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Sketches of Otohistory

Part 4: A Cell by Any Other Name: Cochlear Eponyms

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Preserving one's memory for future generations is an age-old human ambition. A frequent, but perhaps not very creative, penchant is the naming of objects that one has (or claims to have) discovered. Our world is covered with mountains and rivers, countries and continents, animals and plants that make reference to great voyagers and scientists, their sponsors or even imposters. Little wonder, then, that the names of the pioneers of our body's exploration are preserved on the maps of our anatomy, from Alcock's canal to Zinn's ligament. The cochlea is also replete with the eponyms of early anatomists, not to mention that the structure of the entire sensory apparatus carries the name of Alfonso Corti, the subject of an earlier sketch in this series [Hawkins, 2004]. Within the extended neuroepithelium of the cochlea and the surrounding tissues we find the eponyms of Böttcher, Claudius, Deiters, Hardesty, Hensen, Huschke, Nuel, Reissner and Rosenthal (fig. 1).

In honor of the forefathers of our discipline, though, we must admit that they did not claim fame and immortality for themselves. Instead, the eponyms developed slowly. In the early years of morphological investigations, in the 19th century, it was customary for scholars to refer to anatomical structures by the name of the anatomist who first mentioned them, for example, the 'cells that Boettcher described'. This was a convenient reference because the original authors did not necessarily understand the role of the cells or even their precise anatomy and therefore could not propose rational names. Such references to the discoverer may also have helped to alleviate some of the confusion present in the initial naming of the cells. For example, when Deiters discovered the supporting structures that now carry his name, he suggested naming them 'Haarzellen' (hair cells) because of the hair-like phalangeal process. At the time, the cells that we now call 'hair cells' were generally referred to as 'Cortische Zellen' although Corti never named any cell after himself. Later, hair cells became Deiters' cells, Corti's cells became hair cells, and Corti was honored by naming the entire structure after him. Kölliker [1861] was one of the first to attempt to clarify the nomenclature.

Friedrich Christian Rosenthal: 'Ueber den Bau der Spindel im menschlichen Ohr', 1823

Like most scientists of his era, Friedrich Christian Rosenthal was not a specialist of the ear but a general anatomist. The biographical encyclopedia of the German 'Königliche Akademie der Wissenschaften' [Allgemeine Deutsche Biographie 1889] considered him well known for his studies on whales, seals and jelly fish, but did not mention the article that describes what is now known as Rosenthal's canal in the cochlea.

In his publication 'Ueber den Bau der Spindel im menschlichen Ohr' [1823], Rosenthal corrects Scarpa,

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