temporal bone, acoustic trauma (i.e., prolonged exposure to excessive noise), and administration of certain classes of antibiotics and diuretics.

Another example of sensorineural hearing loss often results from aging. Sensorineural hearing loss not only involves a reduction in sound level but also affects the ability to hear clearly or to distinguish speech. A loss of the sensory hair cells or associated nerve fibers begins in the basal turn of the cochlea and progresses apically over time. The characteristic impairment is a high-frequency hearing loss termed **presbycusis** (see presbyopia, page 1004).

In selected patients, the use of a **cochlear implant** can partially restore some hearing function. The cochlear implant is an electronic device consisting of an external microphone, amplifier, and speech processor linked to a receiver implanted under the skin of the mastoid region. The receiver is connected to the multielectrode intracochlear implant inserted along the wall of the cochlear canal. After considerable training and tuning of the speech processor, the patient's hearing can be partially restored to various degrees ranging from recognition of critical sounds to the ability to converse.

Two muscles attach to the ossicles and affect their movement.

The **tensor tympani muscle** lies in a bony canal above the auditory tube; its tendon inserts on the malleus. Contraction of this muscle increases tension on the tympanic membrane. The **stapedius muscle** lies in a bony eminence on the posterior wall of the middle ear; its tendon inserts on the stapes. Contraction of the stapedius tends to dampen the movement of the stapes at the oval window. The stapedius is only a few millimeters long and is the smallest skeletal muscle.

The two muscles of the middle ear are responsible for a protective reflex called the **attenuation reflex** or **acoustic reflex**. In response to intense sound, involuntary contraction of the muscles makes the chain of ossicles more rigid, thus reducing the transmission of vibrations to the internal ear. The muscles will contract on both sides, regardless of which ear is stimulated. This reflex protects the internal ear from the damaging effects of very loud sounds. In certain conditions, such as impulse noise (i.e., fireworks or gun fire), the attenuation reflex is ineffective.

The auditory tube connects the middle ear to the nasopharynx.

The **auditory (Eustachian) tube** is a narrow flattened channel approximately 3.5 cm long. This tube is lined with ciliated pseudostratified columnar epithelium, about one-fifth of which is composed of goblet cells. It vents the middle ear to nasopharynx, equalizing the pressure of the middle ear with atmospheric pressure. In addition, the auditory tube is responsible for draining the secretion produced by the mucous membrane of the middle ear towards the nasopharynx with the aid of the ciliated pseudostratified columnar epithelium. The auditory tube is normally closed; its walls are pressed together but they separate during yawning, chewing, swallowing, and when individual holds the nose and blows. Children are more vulnerable to the middle ear infections, due to the immature development of their auditory tubes which are shorter, narrower, and more horizontal than in the adults. It is common for infections to spread from the pharynx to the middle ear via the auditory tube (causing **otitis media**). A small mass of lymphatic tissue, the **tubal tonsil**, is often found at the pharyngeal orifice of the auditory tube.

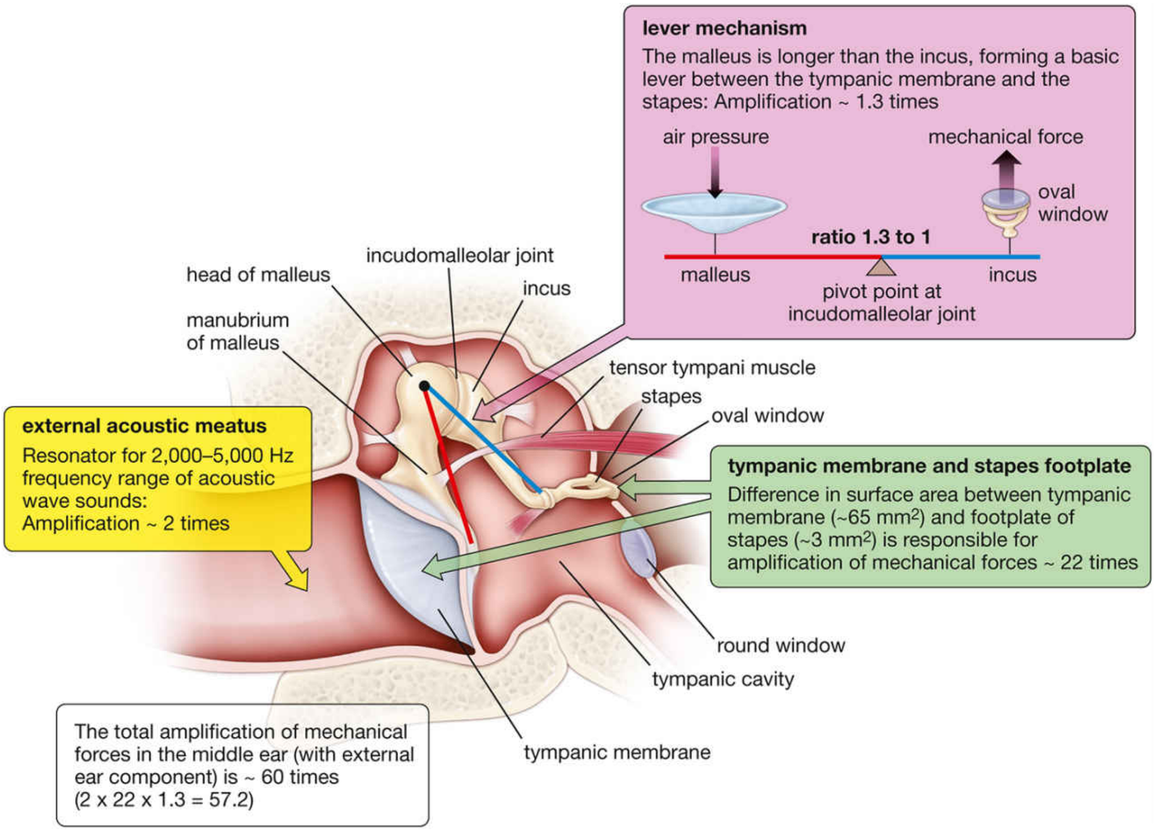
The mastoid air cells extend from the middle ear into the temporal bone.

A system of **air cells** projects into the mastoid portion of the temporal bone from the middle ear. The epithelial lining of these air cells is continuous with that of the tympanic cavity and rests on periosteum. This continuity allows infections in the middle ear to spread into **mastoid air cells**, causing **mastoiditis**. Before the development of antibiotics, repeated episodes of otitis media and mastoiditis usually led to deafness.

The middle ear contributes to the amplification of mechanical forces generated by the vibration of the tympanic membrane.

All three ossicles in the tympanic cavity are involved in the **amplification of the mechanical force** that vibrates the tympanic membrane in two ways:

- The main amplification comes from **differences in the surface area** between the tympanic membrane and the footplate of the stapes. The **tympanic membrane** has a surface area of approximately **$65\ mm^2$**, whereas the footplate of the **stapes** has a surface area of about **$3\ mm^2$**. Sound waves apply force to every square millimeter of the tympanic membrane, and this energy is transferred via the chain of ossicles to the much smaller area of the footplate. Therefore, the pressure applied to the cochlear fluid by the footplate is **about 22 times** the pressure applied to the tympanic membrane (Fig. 25.7).



lever mechanism
The malleus is longer than the incus, forming a basic lever between the tympanic membrane and the stapes: Amplification ~ 1.3 times

external acoustic meatus
Resonator for 2,000–5,000 Hz frequency range of acoustic wave sounds:
Amplification ~ 2 times

tympanic membrane and stapes footplate
Difference in surface area between tympanic membrane (~65 mm^2) and footplate of stapes (~3 mm^2) is responsible for amplification of mechanical forces ~ 22 times

The total amplification of mechanical forces in the middle ear (with external ear component) is ~ 60 times
(2 x 22 x 1.3 = 57.2)

FIGURE 25.7. Summary of amplification of sound entering the ear. This drawing shows the external and middle ear structures and their contributions to the amplification of sound entering the ear. Note that the largest amplification comes from the difference in the surface area

between the tympanic membrane (65 mm^2) and the footplate of the stapes (3 mm^2). This surface area difference results in ~22 times the amplification of the pressure applied by the footplate of the stapes. Another source of amplification comes from the external acoustic meatus and middle ear. The external acoustic meatus acts as a resonator that increases the sound pressure acting on the tympanic membrane by *2 times. Finally, the arrangement of auditory ossicles resembles a basic lever that multiplies the applied mechanical force acting on the footplate of the stapes by* 1.3 times. By multiplying these three amplification factors, the acoustic energy entering the ear is amplified ~60 times.

- Additional amplification comes from the arrangement of **auditory ossicles** that act as **levers** that multiply the mechanical force applied to the stapes. Because the pivot point of the ossicle chain is located farther from the tympanic membrane than from the stapes, the amplification of the mechanical force at the oval window is increased by a factor of **approximately 1.3**. This lever system is adjustable by the action of muscles in the tympanic cavity and may attenuate loud sounds to protect the ear (see Fig. 25.7).

Under normal conditions, the acoustic energy entering the ear is amplified **approximately 60 times**, allowing humans to detect frequencies between 2,000 and 5,000 Hz. The degree of amplification is calculated by multiplying the amplification factors contributed by the external acoustic meatus (~2 times) as described earlier on pages 1018-1019, the surface area differences between the tympanic membrane and the footplate of stapes (~22 times), and the basic lever action of ossicles (~1.3 times). However, this calculation ($2 \times 22 \times 1.3 = 57.2$) must be used with caution owing to variability in the mechanical function of the middle ear and its components, such as ossicular joints, ligaments, muscles, and air volumes, as well as varying frequencies of sound.

INTERNAL EAR

The internal ear consists of two labyrinthine compartments, one contained within the other.

The **bony labyrinth** is a complex system of interconnected cavities and canals in the petrous part of the temporal bone. The **membranous labyrinth** lies within the bony labyrinth and consists of a complex system of small sacs and tubules that also form a continuous space enclosed within a wall of epithelium and connective tissue.

There are three fluid-filled spaces in the internal ear:

- **Endolymphatic spaces** are contained within the membranous labyrinth. The **endolymph** of the membranous labyrinth is similar in composition to **intracellular fluid** (it has a high K^+ concentration and a low Na^+ concentration). The endolymph is produced in the stria vascularis, a specialized area of the cochlear duct (see pages 1032-1034). It drains via the endolymphatic duct to the endolymphatic sac, which terminates in the epidural space of the posterior cranial fossa.
- The **perilymphatic space** lies between the wall of the bony labyrinth and the wall of the membranous labyrinth. The **perilymph** is similar in composition to **extracellular fluid** and **cerebrospinal fluid** (it has a low K^+ concentration and a high Na^+ concentration). Perilymph is produced as an ultrafiltrate from the periosteal microvasculature within the bony labyrinth. It drains via a narrow channel within the temporal bone, called the *cochlear aqueduct*, directly into the cerebrospinal fluid contained within the subarachnoid space of the cranial cavity.
- The **cortilymphatic space** lies within the tunnels of the organ of Corti of the cochlea. It is a true intercellular space. The cells surrounding the space loosely resemble an absorptive epithelium. The cortilymphatic space is filled with **cortilymph**, which has a composition similar to that of **extracellular fluid**.

Structures of the Bony Labyrinth

The bony labyrinth consists of three connected spaces within the temporal bone.

The three spaces of the bony labyrinth, as illustrated in Figure 25.8, are the

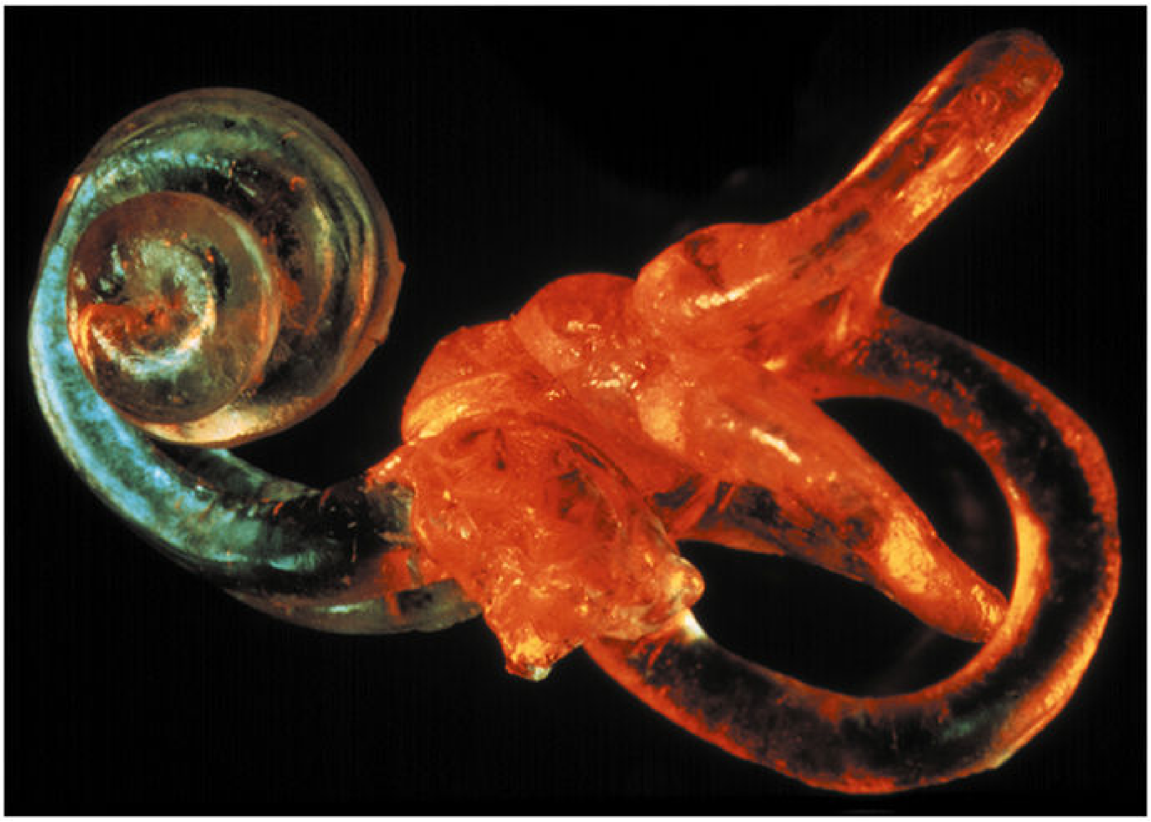


FIGURE 25.8. **Photograph of a cast of the bony labyrinth of the internal ear.** The cochlear portion of the bony labyrinth appears *blue green*; the vestibule and semicircular canals appear *orange red*. (Courtesy of Dr. Merle Lawrence.)

- **semicircular canals**,
- **vestibule**, and
- **cochlea**.

The vestibule is the central space that contains the utricle and saccule of the membranous labyrinth.

The **vestibule** is the small oval chamber located in the center of the bony labyrinth. The **utricle** and **saccule** of the membranous labyrinth lie in elliptical and spherical recesses, respectively. The **semicircular canals** extend from the vestibule posteriorly, and the **cochlea** extends from the vestibule anteriorly. The oval window into which the footplate of the stapes inserts lies in the lateral wall of the vestibule.

The semicircular canals are tubes within the temporal bone that lie at right angles to each other.

Three semicircular canals, each forming about three-quarters of a circle, extend from the wall of the vestibule and return to it. The semicircular canals are identified as anterior, posterior, and lateral and lie within the temporal bone at approximately right angles to each other. They occupy three planes in space—sagittal, frontal, and horizontal. The end of each semicircular canal closest to the vestibule is expanded to form the **ampulla** (Fig. 25.9a and b). The three canals open into the vestibule through five orifices; the anterior and posterior semicircular canals join at one end to form the **common bony limb** (see Fig. 25.9a).

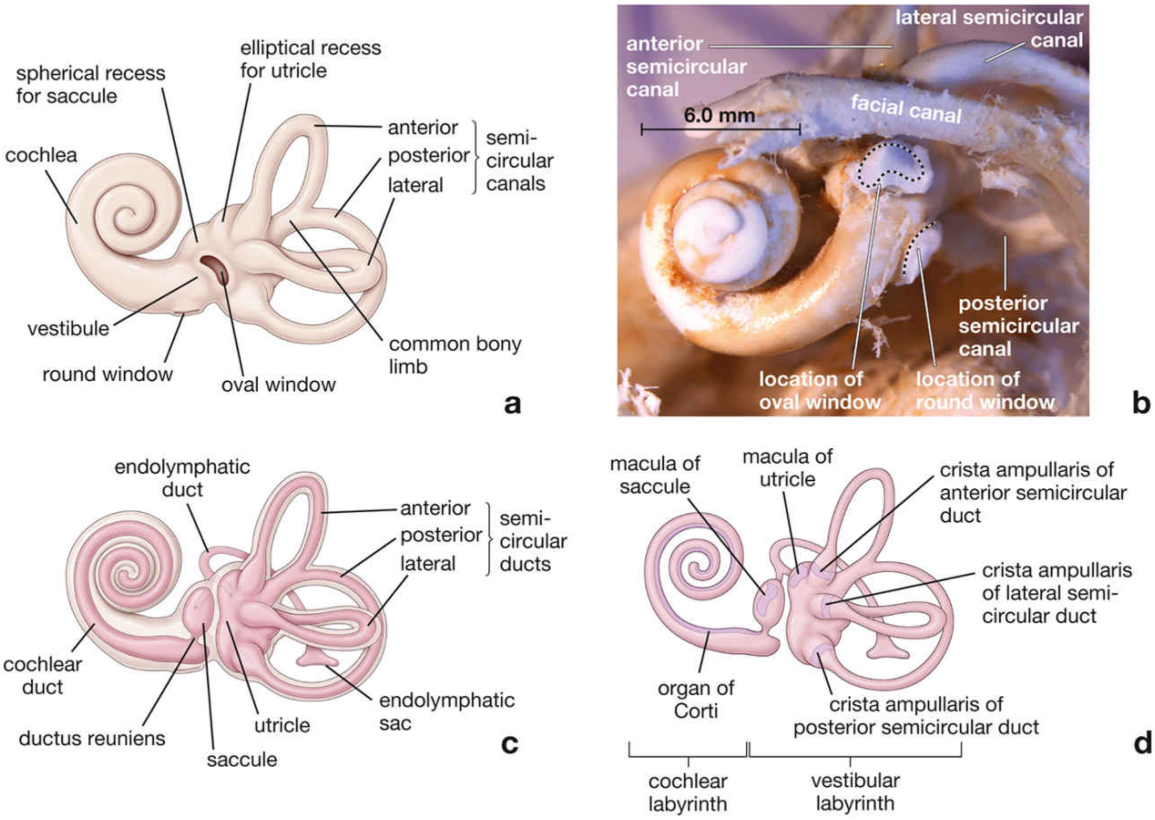


FIGURE 25.9. Diagrams and photograph of the human internal ear. a. This lateral view of the left bony labyrinth shows its divisions: the vestibule, cochlea, and three semicircular canals. The openings of the oval window and the round window can be observed. **b.** This photograph of a cast obtained by injection of polyester resin into the human internal ear shows an authentic shape of the bony labyrinth. Note that the cast material is pouring out of the cochlea through the oval and round windows. Also, in this image, the cast of the facial canal that contains the facial nerve is visible. ×5. (Courtesy of Dr. Elsa Erixon.) **c.** Diagram of a membranous labyrinth of the internal ear lying within the bony labyrinth. The cochlear duct can be seen spiraling within the bony cochlea. The saccule and utricle are positioned within the vestibule, and the three semicircular ducts are lying within their respective canals. This view of the left membranous labyrinth allows the endolymphatic duct and sac to be observed. **d.** This view of the left membranous labyrinth shows the sensory regions of the internal ear for equilibrium and hearing. These regions are the macula of the saccule and macula of the utricle, the cristae

ampullares of the three semicircular ducts, and the spiral organ of Corti of the cochlear duct.

The cochlea is a cone-shaped helix connected to the vestibule.

The spiral lumen of the **cochlea**, called the **cochlear canal** (like the semicircular canals), is continuous with that of the vestibule. It connects to the vestibule via two openings, the **round window** and the **oval window**, both of which are located on the side opposite the openings of the semicircular canals. Between its base and the apex, the cochlear canal makes approximately 2.75 turns around a central core of spongy bone called the **modiolus** (Plate 25.1, page 1042). A sensory ganglion, the **spiral ganglion**, lies in the modiolus. A thin membrane (the secondary tympanic membrane) covers the round window, whereas the footplate of the stapes is positioned within the oval window. These two openings are located at the base of the cochlear canal.

Structures of the Membranous Labyrinth

The membranous labyrinth contains the endolymph and is suspended within the bony labyrinth.

The **membranous labyrinth** consists of a series of communicating sacs and ducts containing endolymph. It is suspended within the bony labyrinth (Fig. 25.9c), and the remaining space is filled with perilymph. The membranous labyrinth is composed of two divisions: the **cochlear labyrinth** and the **vestibular labyrinth** (Fig. 25.9d).

The vestibular labyrinth contains the following:

- Three **semicircular ducts** lie within the semicircular canals and are continuous with the utricle.
- The **utricle** and the **saccule**, which are contained in recesses in the vestibule, are connected by the membranous **utriculosaccular duct**.

The cochlear labyrinth contains the **cochlear duct**, which is contained within the cochlea and is continuous with the saccule (see Fig. 25.9c and d).

Sensory cells of the membranous labyrinth

Specialized sensory cells are located in six regions in the membranous labyrinth.

Six sensory regions of membranous labyrinth are composed of sensory **hair cells** and accessory **supporting cells**. These regions project from the wall of the membranous labyrinth into the endolymphatic space in each internal ear (see Fig. 25.9d):

- Three **cristae ampullares (ampullary crests)** are located in the membranous ampullae of the semicircular ducts. They are sensitive to the angular acceleration of the head (i.e., turning the head).
- Two maculae, one in the utricle (**macula of utricle**) and the other in the saccule (**macula of saccule**), sense the position of the head and its linear movement.
- The **spiral organ of Corti** projects into the endolymph of the cochlear duct. It functions as a sound receptor.

Hair cells are epithelial mechanoreceptors of the vestibular and cochlear labyrinth.

The **hair cells** of the vestibular and cochlear labyrinths function as **mechanoelectrical transducers**; they convert mechanical energy into electrical energy that is then transmitted via the vestibulocochlear nerve to the brain. The hair cells derive their name from the organized bundle of rigid projections at their apical surface. This surface holds a **hair bundle** that is formed by rows of stereocilia called *sensory hairs*. The rows increase in height in one particular direction across the bundle (Fig. 25.10). In the vestibular system, each hair cell possesses a single true cilium called a **kinocilium**, which is located behind the row of longest stereocilia (Fig. 25.11). In the auditory system, the hair cells lose their cilium during development but retain the **basal body**. The position of the kinocilium (or basal body) behind the longest row of stereocilia defines the polarity of this asymmetric hair bundle. Therefore, movement of the stereocilia toward the kinocilium is perceived differently than movement in the opposite direction (see later).

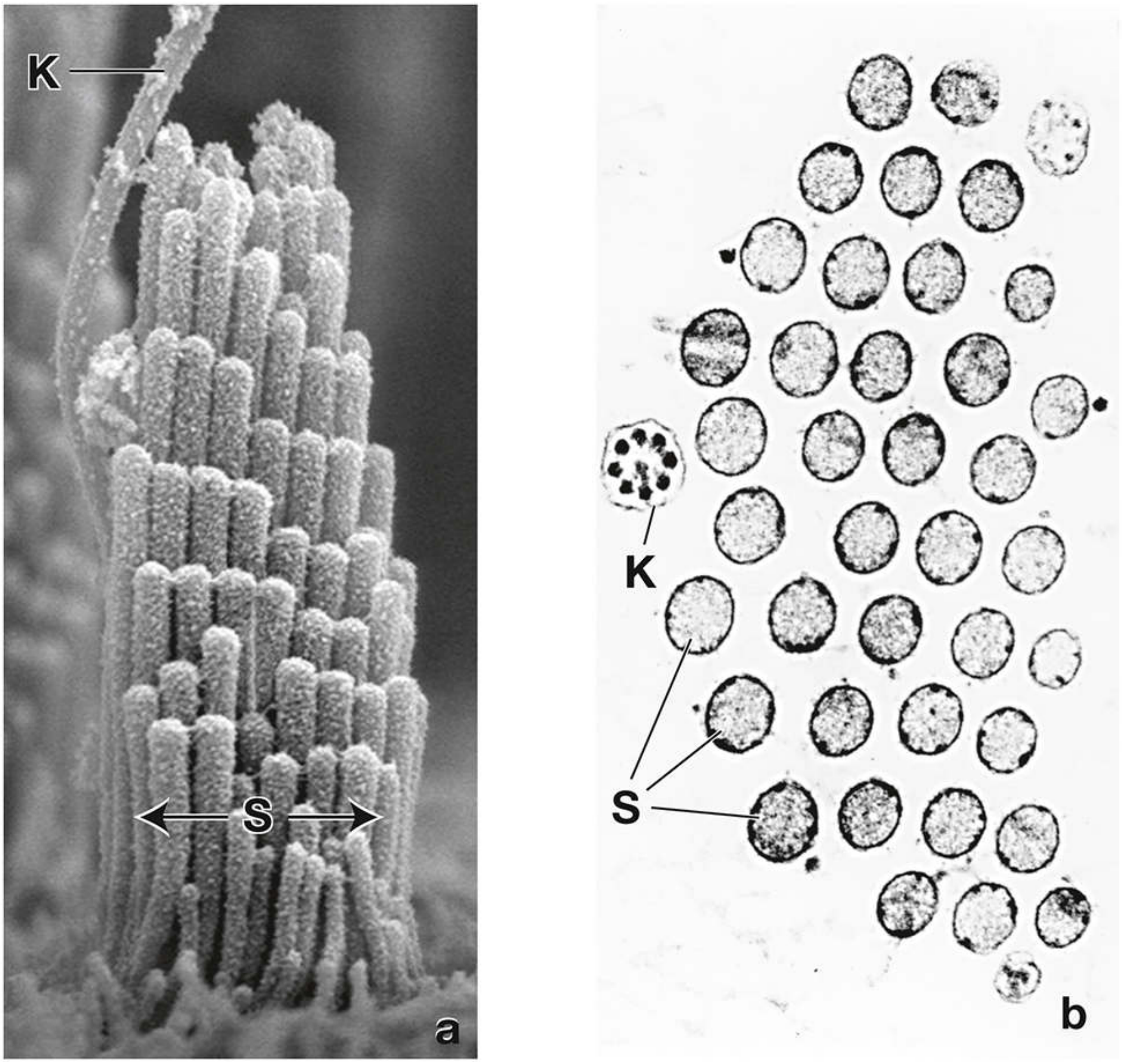


FIGURE 25.10. Electron micrographs of the kinocilium and stereocilia of a vestibular sensory hair cell. a. Scanning electron micrograph of the apical surface of a sensory hair cell from the macula of the utricle. Note the relationship of the kinocilium (*K*) to the stereocilia (*S*). ×47,500. **b.** Transmission electron micrograph of the kinocilium (*K*) and stereocilia (*S*) of a vestibular hair cell in cross section. The kinocilium has a larger diameter than the stereocilia. ×47,500. (**a.** Reprinted with permission from Rzadzinska AK, Schneider ME, Davies C, *et al.* An actin molecular treadmill and myosins maintain stereocilia functional architecture and self-renewal. *J Cell Biol.* 2004;164:887–897. **b.** Reprinted with permission from Hunter-Duvar IM, Hinojosa R. Vestibule: sensory epithelia. In: Friedmann I, Ballantyne J, eds. *Ultrastructural Atlas of the Inner Ear*. Butterworth; 1984.)

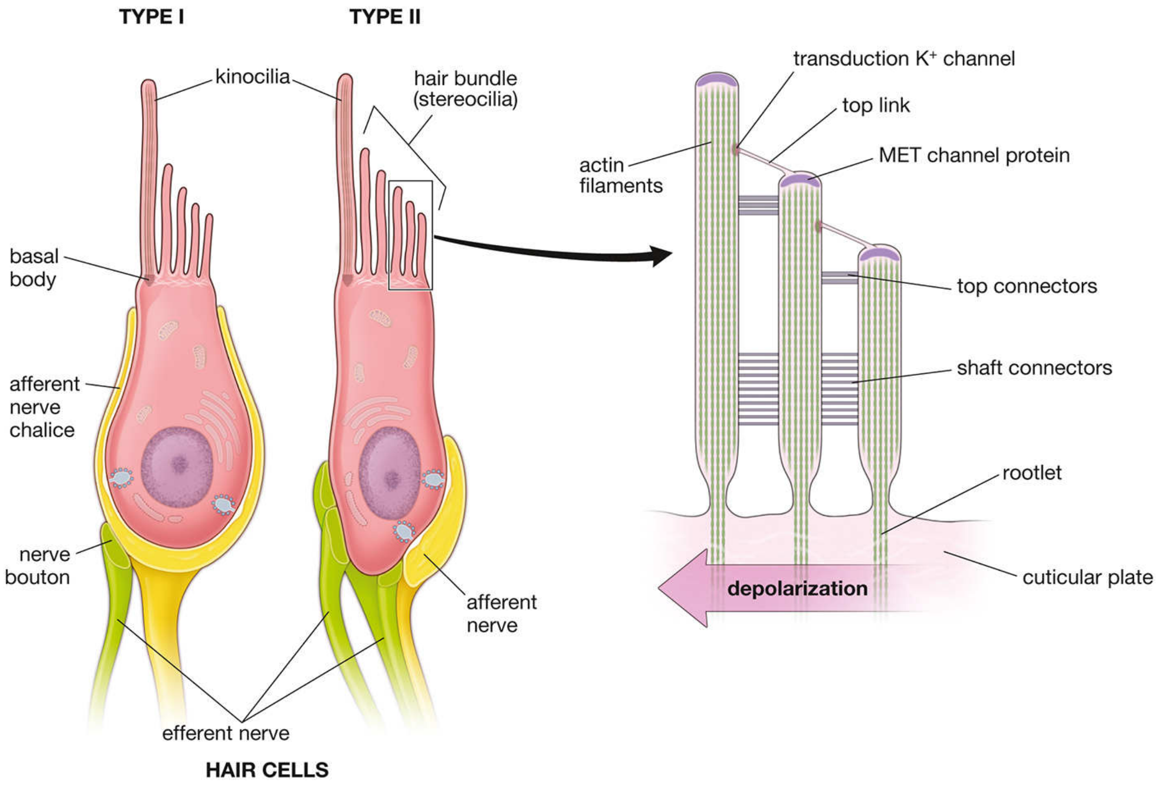


FIGURE 25.11. Diagram of two types of sensory hair cells in the sensory areas of the membranous labyrinth. The type I hair cell has a flask-shaped structure with a rounded base. The base is enclosed in a chalice-like afferent nerve ending containing several ribbon synapses in addition to several synaptic boutons for efferent nerve endings. Note the apical surface specializations of this cell, which include a kinocilium and hair bundle. The apical cytoplasm of hair cells contains basal bodies for the attachment of the kinocilium and a terminal web for the attachment of stereocilia. The type II hair cell is cylindrical and possesses several nerve terminals at its base for both afferent and efferent nerve fibers. The apical surface specializations are identical to those of the type I cell. The molecular organization of the stereocilia is depicted in the diagram on the *right*. The top link connects the lateral plasma membrane of the stereocilium shaft (where K^+ transduction channels are located) with the tip of the shorter stereocilium (where the mechanoelectrical transduction [*MET*] channel protein is located). Movement of the stereocilia toward the kinocilium opens the *MET* channels, causing depolarization of the hair cell, whereas movement in the opposite direction (away from the kinocilium) causes hyperpolarization. Note that the proximal end of each stereocilium is tapered and its narrow rootlets are anchored within the terminal web (cuticular plate) of the hair cell. Several other fibrillar connectors between neighboring stereocilia are also shown.

Stereocilia of hair cells are rigid structures that contain mechanoelectrical transducer channel proteins at their distal ends.

The **stereocilia of hair cells** have a molecular structure similar to those described on pages 127-128. Tightly packed **actin filaments** cross-linked by **fimbrin** and **espin** (actin-bundling proteins) form their internal core structure. Espins provide the most rigid cross-linking for stereocilia; mutations that alter their structure cause cochlear and vestibular dysfunction. The high density of actin filaments and the extensive cross-linking pattern impart rigidity and stiffness to the shaft of the stereocilium. The shaft tapers at its proximal end near the apical surface of the cell, where the core filaments of each stereocilium are anchored within the terminal web (cuticular plate). When stereocilia are deflected, they pivot at their proximal ends like stiff rods (see Fig. 25.11).

Transmission electron microscope examination of the distal free end of the stereocilium reveals an electron-dense plaque at the cytoplasmic site of the plasma membrane. This plaque represents the **mechanoelectrical transducer (MET) channel complex**. A fibrillar cross-link called the **tip link** connects the tip of the stereocilium with the shaft of an adjacent longer stereocilium (see Fig. 25.11). These tip links are anchored to mechanically gated ion channels on both ends. The upper insertion of the tip link to the shaft of neighboring stereocilium contains a cluster of motor proteins (unconventional myosin VIIa) that maintains a resting tension on the tip link. The lower insertion to the distal free end of the stereocilium is connected to the MET channel complex. The tip link is composed of **cadherin-23** (CDH23) and **protocadherin-15** (PCDH15); however, the molecular composition of the MET channel complex remains elusive. Recently, two transmembrane channel-like (TMC) proteins, TMC1 and TMC2, have been identified in the MET channels that are expressed in developing hair cells. Mutations in the genes encoding TMC1 cause **deafness** in humans.

The tip link plays an important role in activating the MET channel complex at the tip of the stereocilia and opening additional transduction K^+ channels at the site of its attachment to the shaft of neighboring stereocilium (see Fig. 25.11). The molecular structure of the transduction K^+ channels is unknown.

A mutation that disrupts the gene that encodes the actin-bundling protein **espin** causes cochlear and vestibular symptoms in experimental mice. They lose their hearing early in life; these animals also spend most of their time walking or spinning in circles. The stereocilia of these animals do not maintain the rigidity necessary for the proper functioning of the **MET channels**. In humans, mutations in a gene located on chromosome 1 that encodes espin are associated with deafness without vestibular involvement.

All hair cells use mechanically gated ion channels to generate action potentials.

All hair cells of the internal ear appear to function by moving (pivoting) their rigid stereocilia. Mechanoelectrical transduction occurs in stereocilia that are deflected toward its tallest edge (toward the kinocilium, if present). This movement exerts tension on the fibrillar tip links, and the generated force is used to open **mechanically gated ion channels** near the tip of the stereocilium. This allows for an influx of K^+, causing depolarization of the receptor cell. This depolarization results in the opening of voltage-gated Ca^{2+} channels in the basolateral surface of the hair cells and the secretion of a neurotransmitter that generates an action potential in afferent nerve endings. Movement in the opposite direction (away from the kinocilium) closes the MET channels, causing hyperpolarization of the receptor cell. The means by which stereocilia are deflected varies from receptor to receptor; these are discussed in the sections describing each receptor area.

Hair cells communicate with afferent nerve fibers through ribbon synapses, a specialized type of chemical synapse.

Deflection of the stereocilia on hair cells generates a high rate of prolonged impulses that are quickly transmitted to the afferent nerve fibers. To ensure rapid release of the glutamate neurotransmitter from synaptic vesicles, hair cells possess specialized **ribbon synapses** that contain unique organelles called **ribbons**. In electron microscopy, ribbons appear as ovoid, 30-nm-thick, electron-dense plates that are anchored to the presynaptic membrane by electron-dense structures (Fig. 25.12). This arrangement allows the ribbons to float just above the presynaptic plate like balloons on a short leash. The ribbons tether a large number of synaptic vesicles on their surface that are primed for fusion with the presynaptic membrane, which contains a high density of voltage-gated Ca^{2+} channels (see Fig. 25.12). After activation of the Ca^{2+} channels, the ribbon serves as a fast-moving conveyor belt, delivering the vesicles to the presynaptic membrane for fusion. The tethered pool of synaptic vesicles is approximately fivefold greater than the pool of the remaining vesicles. The ribbons contain several proteins, including the active-zone protein RIM that interacts with rab3, a GTPase enzyme expressed on the surface of synaptic vesicles. Other proteins of the ribbon complex include presynaptic matrix proteins, such as RIBEYE, Bassoon, and Piccolo. A hair cell typically contains about 10–20 ribbons. These ribbon synapses are also found in the photoreceptors and bipolar cells of the retina.

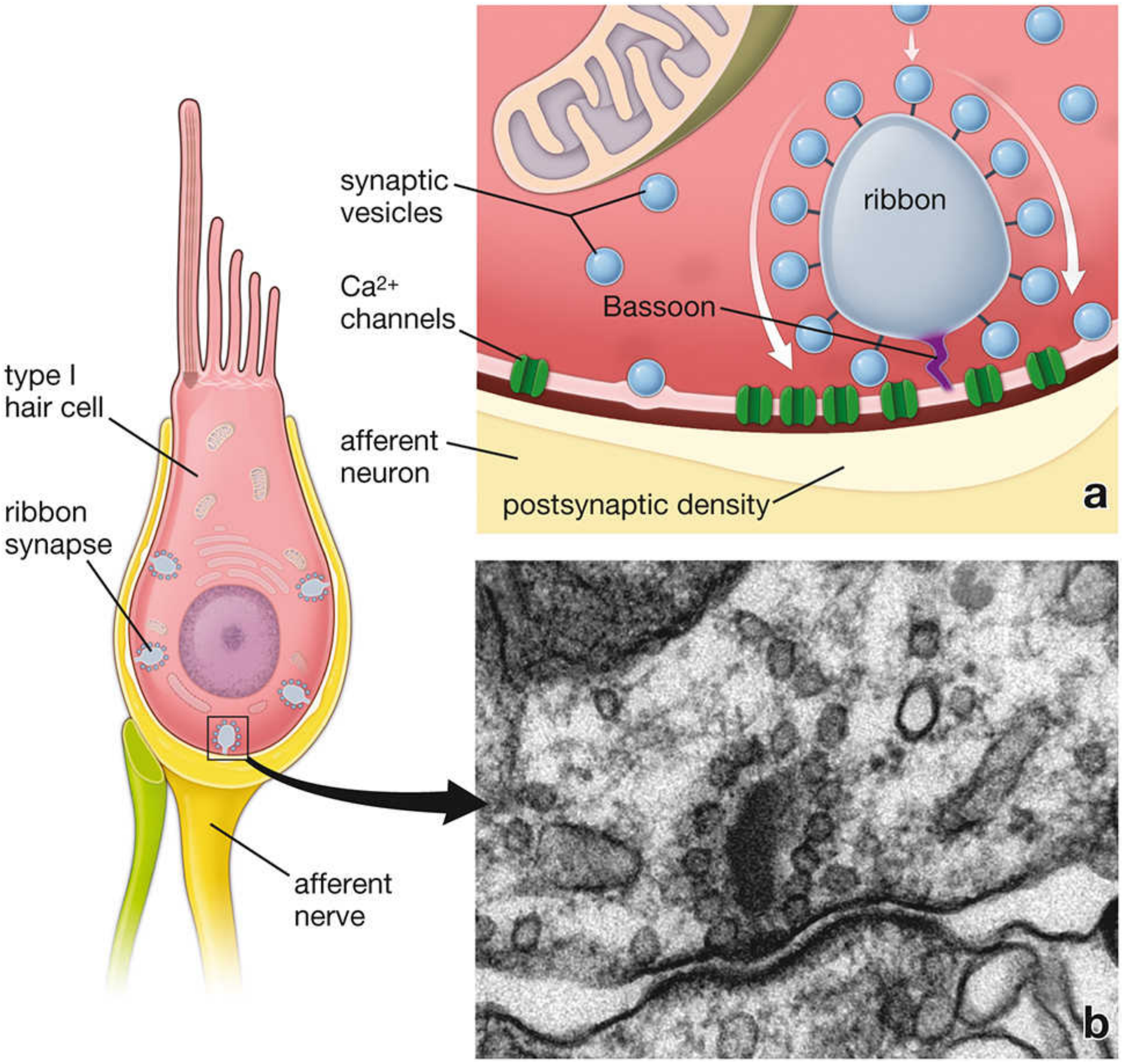


FIGURE 25.12. Diagram and electron micrograph of a ribbon synapse in a hair cell. Diagram on the *left* shows a type I hair cell with several ribbon synapses that are specialized for transmitting long-lasting and high-volume impulses to the afferent nerve cell endings (*yellow*). **a.** This schematic view of a ribbon synapse shows the ribbon protein complex that contains several presynaptic matrix proteins (RIM, RIBEYE, and Piccolo) and is anchored into the presynaptic plate by another protein called *Bassoon*. The surface of the ribbon serves as the tethering platform for multiple synaptic vesicles. Note the presence of voltage-sensitive Ca^{2+} channels in the presynaptic membrane next to the attachment of the ribbon. Upon influx of Ca^{2+}, the ribbon accelerates movement of the attached vesicles toward the presynaptic membrane for fusion (similar to the action of a fast-moving conveyor belt). **b.** This electron micrograph of a ribbon synapse from a mouse cochlear hair cell shows the ribbon protein complex with attached synaptic vesicles. ×27,400. (Reprinted with permission from Neef A, Khimich D, Pirih P, *et al.* Probing the mechanism of exocytosis at the hair cell ribbon synapse. *J Neurosci*. 2007;27:12933–12944.)

Two types of hair cells are present in the vestibular labyrinth.

Both **hair cell** types are associated with **afferent** and **efferent nerve endings** (see Fig. 25.11). **Type I hair cells** are flask shaped, with a rounded base and thin neck, and are surrounded by an afferent nerve chalice and a few efferent nerve fibers. **Type II hair cells** are cylindrical and have afferent and efferent bouton nerve endings at the base of the cell (see Fig. 25.11).

Sensory receptors of the membranous labyrinth

The crista ampullaris senses angular movements of the head.

Each ampulla of the semicircular duct contains a **crista ampullaris**, which is a sensory receptor for angular movements of the head (Figs. 25.13 and 25.14). The crista ampullaris is a thickened transverse epithelial ridge that is oriented perpendicularly to the long axis of the semicircular canal and consists of the epithelial hair cells and supporting cells (Plate 25.1, page 1042).

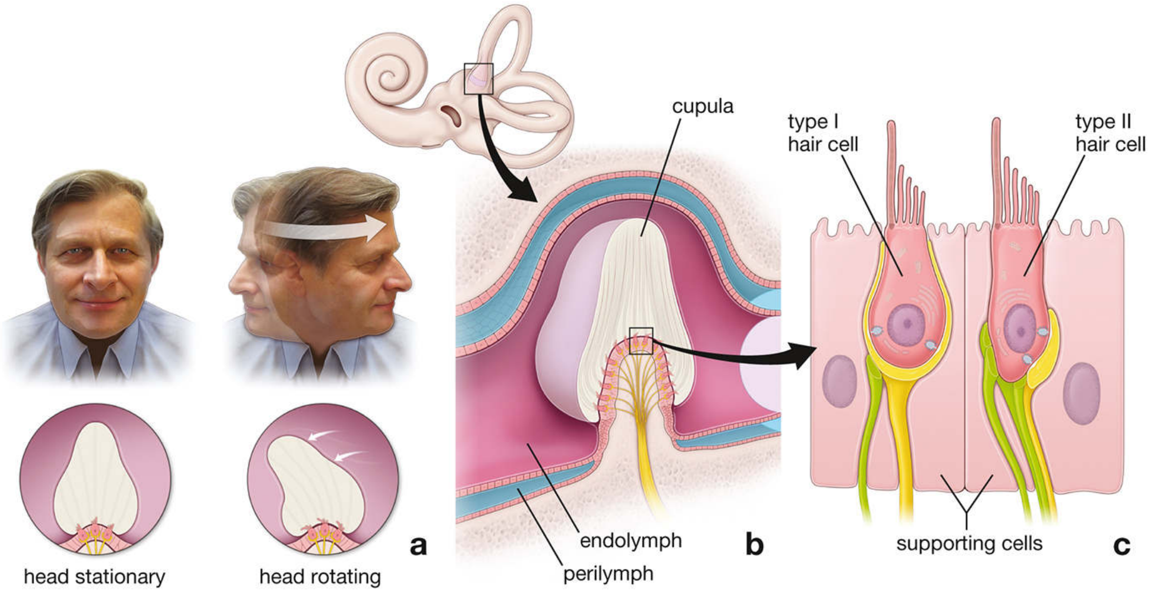


FIGURE 25.13. Diagram of function and structure of the crista ampullaris within a semicircular duct. a. As shown in this drawing, the crista ampullaris functions as the sensor for angular movement of the head. For example, when the head of the individual shown in this diagram rotates toward the left side, the bony labyrinth also rotates at the same speed together with the head. However, the endolymph lags behind due to its own fluid inertia. Because the crista ampullaris is attached to the wall of the bony labyrinth, it will be swayed by the lagging endolymph in the opposite direction to the movement of the head. **b.** The structure of the crista ampullaris includes sensory epithelium and large cupula made of a gelatinous protein–

polysaccharide mass that projects toward the nonsensory wall of the ampulla. Note that the membranous ampulla is filled with endolymph and is surrounded by perilymph. **c.** The sensory epithelium of the crista ampullaris is composed of both type I and type II hair cells and supporting cells. The stereocilia and kinocilium of each hair cell are embedded in the cupula. Their mechanical deflection opens the K^+ channels, causing depolarization of the cell.

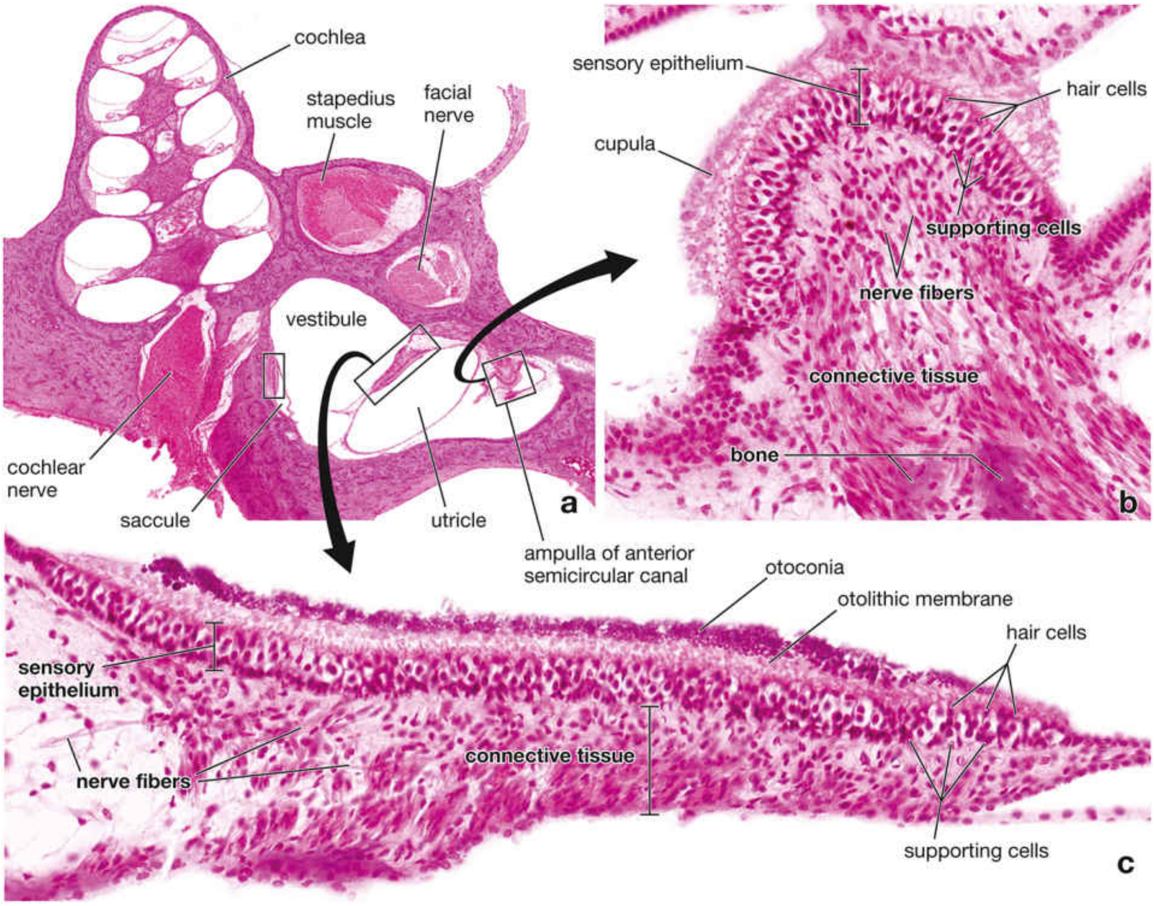


FIGURE 25.14. Photomicrograph of the crista ampullaris and macula of the utricle of the internal ear. a. This low-magnification view of a horizontal section of the temporal bone reveals several regions of the internal ear. The prominent *cochlea* contains a well-preserved cochlear duct with a *cochlear nerve* emerging from the base of the modiolus. Note the cross section of the *stapedius muscle* and *facial nerve*. The central cavity of the slide represents the vestibule that contains three parts of the membranous labyrinth: the *utricle*, *saccule*, and *ampulla of the anterior semicircular canal*. The locations of sensory receptors (macula of utricle, macula of saccule, and crista ampullaris) are enclosed within the rectangles. ×20. **b.** This high-magnification view of the crista ampullaris from the anterior semicircular canal shows a thick *sensory epithelium* that contains two types of cells: the *hair cells* in the upper layer and the *supporting cells* in the basal layer. Note that the sensory hair processes of the cells are barely discernable and are

covered by the *cupula*. The underlying loose *connective tissue* extends to the wall of the bony labyrinth and contains nerve fibers with associated Schwann cells, fibroblasts, capillaries, and other connective tissue cells. ×380. **c.** This high-magnification view of the macula of the utricle shows *sensory epithelium* similar to that of the crista ampullaris. The sensory epithelium is overlaid by the *otolithic membrane* containing a darker stained layer of *otoconia* (otoliths) on its surface. ×380. (Copyright 2010 Regents of the University of Michigan. Reprinted with permission.)

A gelatinous protein–polysaccharide mass, known as the **cupula**, is attached to the hair cells of each crista (see Fig. 25.13). The cupula projects into the lumen and is surrounded by endolymph. During rotational movement of the head, the walls of the semicircular canal and the membranous semicircular ducts move, but the endolymph contained within the ducts tends to lag behind because of inertia. The cupula, projecting into the endolymph, is swayed by the movement differential between the crista fixed to the wall of the duct and the endolymph. Deflection of the stereocilia in the narrow space between the hair cells and the cupula generates nerve impulses in the associated nerve endings.

The maculae of the saccule and utricle are sensors of gravity and linear acceleration.

The **maculae** of the saccule and utricle are innervated sensory thickenings of the epithelium that face the endolymph of the saccule and utricle (see Figs. 25.14 and 25.15). As in the cristae, each macula consists of **type I** and **type II hair cells**, supporting cells, and nerve endings associated with the hair cells. The maculae of the utricle and saccule are oriented at right angles to each another. When a person is standing, the macula of the utricle is in a horizontal plane and the macula of the saccule is in a vertical plane.

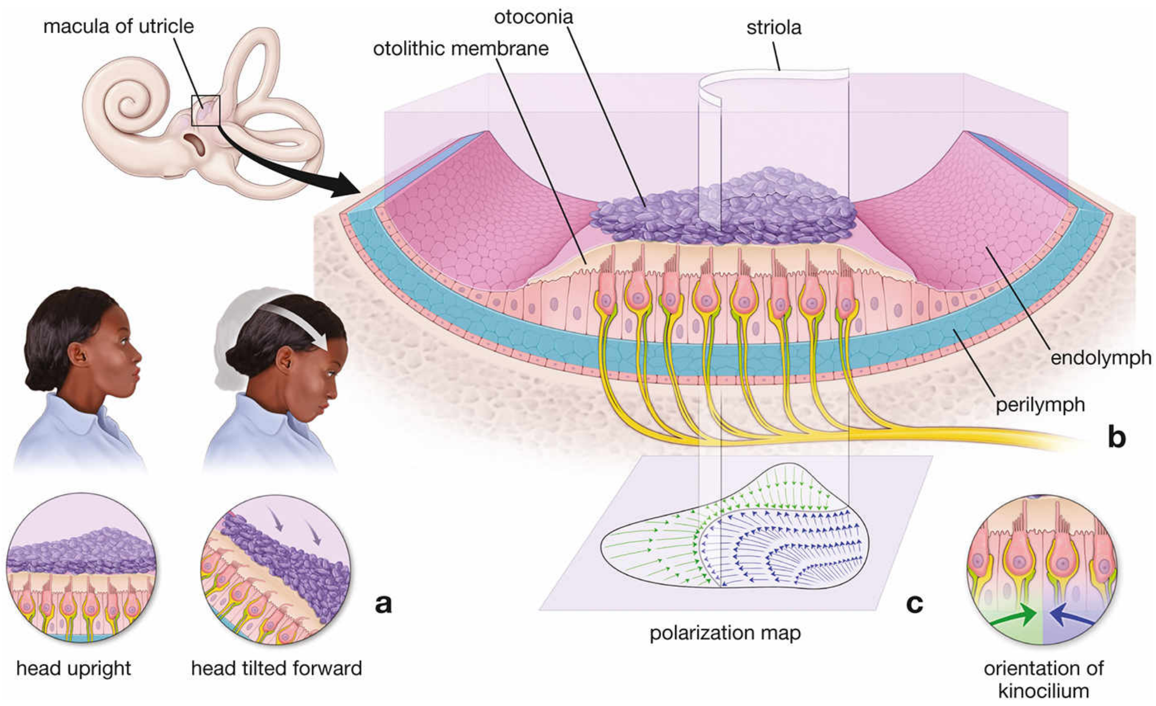


FIGURE 25.15. Diagram of function and structure of the macula within the utricle. a. As shown in this drawing, the macula of the utricle (as well as macula of the saccule) functions as a sensor for gravity and linear acceleration. For example, when the head of the individual shown in this diagram is tilted forward, tiny crystals of calcium carbonate called *otoconia* are shifted on the surface of the otolithic membrane. This movement is detected by the underlying hair cells. **b.** The macula is composed of a sensory epithelium containing both type I and type II hair cells. The hair cell processes are embedded in the gelatinous polysaccharide otolithic membrane. The luminal surface of the membrane is covered by otoconia that are heavier than endolymph. **c.** As visible on the map below the macula, the hair cells are polarized with respect to the striola, an imaginary plane that curves through the center of each macula. Note that on each side of the striola, the kinocilia of the hair cells are oriented in opposite directions facing toward the striola (see direction of the *blue* and *green arrows* on the polarization map of the utricle). This arrangement is only seen in the utricle because in the macula of the saccule, the kinocilia of the hair cells are turned away from the striola.

Hair cells are polarized with respect to the **striola**, an imaginary plane that curves through the center of each macula (see Fig. 25.15). On each side of the striola, the kinocilia of the hair cells are oriented in opposite directions, facing toward the striola in the utricle and turning away from the striola in the saccule. Owing to polarization of the hair cells, the maculae of the saccule and utricle are sensitive to multiple directions of linear accelerations.

The gelatinous polysaccharide material that overlies the maculae is called the **otolithic membrane** (see Fig. 25.15). Its outer surface contains 3-to 5-µm crystalline bodies of calcium carbonate and a protein (Fig. 25.16). **Otoliths**, also called **otoconia**, are heavier than endolymph. The outer surface of the otolithic membrane lies opposite the surface in which the stereocilia of the hair cells are embedded. The otolithic membrane moves on the macula in a manner analogous to that by which the cupula moves on the crista. Stereocilia of the hair cells are deflected by gravity in the stationary individual when the otolithic membrane and its otoliths pull on the stereocilia. They are also displaced during linear movement when the individual is moving in a straight line and the otolithic membrane drags on the stereocilia because of inertia. In both cases, movement of the otolithic membrane causes the stereocilia to move toward the kinocilium, activating MET channels. This depolarizes hair cells and generates an action potential. Displacement of stereocilia in the opposite direction away from the kinocilium causes hyperpolarization of hair cells and inhibits the generation of the action potential.

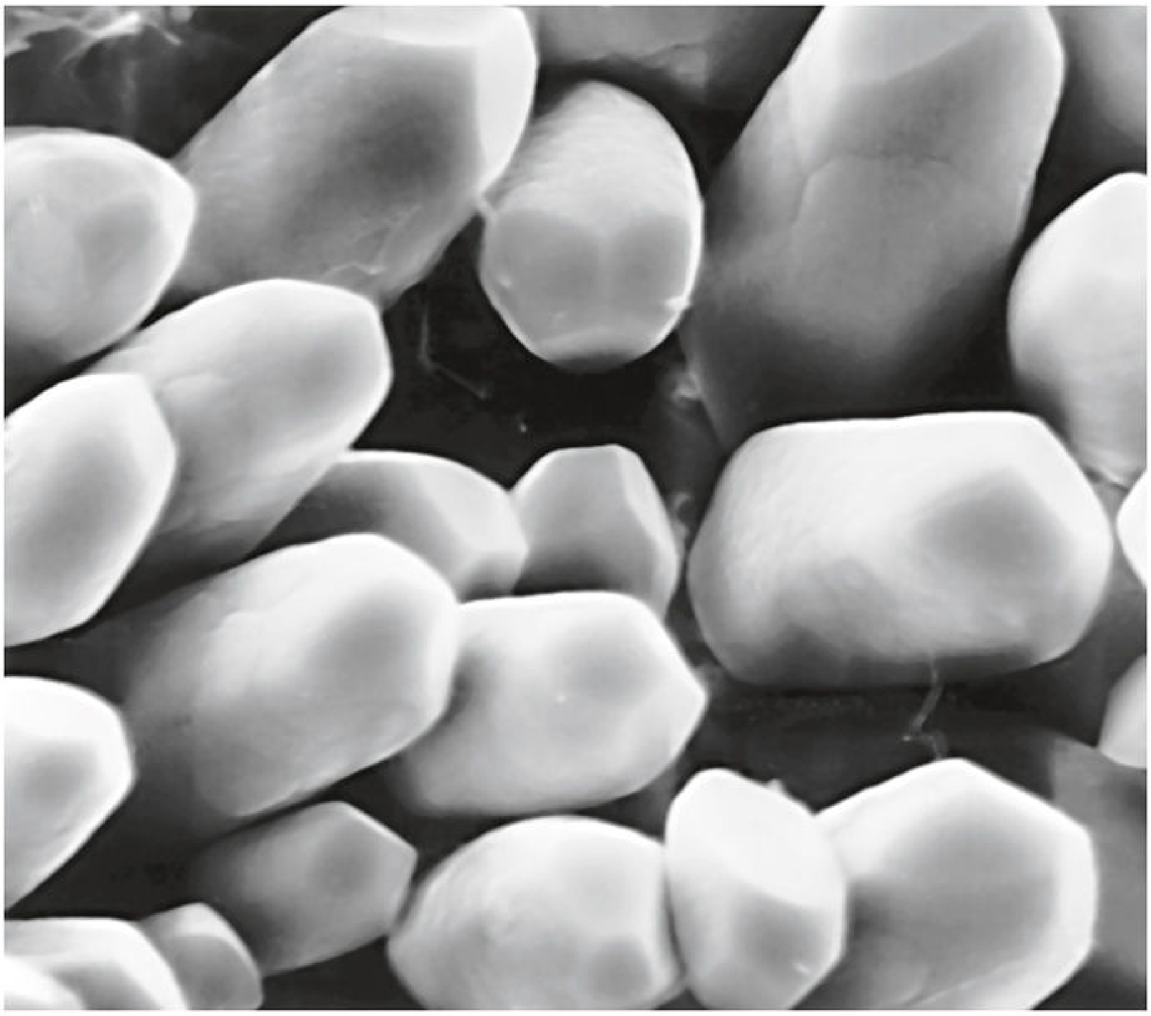


FIGURE 25.16. Scanning electron micrograph of human otoconia. Each otoconium has a long cylindrical body with a three-headed facet on each end. ×5,000.

The spiral organ of Corti is the sensor of sound vibrations.

The **cochlear duct** divides the cochlear canal into three parallel compartments or scalae:

- **Scala media**, the middle compartment in the cochlear canal
- **Scala vestibule**
- **Scala tympani**

The **cochlear duct** itself is the **scala media** (Fig. 25.17). The scala vestibuli and scala tympani are the spaces above and below, respectively, the scala media. The scala media is an **endolymph-containing space** that is continuous with the lumen of the saccule and contains the spiral organ of Corti, which rests on its lower wall (see Fig. 25.17).

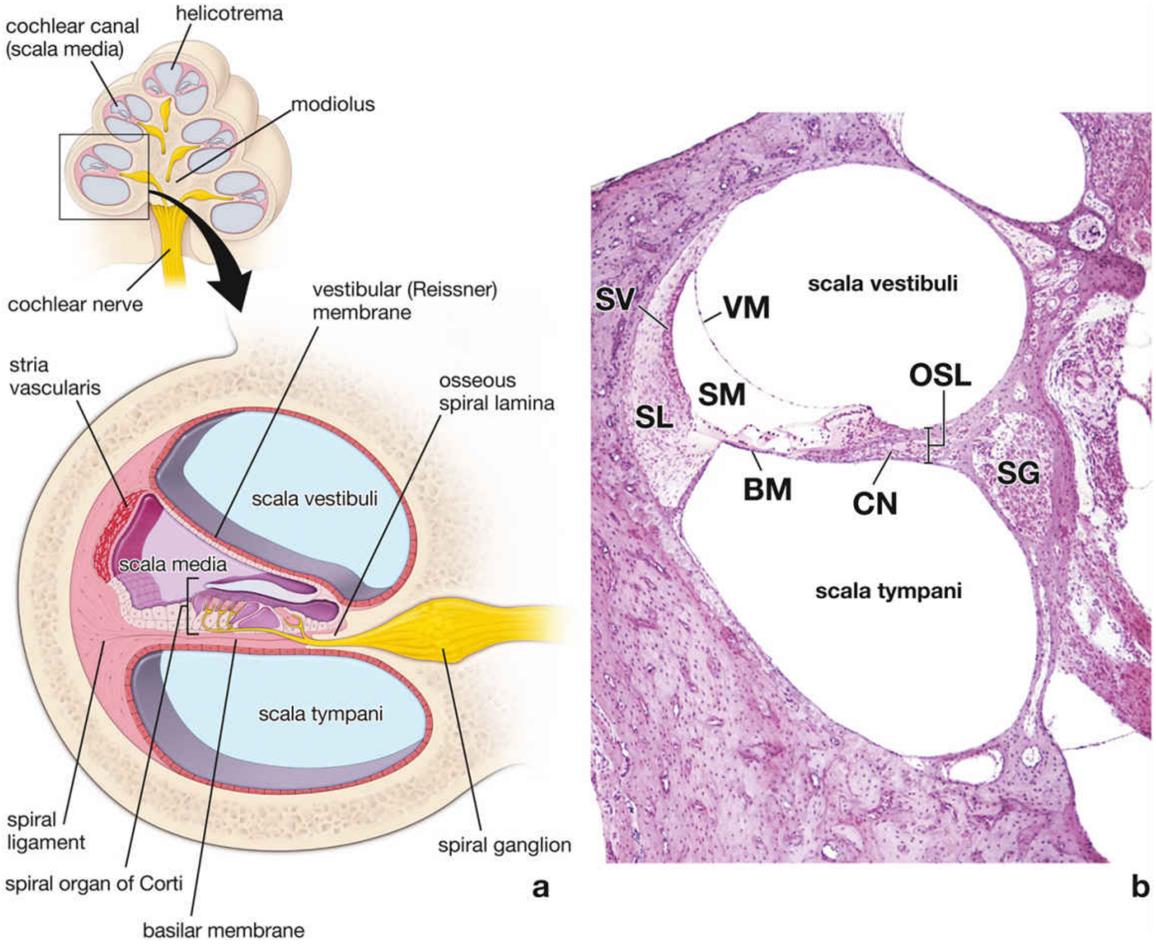


FIGURE 25.17. Schematic diagram and photomicrograph of the cochlear canal. a. Cross section of the basal turn of the cochlear duct is

shown in the *box* on the smaller orientation view. This view of a midmodiolar section of the cochlea illustrates the position of the cochlear duct within the 2.75 turns of the bony cochlea. Observe that at the top of the cochlea, the scala vestibuli and scala tympani communicate with each other at the helicotrema. The scala media and the osseous spiral lamina divide the cochlea into the scala vestibuli and the scala tympani, which are filled with perilymph. The scala media (the space within the cochlear duct) is filled with endolymph and contains the organ of Corti. **b.** This photomicrograph shows a section of the basal turn of the cochlear canal. The osseous spiral lamina (*OSL*) and its membranous continuation, the basilar membrane (*BM*) as well as the vestibular membrane (*VM*) are visible. Note the location of the *scala vestibuli*, the scala media (*SM*) or cochlear duct, and the *scala tympani*. The three walls of the scala media are formed by the basilar membrane inferiorly, the stria vascularis (*SV*) and underlying spiral ligament (*SL*) laterally, and the vestibular membrane superiorly. The spiral organ of Corti resides on the inferior wall of the cochlear duct. Dendrites of the cochlear nerve (*CN*) that originate in the spiral ganglion (*SG*) enter the spiral organ of Corti. The axons of the spiral ganglion cells form the cochlear part of the vestibulocochlear nerve. ×65.

The **scala vestibuli** and the **scala tympani** are **perilymph-containing spaces** that communicate with each other at the apex of the cochlea through a small channel called the **helicotrema** (see Fig. 25.17b). The scala vestibuli begins at the **oval window**, and the scala tympani ends at the **round window**.

The scala media is a triangular space with its acute angle attached to the modiolus.

In transverse section, the **scala media** appears as a triangular space with its most acute angle attached to a bony extension of the modiolus, the **osseous spiral lamina** (see Fig. 25.17). The upper wall of the scala media, which separates it from the scala vestibuli, is the **vestibular (Reissner) membrane** (Fig. 25.18). The lateral or outer wall of the scala media is bordered by a unique epithelium, the **stria vascularis**. It is responsible for the production and maintenance of endolymph. The stria vascularis encloses a complex capillary network and contains three types of cells (Fig. 25.19). The marginal cells, primarily involved in K^+ transport, line the endolymphatic space of the scala media. Intermediate pigment-containing cells are scattered among capillaries. The basal cells separate stria vascularis from the underlying spiral ligament. The lower wall or floor of the scala media is formed by a relatively flaccid **basilar membrane** that increases in width and decreases in stiffness as it coils from the base to apex of the cochlea. The spiral organ of Corti rests on the basilar membrane and is overlain by the **tectorial membrane**.

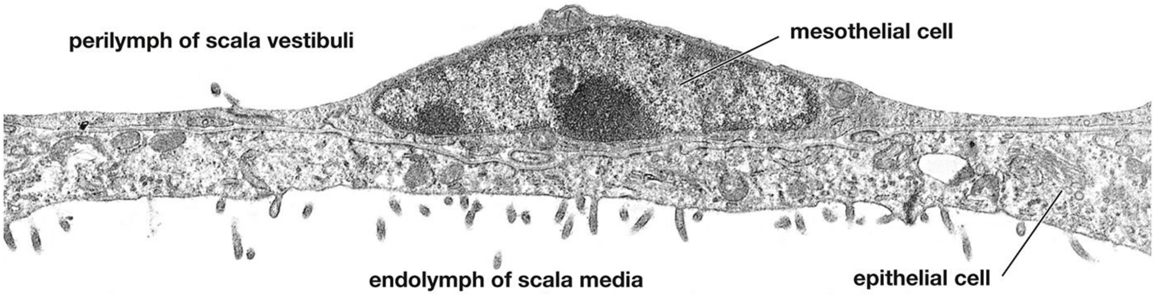


FIGURE 25.18. Transmission electron micrograph of the vestibular (Reissner) membrane. Two cell types can be observed: a mesothelial cell, which faces the scala vestibuli and is bathed by perilymph, and an epithelial cell, which faces the scala media and is bathed by endolymph. ×8,400.

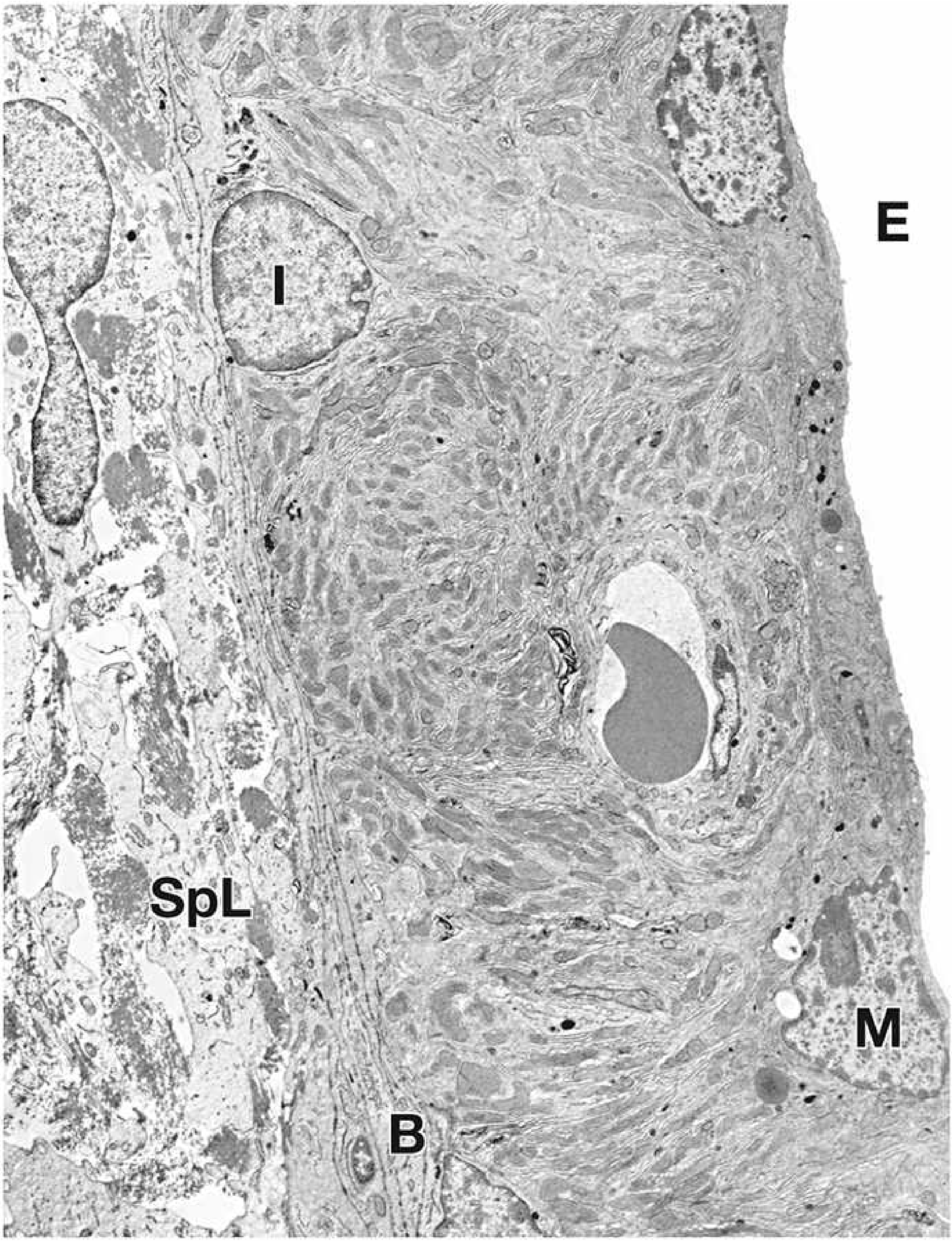


FIGURE 25.19. Transmission electron micrograph of the stria vascularis. The apical surfaces of the marginal cells (*M*) of the stria are bathed by endolymph (*E*) of the scala media. Intermediate cells (*I*) are positioned between the marginal cells and the basal cells (*B*). The basal cells separate the other cells of the stria vascularis from the spiral ligament (*SpL*). ×4,700.

The spiral organ of Corti is composed of hair cells, phalangeal cells, and pillar cells.

The **spiral organ of Corti** is a complex epithelial layer on the floor of the scala media (Fig. 25.20 and Plate 25.2, page 1044). It is formed by the following:

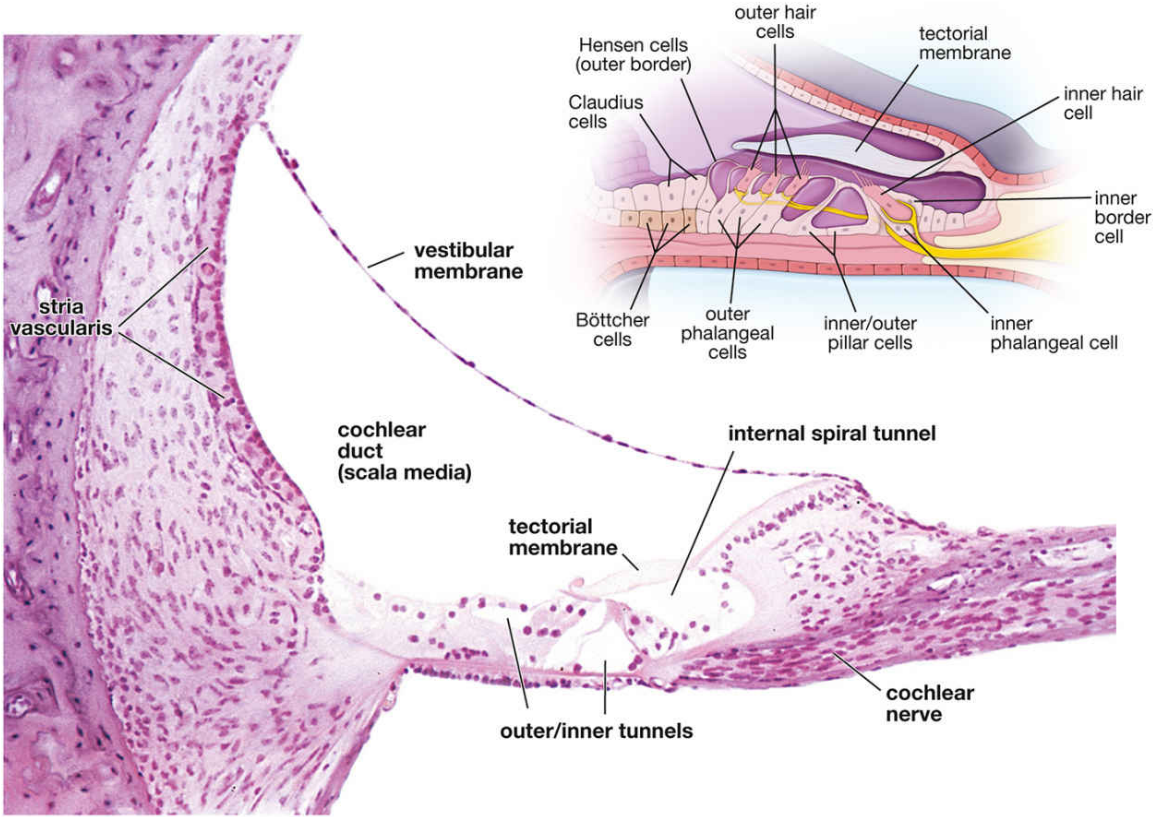


FIGURE 25.20. Photomicrograph of the vestibular duct and spiral organ of Corti. This higher magnification photomicrograph of the cochlear duct shows the structure of the spiral organ of Corti. Relate this structure to the *inset*, which labels the structural features of the spiral organ. ×180. **Inset.** Diagram of the sensory and supporting cells of the spiral organ of Corti. The sensory cells are divided into an inner row of sensory hair cells and three rows of outer sensory hair cells. The supporting cells are the inner and outer pillar cells, inner and outer (Deiters) phalangeal cells, outer border cells (Hensen cells), inner border cells, Claudius cells, and Böttcher cells.

- **Inner hair cells** (close to the spiral lamina) and **outer hair cells** (farther from the spiral lamina)
- **Inner phalangeal (supporting) cells** and **outer phalangeal cells**
- **Pillar cells**

Several other named cell types of unknown function are also present in the spiral organ.

The hair cells are arranged in inner and outer rows of cells.

The **inner hair cells** form a single row of cells throughout all 2.75 turns of the cochlear duct. The number of cells forming the width of the continuous row of **outer hair cells** is variable. Three ranks of hair cells are found in the basal part of the coil (Fig. 25.21). The width of the row gradually increases to five ranks of cells at the apex of the cochlea.

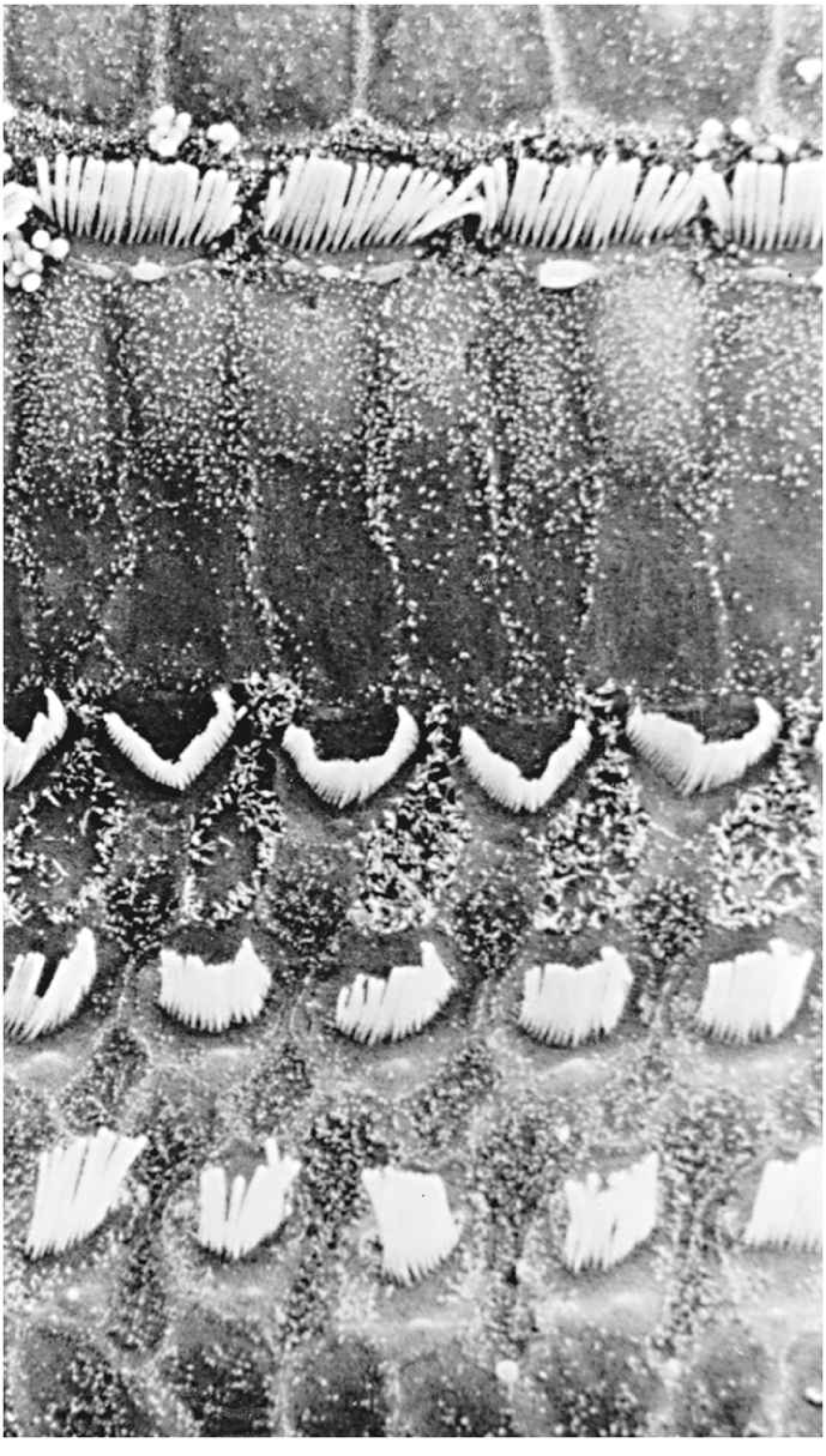


FIGURE 25.21. Scanning electron micrograph of the spiral organ of Corti. This electron micrograph illustrates the configuration of stereocilia on the apical surfaces of the inner row and three outer rows of the cochlear sensory hair cells. ×3,250.

The phalangeal and pillar cells provide support for the hair cells.

Phalangeal cells are supporting cells for both rows of hair cells. The phalangeal cells associated with the inner hair cells surround the cells completely (Fig. 25.22a). The phalangeal cells associated with the outer hair cells surround only the basal portion of the hair cell completely and send apical processes toward the endolymphatic space (Fig. 25.22b). These processes flatten near the apical ends of the hair cells and collectively form a complete plate surrounding each hair cell (Fig. 25.23).

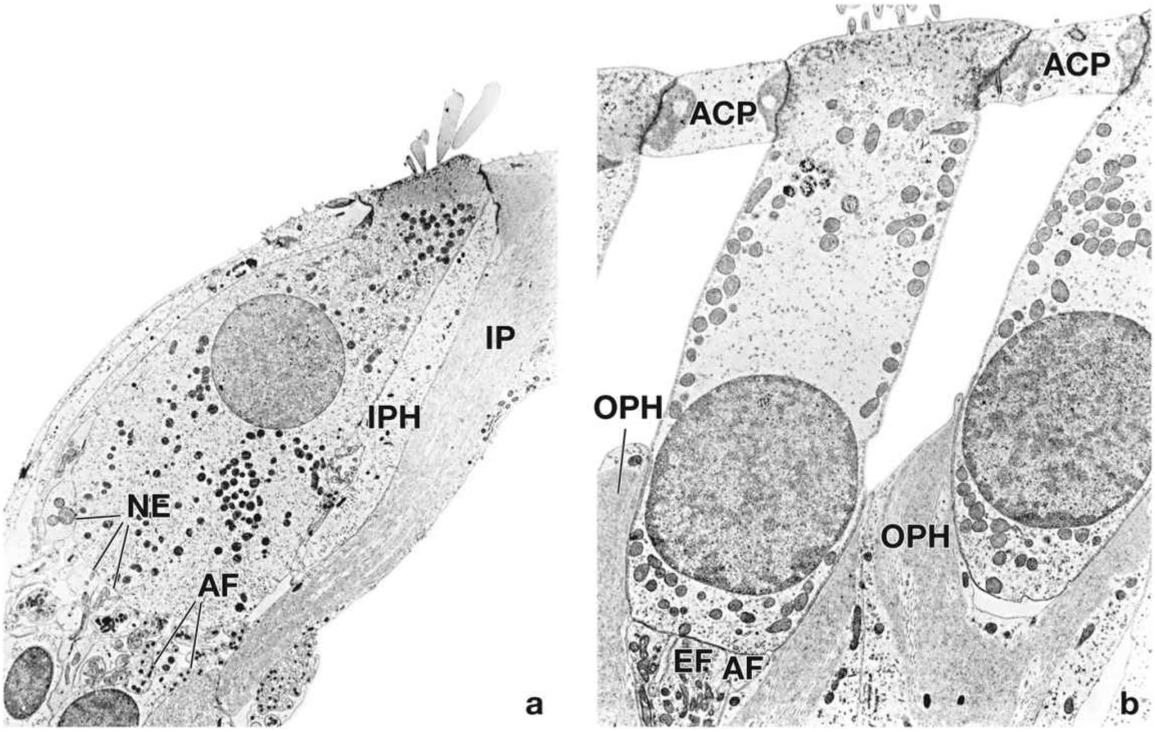


FIGURE 25.22. Electron micrograph of an inner and outer hair cell. a. Observe the rounded base and constricted neck of the inner hair cell. Nerve endings (*NE*) from afferent nerve fibers (*AF*) to the inner hair cells are seen basally. *IP*, inner pillar cell; *IPH*, inner phalangeal cell. ×6,300. **b.** Afferent (*AF*) and efferent (*EF*) nerve fiber endings on the base of an outer sensory hair cell are evident. Outer phalangeal cells (*OPH*) surround the outer hair cells basally. Their apical projections form the apical cuticular plate (*ACP*). Note that the lateral domains in the middle third of the outer hair cells are not surrounded by supporting cells. ×6,300. (Reprinted with permission from Kimura RS. Sensory and accessory epithelia of the cochlea. In: Friedmann I, Ballantyne J, eds. *Ultrastructural Atlas of the Inner Ear*. Butterworth; 1984.)

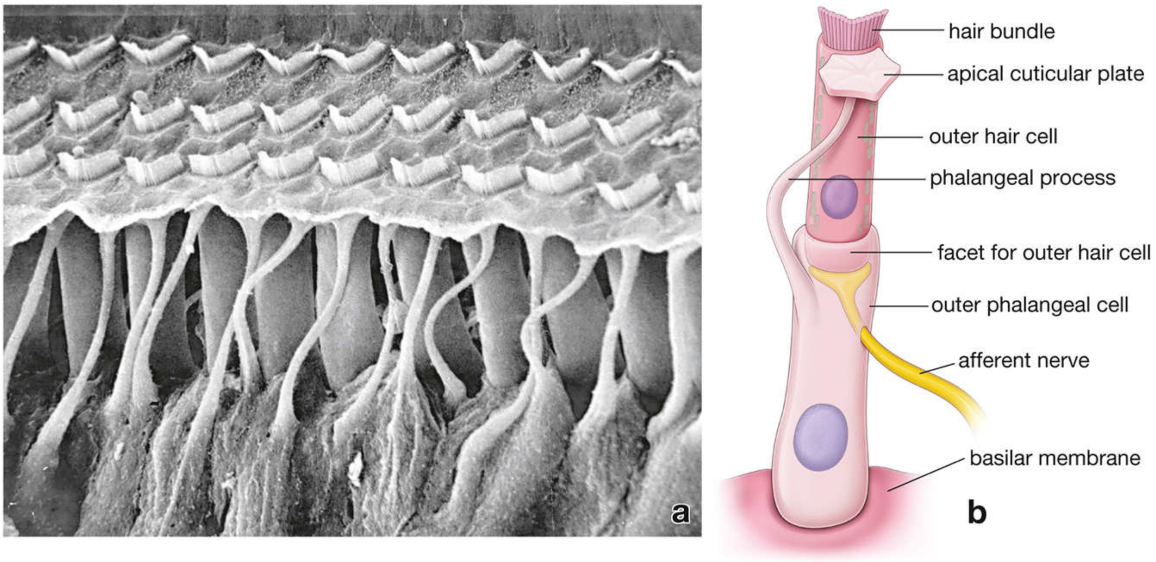


FIGURE 25.23. Structure of the outer phalangeal cell. a. This scanning electron micrograph illustrates the architecture of the outer phalangeal (Deiters) cells. Each phalangeal cell cups the basal surface of an outer hair cell and extends its phalangeal process apically to form an apical cuticular plate that supports the outer sensory hair cells. ×2,400. **b.** Schematic drawing showing the relationship of an outer phalangeal cell to an outer hair cell.

The apical ends of the phalangeal cells are tightly bound to one another and to the hair cells by elaborate tight junctions. These junctions form the **reticular lamina** that separates the endolymphatic compartment from the true intercellular spaces of the organ of Corti (see Figs. 25.20 and 25.22b). The extracellular fluid in this intercellular space is **cortilymph**. Its composition is similar to that of other extracellular fluids and to perilymph.

Pillar cells have broad apical and basal surfaces that form plates and a narrowed cytoplasm. The inner pillar cells rest on the tympanic lip of the spiral lamina; the outer pillar cells rest on the basilar membrane. Between them, they form a triangular tunnel, the **inner spiral tunnel** (see Fig. 25.20).

The tectorial membrane extends from the spiral limbus over the cells of the spiral organ of Corti.

The **tectorial membrane** is attached medially to the modiolus. Its lateral free edge projects over and attaches to the organ of Corti by the stereocilia of the hair cells. It is formed from the radially oriented bundles of collagen types II, V, and IX embedded in a dense amorphous ground substance. Glycoproteins unique to the internal ear, called **otogelin** and **tectorin**, are associated with the collagen bundles. These proteins are also present in the otolithic membranes overlying the maculae of the utricle and saccule as well as in the cupulae of the cristae in the semicircular canals.

Sound Perception

As described on pages 1018-1019, sound waves striking the tympanic membrane are translated into simple mechanical vibrations. The ossicles of the middle ear convey these vibrations to the cochlea.

In the internal ear, the vibrations of the ossicles are transformed into waves in the perilymph.

Movement of the stapes in the oval window of the vestibule sets up vibrations or traveling waves in the perilymph of the scala vestibuli. The vibrations are transmitted through the vestibular membrane to the scala media (cochlear duct), which contains endolymph, and are also propagated to the perilymph of the scala tympani. Pressure changes in this closed perilymphatic–endolymphatic system are reflected in movements of the membrane that covers the round window in the base of the cochlea.

As a result of **sound vibrations** entering the internal ear, a traveling wave is set up in the basilar membrane (Fig. 25.24). A sound of a specified frequency causes displacement of a relatively long segment of the basilar membrane, but the region of maximal displacement is narrow. The point of maximal displacement of the basilar membrane is specified for a given frequency of sound and is the morphologic basis of frequency discrimination. High-frequency sounds cause maximal vibration of the basilar membrane near the base of the cochlea; low-frequency sounds cause maximal displacement nearer the apex. Amplitude discrimination (i.e., perception of sound intensity or loudness) depends on the degree of displacement of the basilar membrane at any given frequency range. Thus, coding acoustic information into nerve impulses depends on the vibratory pattern of the basilar membrane.

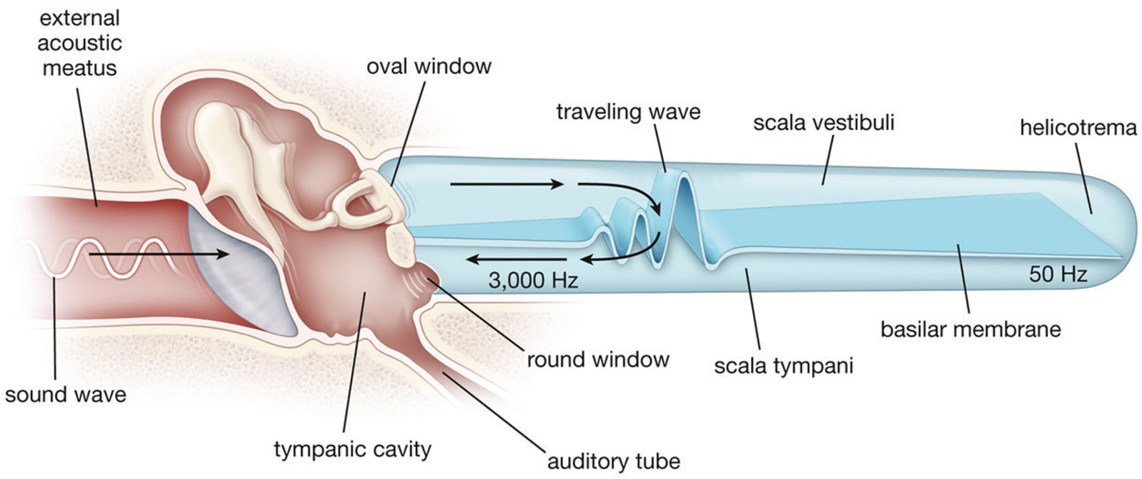


FIGURE 25.24. Schematic diagram illustrating the dynamics of the three divisions of the ear. The cochlear duct is shown here as if straightened. Sound waves are collected and transmitted from the external ear to the middle ear, where they are converted into mechanical vibrations. The mechanical vibrations are then converted at the oval window into fluid vibrations within the internal ear. Fluid vibrations cause displacement of the basilar membrane (traveling wave) on which rest the auditory sensory hair cells. Such displacement leads to stimulation of the hair cells and a discharge of neural impulses from them. Note that high-frequency sounds cause vibrations of the narrow, thick portion of the basilar membrane at the base of the cochlea, whereas low-frequency sounds displace basilar membrane toward the apex of the cochlea near its helicotrema.

Movement of the stereocilia of the hair cells in the cochlea initiates neuronal transduction.

Hair cells are attached through the **phalangeal cells** to the basilar membrane, which vibrates during sound reception. The **stereocilia** of these hair cells are, in turn, attached to the tectorial membrane, which also vibrates. However, the **tectorial membrane** and the **basilar membrane** are hinged at different points. Thus, a shearing effect occurs between the basilar membrane (and the cells attached to it) and the tectorial membrane when sound vibrations impinge on the internal ear.

Because they are inserted into the tectorial membrane, the stereocilia of the hair cells are the only structures that connect the basilar membrane and its complex epithelial layer to the tectorial membrane. The shearing effect between the basilar membrane and the tectorial membrane deflects the stereocilia and thus the apical portion of the hair cells. This deflection activates **MET channels** located at the tips of stereocilia and generates action potentials that are conveyed to the brain via the **cochlear nerve** (cochlear division of the vestibulocochlear nerve, cranial nerve VIII).

Innervation of the Internal Ear

The vestibular nerve originates from the sensory receptors associated with the vestibular labyrinth.

The **vestibulocochlear nerve (cranial nerve VIII)** is a special sensory nerve and is composed of two divisions: a vestibular division called the *vestibular nerve* and a cochlear division called the *cochlear nerve*. The **vestibular nerve** is associated with equilibrium and carries impulses from the sensory receptors located within the vestibular labyrinth. The **cochlear nerve** is associated with hearing and conveys impulses from the sensory receptors within the cochlear labyrinth (Fig. 25.25).

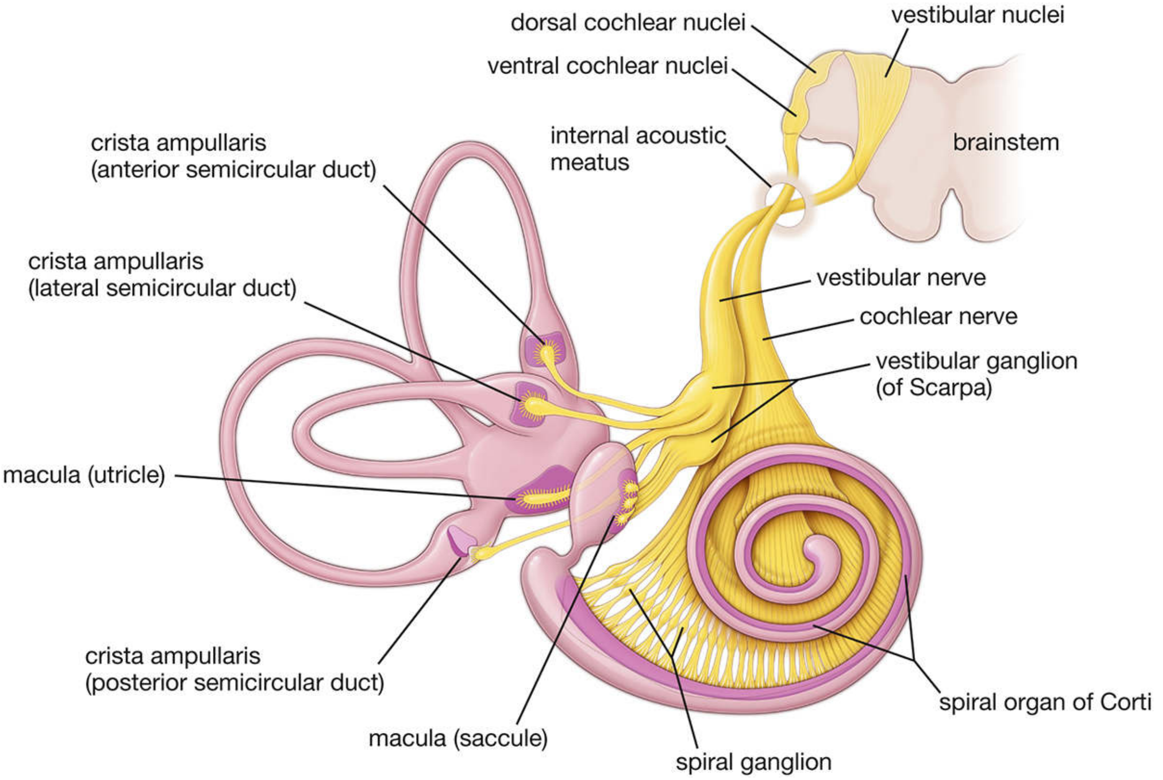


FIGURE 25.25. Diagram illustrating the innervation of the sensory regions of the membranous labyrinth. Note that cochlear and vestibular nerves form the vestibulocochlear nerve (cranial nerve VIII). The cochlear nerve carries the sound impulses from the spiral organ of Corti located within the cochlear duct; the vestibular nerve carries balance information from the three cristae ampullares of the semicircular canals, utricle, and saccule. The cell bodies of these sensory fibers are located in the spiral ganglion (for hearing) and vestibular ganglion (for equilibrium).

The cell bodies of the bipolar neurons of the **vestibular nerve** are located in the **vestibular ganglion (of Scarpa)** in the internal acoustic meatus. Dendritic processes of the vestibular ganglion cells originate in the cristae ampullares of the three semicircular ducts, the macula of the utricle, and the macula of the saccule. They synapse at the base of the vestibular sensory hair cells, either as a chalice around a type I hair cell or as a bouton associated with a type II hair cell. The axons of the vestibular nerve originate from the vestibular ganglion, enter the brainstem, and terminate in four vestibular nuclei. Some secondary neuronal fibers travel to the cerebellum and to the nuclei of cranial nerves III, IV, and VI, which innervate the muscles of the eye.

The cochlear nerve originates from the sensory receptors of the spiral organ of Corti.

Neurons of the **cochlear nerve** are also bipolar, and their cell bodies are located in the **spiral ganglion of Corti** within the modiolus. Dendritic processes of spiral ganglion cells exit the modiolus through the small openings in the bony spiral lamina and enter the spiral organ. Approximately 90% of dendrites originating from the spiral ganglion cells synapse with the inner hair cells; the remaining 10% of dendrites synapse with the outer hair cells of the spiral ganglion. The axons of the spiral ganglion cells form the cochlear nerve, which enters the bony cochlea through the modiolus to appear in the internal acoustic meatus (see Fig. 25.25). From the internal acoustic meatus, the cochlear nerve enters the brainstem and terminates in the cochlear nuclei of the medulla. Nerve fibers from these nuclei pass to the geniculate nucleus of the thalamus and then to the auditory cortex of the temporal lobe.

The organ of Corti also receives a small number of efferent fibers conveying impulses from the brain that pass parallel to the afferent nerve fibers of the vestibulocochlear nerve (olivocochlear tract, cochlear efferents of Rasmussen). Efferent nerve fibers from the brainstem pass through the vestibular nerve. They synapse either on afferent endings of the inner hair cell or on the basal aspect of an outer hair cell. Efferent fibers are thought to affect the control of auditory and vestibular input to the central nervous system, presumably by enhancing some afferent signals while suppressing other signals. Damage to the organ of Corti, cochlear nerve, nerve pathways, or auditory cortex is responsible for **sensorineural hearing loss** (see Folder 25.2).

FOLDER 25.3

CLINICAL CORRELATION: VERTIGO

The sensation of rotation without equilibrium (**dizziness**, **vertigo**) signifies dysfunction of the vestibular system. Causes of vertigo include viral infections, certain drugs, and tumors such as **acoustic neuroma**. Acoustic neuromas develop in or near the internal acoustic meatus and exert pressure on the vestibular division of cranial nerve VIII or branches of the labyrinthine artery. Vertigo can also be produced normally in individuals by excessively stimulating the semicircular ducts. Similarly, excessive stimulation of the utricle can produce motion sickness (seasickness, carsickness, or airsickness) in some individuals.

The most common vestibular disorder is **benign paroxysmal positional vertigo (BPPV)**. In this condition, otoconia become detached from the macula of the utricle and lodge in one of the three cristae ampullares. The anatomic position of the posterior semicircular canal (it has an opening inferior to the macula) makes it the most common site for the detached otoconia to enter (81%–90%). The otoconia remain either free floating within the canal (**canalithiasis**) or are attached to the cupula (**cupulolithiasis**), causing inappropriate movement of the stereocilia at the apical surface of the receptor hair cells. Individuals with BPPV report episodes of an erroneous sensation of spinning evoked by certain movements of the head. Otoconia may detach following trauma or viral infections, but in many instances, it occurs idiopathically.

Some diseases of the internal ear affect both hearing and equilibrium. For example, people with **Ménière disease** initially complain of episodes of dizziness and tinnitus (ringing in the ears) and later develop low-frequency hearing loss. The causes of Ménière disease are related to blockage of the cochlear aqueduct, which drains excess endolymph from the membranous labyrinth. Blockage of this duct causes an increase in endolymphatic pressure and distension of the membranous labyrinth (endolymphatic hydrops).

Blood Vessels of the Membranous Labyrinth

Arterial blood is supplied to the membranous labyrinth by the labyrinthine artery; venous blood drainage is to the venous dural sinuses.

The blood supply to the external ear, middle ear, and bony labyrinth of the internal ear is from vessels associated with the external carotid arteries. The **arterial blood supply** to tissues of the membranous labyrinth of the internal ear is from the intracranial **labyrinthine artery**, a common branch of the anterior inferior cerebellar or basilar artery. The labyrinthine artery is a terminal artery: It has no anastomoses with other surrounding arteries. Branches of this artery are exactly parallel to the distribution of the superior and inferior parts of the vestibular nerve.

Venous drainage from the cochlear labyrinth is via the posterior and anterior spiral modiolar veins that form the **common modiolar vein**. The common modiolar vein and the vestibulocochlear vein form the vein of the cochlear aqueduct, which empties into the inferior petrosal sinus. Venous drainage from the vestibular labyrinth is via **vestibular veins** that join the vein of the cochlear aqueduct and by the vein of vestibular aqueduct, which drains into the sigmoid sinus.

EAR

OVERVIEW OF THE EAR

- The **ear** is a paired specialized sensory organ that is responsible for sound perception and balance.
- Tissues of the ear are derived from **surface ectoderm** (epithelia lining of the membranous labyrinth) and components of the **first pharyngeal pouch** (auditory tube and middle ear cavity), **first pharyngeal groove** (external acoustic meatus), **first pharyngeal arch** (malleus, incus, and anterior part of the auricle), and **second pharyngeal arch** (stapes and posterior part of the auricle).

EXTERNAL EAR

- The **auricle** is the external component of the ear that collects and amplifies sound.
- The **external acoustic meatus** extends from the auricle to the tympanic membrane. It is lined by skin that contains hair follicles as well as sebaceous and ceruminous glands (which produce **cerumen**, or **earwax**).

MIDDLE EAR

- The **middle ear** is an air-filled space lined by a mucous membrane that contains three **auditory ossicles** (malleus, incus, and stapes). It is separated from the external acoustic meatus by the tympanic membrane and is connected by the **auditory (Eustachian) tube** to the nasopharynx.
- The middle ear **amplifies mechanical forces** generated by the vibration of the tympanic membrane.
- The **tympanic membrane** is composed of skin of the external auditory meatus, a thin core of connective tissue, and mucous membrane of the middle ear.
- The auditory ossicles (**malleus**, **incus**, and **stapes**) cross the space of the middle ear in series and connect the tympanic membrane to the oval window. Movement of the ossicles is modulated by the **tensor tympani muscle** that inserts to the malleus and the **stapedius muscle** that inserts to the stapes.

COMPARTMENTS OF THE INTERNAL EAR

- The **internal ear** consists of two compartments within the temporal bone: the **bony labyrinth** and the **membranous labyrinth**, which is contained within the bony labyrinth.
- The internal ear has three fluid-filled spaces: the **endolymphatic space** within the membranous labyrinth (which has a high K^+ and a low Na^+ concentration), the **perilymphatic space** between the wall of the bony and membranous labyrinth (which has a low K^+ and a high Na^+ concentration), and the **cortilymphatic space** that lies within the tunnels of the organ of Corti of the cochlea.
- The **bony labyrinth** consists of three connected spaces: **semicircular canals**, **vestibule**, and **cochlea**, each containing different parts of the membranous labyrinth.
- The **membranous labyrinth** consists of a series of communicating sacs (**utricle**, **saccule**, and endolymphatic sac) and ducts (**three semicircular ducts**, **cochlear duct**, utriculosaccular duct, endolymphatic duct, and ductus reuniens) that contain **endolymph**.

SENSORY RECEPTORS OF THE MEMBRANOUS LABYRINTH

- Specialized sensory cells are located in six regions in the membranous labyrinth: three **cristae ampullares** in the ampullae of the semicircular ducts (receptors for angular acceleration of the head), two **maculae** in the utricle and saccule (receptors for position of the head and its linear movements), and the **spiral organ of Corti** (receptors for sound).

- Utricle and saccule maculae contain **hair cells** that are epithelial mechanoreceptors. These hair cells contain **hair bundles** on their apical surfaces (formed by rows of stereocilia with a single kinocilium) and are overlaid with a gelatin-like **otolithic membrane** that contains otoliths (otoconia).
- Movement of the **otoliths** is detected by the hair bundles, which activate **mechanically gated ion channels** to generate an action potential.
- Sensory receptors in the **crista ampullaris** are also covered by a gelatin-like mass without otoliths called the **cupula**. The cupula is deflected during the flow of endolymph through the semicircular canal. Movement of the cupula stimulates **mechanically gated ion channels** to generate an action potential.
- The **cochlear canal** is divided into three parallel compartments: **scala media** or **cochlear duct** (the middle compartment filled with endolymph that contains the spiral organ of Corti), **scala vestibuli**, and **scala tympani** (both containing perilymph).
- The **scala media** is a triangular space with its lower wall forming the **basilar membrane** on which the spiral organ of Corti resides. The upper wall (**vestibular membrane**) separates the scala media from scala vestibuli, and the lateral wall contains the **stria vascularis** that produces endolymph.
- The **spiral organ of Corti** is composed of **hair cells** (arranged in inner and outer rows), supportive **phalangeal cells**, and **pillar cells**. Movement of the stereocilia on hair cells during interaction with the overlying **tectorial membrane** generates electrical impulses that are transmitted to the cochlear nerve.
- **Sound waves** are transmitted from the vibrating tympanic membrane by the ossicles to the oval window, where they produce movement (waves) of the perilymph in the scala vestibule. This movement deflects the basilar membrane and spiral organ of Corti to generate electrical nerve impulses, which are perceived by the brain as sounds.
- Nerve impulses from the cristae ampullares and maculae travel with the **vestibular nerve**, and the impulses from the spiral organ of Corti travel with the **cochlear nerve**. These two nerves join together in the internal acoustic meatus to form the **vestibulocochlear nerve (cranial nerve VIII)**.

PLATE 25.1 ■ EAR

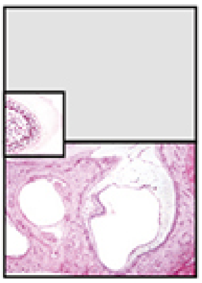
The **internal ear**, located in the temporal bone, consists of a system of chambers and canals that contain a network of membranous channels. These are referred to, respectively, as the **bony labyrinth** and **membranous labyrinth**. In some areas, the membranous labyrinth forms the lining of the bony labyrinth; in others, they are separated. Within the space lined by the membranous labyrinth is a watery fluid called **endolymph**. External to the membranous labyrinth, that is, between the membranous and bony labyrinths, is an additional fluid called **perilymph**.

The bony labyrinth is divided into three parts: **cochlea**, **semicircular canals**, and **vestibule**. The cochlea and semicircular canals contain membranous counterparts of the same shape; however, the membranous components of the vestibule are more complex in form, being composed of ducts and two chambers, the **utricle** and **saccule**. The cochlea contains the receptors for hearing (the **organ of Corti**); the semicircular canals contain the receptors for movement of the head; and the utricle and saccule contain receptors for position of the head.

Internal ear, ear, guinea pig, hematoxylin and eosin (H&E) ×20.

In this section through the **internal ear**, bone surrounds the entire internal ear cavity. Because of its labyrinthine character, sections of the internal ear appear as a number of separate chambers and ducts. However, these structures are all interconnected (except for the perilymphatic and endolymphatic spaces, which remain separate). The largest chamber is the **vestibule** (*V*). The left side of this chamber (*black arrow*) leads into the **cochlea** (*C*). Just below the *black arrow* and to the right is the oval ligament (*OL*) surrounding the base of the stapes (*S*). Both structures have been cut obliquely and are not seen in their entirety. The facial nerve (*FN*) is in an osseous tunnel to the left of the oval ligament. The communication of the vestibule with one of the semicircular canals is marked by the *white arrow*. Note the crista ampullaris (*CA*) that is projecting into the lumen of the semicircular canal. At the *upper right* are cross sections of the membranous labyrinth passing through components of the semicircular duct system (*DS*).

The cochlea is a spiral, cone-shaped structure. The specimen illustrated here makes 3½ turns (in humans, there are 2¾ turns). The section goes through the central axis of the cochlea. This consists of a bony stem called the **modiolus** (*M*). It contains the beginning of the cochlear nerve (*CN*) and the spiral ganglion (*SG*). Because of the plane of section and the spiral arrangement of the cochlear tunnel, the tunnel is cut crosswise in seven places (note 3½ turns). A more detailed examination of the cochlea and the organ of Corti is provided in Plate 25.2 (page 1044).



Semicircular canal, ear, guinea pig, H&E ×85; inset ×380.

A higher magnification of one of the semicircular canals and of the **crista ampullaris** (*CA*) within the canal seen in the *lower right* corner of the previous figure is provided here. The receptor for movement, the crista ampullaris (note its relationships in the previous figure), is present in each of the semicircular canals. The epithelial (*EP*) surface of the crista consists of two cell types, supporting cells and receptor hair cells. (Two types of hair cells are distinguished with the electron microscope.) It is difficult to identify the hair and supporting cells on the basis of specific characteristics; they can, however, be distinguished on the basis of location (see *inset*), as the **hair cells** (*HC*) are situated in a more superficial location than the supporting cells (*SC*). A gelatinous mass, the cupula (*Cu*), surmounts the epithelium of the crista ampullaris. Each receptor cell sends a hair-like projection deep into the substance of the cupula.

The epithelium rests on a loose, cellular connective tissue (*CT*) that also contains the nerve fibers associated with the receptor cells. The nerve fibers are difficult to identify because they are not organized into a discrete bundle.

C, cochlea
CA, crista ampullaris
CN, cochlear nerve
CT, connective tissue
Cu, cupula
DS, duct system (of membranous labyrinth)
EP, epithelium
FN, facial nerve
HC, hair cell
M, modiolus
OL, oval ligament
S, stapes
SC, supporting cell
SG, spiral ganglion
V, vestibule
black arrow, entry to cochlea
white arrow, entry to semicircular canal

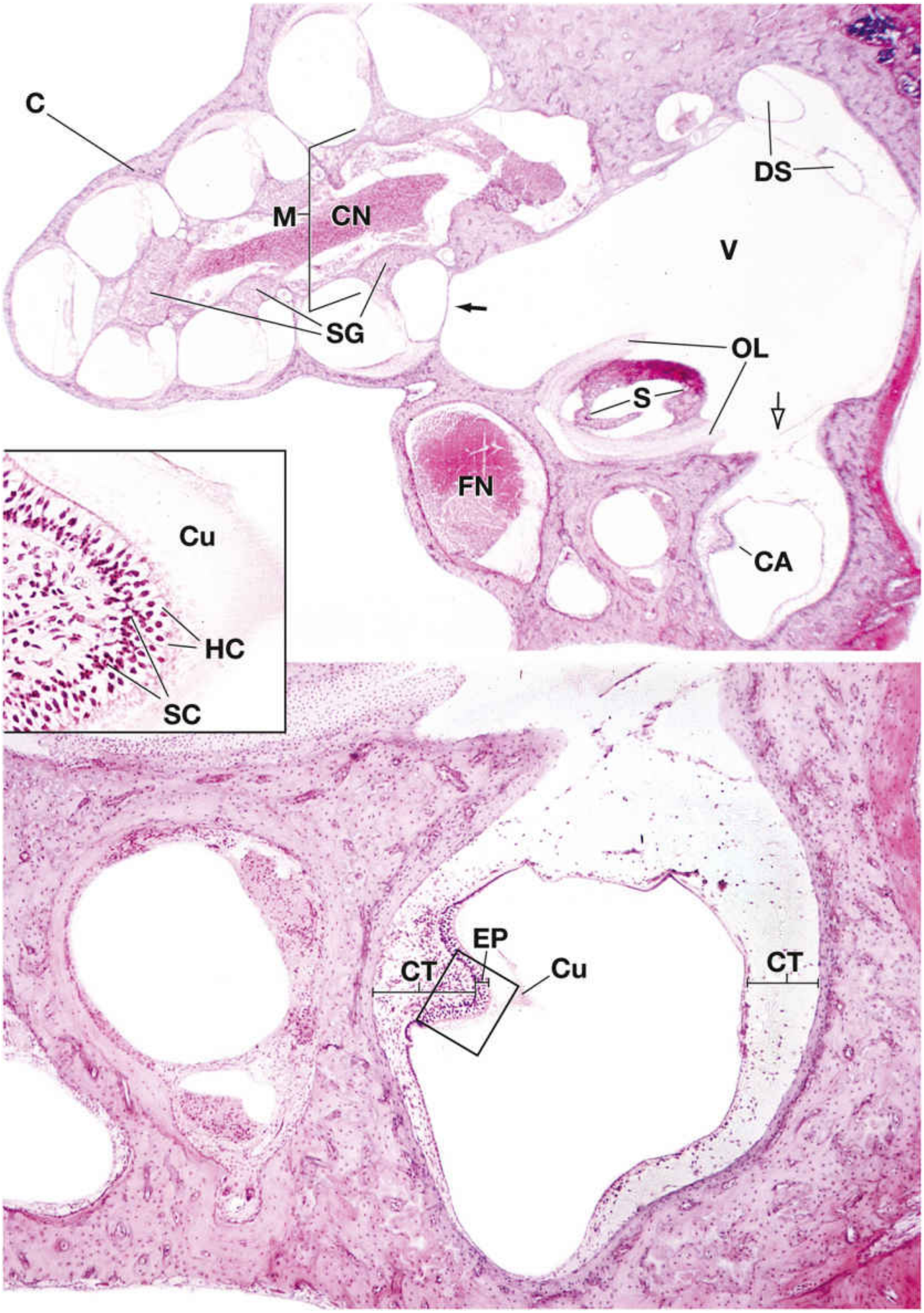

C
M
CN
DS
V
SG
OL
S
FN
CA
Cu
HC
SC
EP
CT
Cu
CT

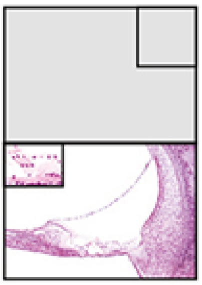
PLATE 25.2 ■ COCHLEAR CANAL AND ORGAN OF CORTI

The **hair cell**, a nonneuronal mechanoreceptor, is the common receptor cell of the vestibulocochlear system. Hair cells are epithelial cells that possess numerous **stereocilia**, modified microvilli also called **sensory hairs**. They convert mechanical energy to electrical energy that is transmitted via the vestibulocochlear nerve (cranial nerve VIII) to the brain. Hair cells are associated with afferent, as well as efferent, nerve endings. All hair cells have a common basis of receptor cell function that involves bending or flexing of their stereocilia. The specific means by which the stereocilia are bent varies from receptor to receptor, but in each case, stretching of the plasma membrane caused by the bending of the stereocilia generates transmembrane potential changes that are transmitted to the afferent nerve endings associated with each cell. Efferent nerve endings on the hair cells serve to regulate their sensitivity.

Cochlear canal, ear, guinea pig, hematoxylin and eosin (H&E) ×65; inset ×380.

A section through one of the turns of the cochlea is shown here. The most important functional component of the cochlea is the organ of Corti, enclosed by the *rectangle* and shown at higher magnification in the next figure. Other structures are included in this figure. The spiral ligament (*SL*) is a thickening of the periosteum on the outer part of the tunnel. Two membranes, the basilar membrane (*BM*) and the vestibular membrane (*VM*), join with the spiral ligament and divide the cochlear tunnel into three parallel canals, namely, the **scala vestibuli** (*SV*), the **scala tympani** (*ST*), and the **cochlear duct** (*CD*). Both the scala vestibuli and the scala tympani are perilymphatic spaces; these communicate at the apex of the cochlea. The cochlear duct is the space of the membranous labyrinth and is filled with endolymph. It is thought that the endolymph is formed by the portion of the spiral ligament that faces the cochlear duct, the stria vascularis (*StV*). This is highly vascularized and contains specialized "secretory" cells.

A shelf of bone, the osseous spiral lamina (*OSL*), extends from the modiolus to the basilar membrane. Branches of the cochlear nerve (*CN*) travel along the spiral lamina to the modiolus, where the main trunk of the nerve is formed. The components of the cochlear nerve are bipolar neurons whose cell bodies constitute the spiral ganglion (*SG*). These cell bodies are shown at higher magnification in the *inset* (*upper right*). The spiral lamina supports an elevation of cells, the limbus spiralis (*LS*). The surface of the limbus is composed of columnar cells.



Organ of Corti, ear, guinea pig, H&E ×180; inset ×380.

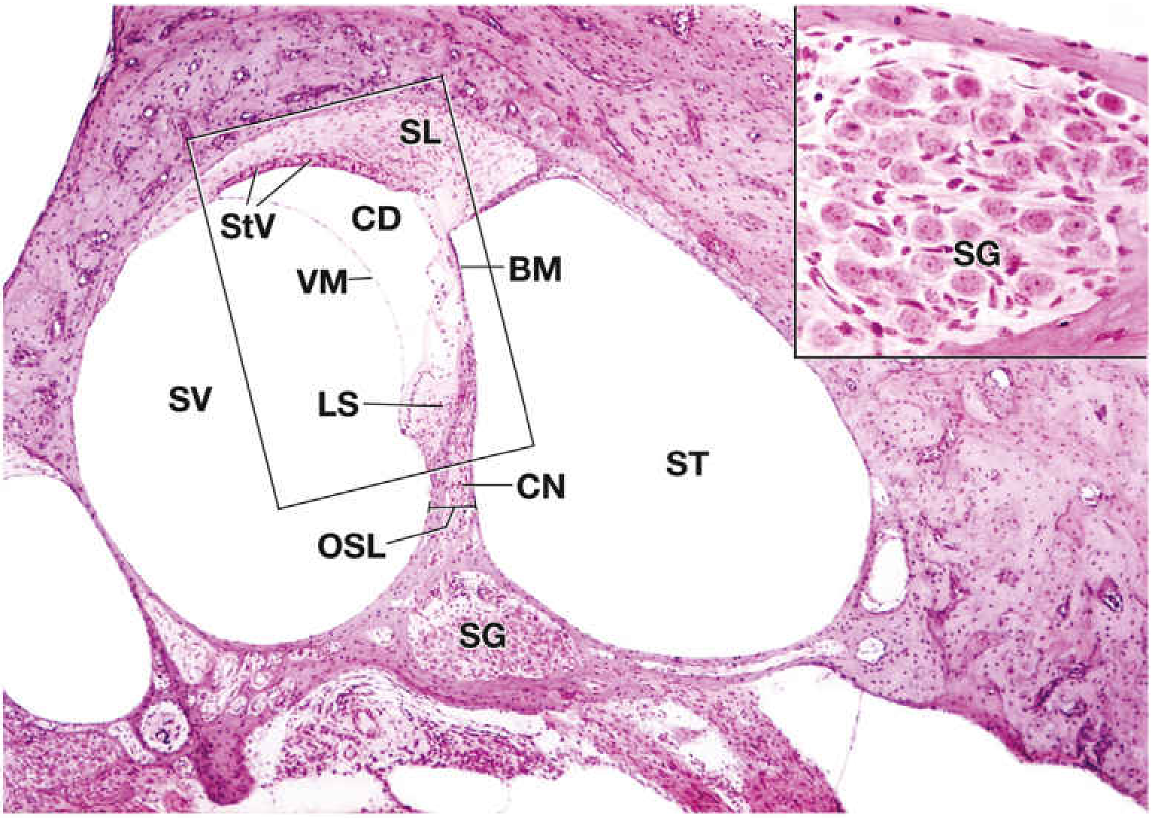
The cross section of the **cochlear canal** (*CD*) visible in this image appears as a triangular space. The upper wall (roof) of this canal is formed by the vestibular membrane (*VM*) that separates it from the scala vestibuli (*SV*). The lateral (outer) wall of the cochlear canal is bordered the stria vascularis (*StV*) and underlying spiral ligament (*SL*). The lower wall (or floor) is formed by the basilar membrane, an extension of the osseous spiral lamina with visible branches of the cochlear nerve (*CN*). The basilar membrane supports the spiral **organ of Corti**. The components of the organ of Corti, beginning at the limbus spiralis (*LS*), are as follows: inner border cells (*IBC*), inner phalangeal and hair cells (*IP&HC*), and inner pillar cells (*IPC*). The sequence continues, repeating itself in reverse as follows: outer pillar cells (*OPC*), hair cells (*HC*) and outer phalangeal cells (*OP*), and outer border cells or cells of Hensen (*CH*). Hair cells are receptor cells; the other cells are collectively referred to as *supporting cells*. The hair and outer phalangeal cells can be distinguished in this figure by their location (see *inset*) and because their nuclei are well aligned. Because the hair cells rest on the phalangeal cells, it can be concluded that the upper three nuclei belong to outer hair cells, whereas the lower three nuclei belong to outer phalangeal cells.

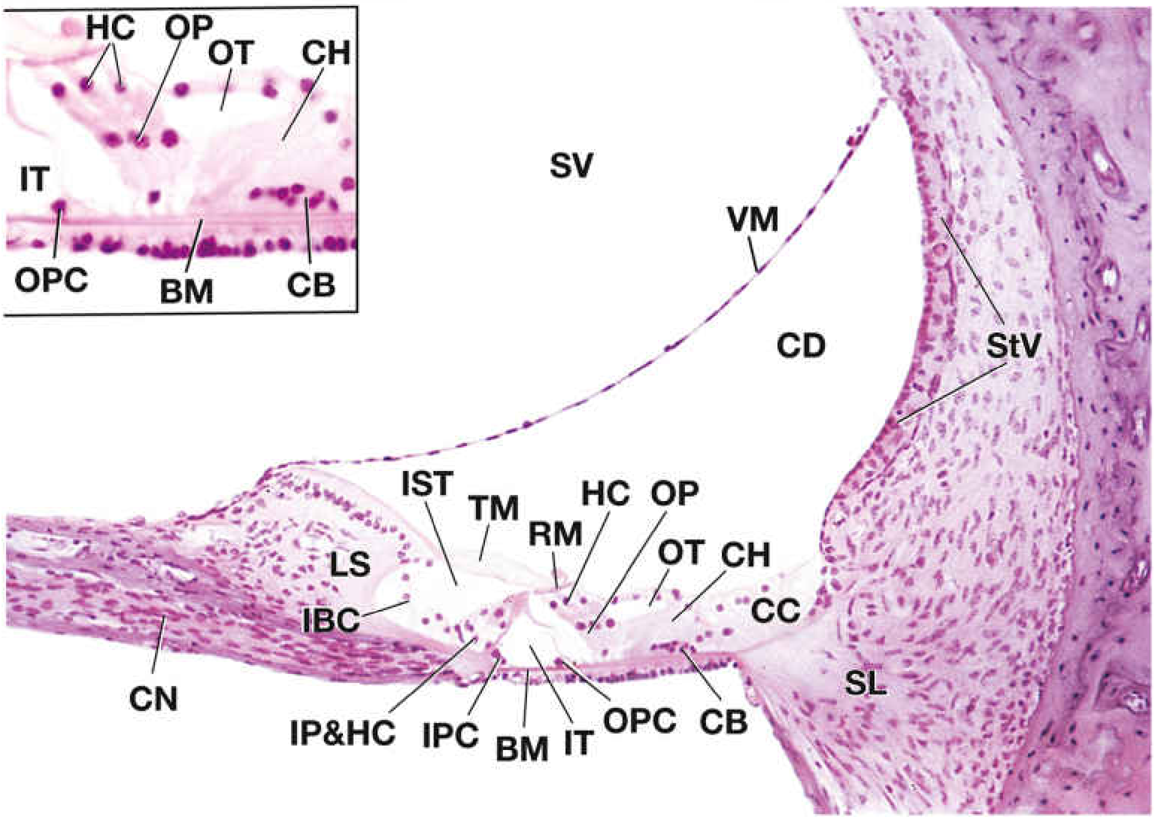
The supporting cells extend from the basilar membrane (*BM*) to the surface of the organ of Corti (this is not evident here but can be seen in the *inset*), where they form a reticular membrane (*RM*). The free surface of the receptor cells fits into openings in the reticular membrane, and the "hairs" of these cells project toward, and make contact with, the tectorial membrane (*TM*). The latter is a cuticular extension from the columnar cells of the limbus spiralis. In ideal preparations, nerve fibers can be traced from the hair cells to the cochlear nerve (*CN*).

In their course from the basilar membrane to the reticular membrane, groups of supporting cells are separated from other groups by spaces that form spiral tunnels. These tunnels are named the inner tunnel (*IT*), the outer tunnel (*OT*), and the internal spiral tunnel (*IST*). Beyond the supporting cells are two additional groups of cells, the cells of Claudius (*CC*) and the cells of Böttcher (*CB*).

BM, basilar membrane
CB, cells of Böttcher
CC, cells of Claudius
CD, cochlear duct
CH, cells of Hensen
CN, cochlear nerve
HC, hair cells

IBC, inner border cells
IPC, inner pillar cells
IP&HC, inner phalangeal and hair cells
IST, internal spiral tunnel
IT, inner tunnel
LS, limbus spiralis
OP, outer phalangeal cells
OPC, outer pillar cells
OSL, osseous spiral lamina
OT, outer tunnel
RM, reticular membrane
SG, spiral ganglion
SL, spiral ligament
ST, scala tympani
StV, stria vascularis
SV, scala vestibule
TM, tectorial membrane
VM, vestibular membrane


SL
StV
CD
VM
BM
SV
LS
ST
CN
OSL
SG
SG


HC
OP
OT
CH
IT
OPC
BM
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SV
VM
CD
StV
IST
TM
HC
OP
RM
OT
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LS
CC
IBC
CN
SL
IP&HC
IPC
BM
IT
OPC
CB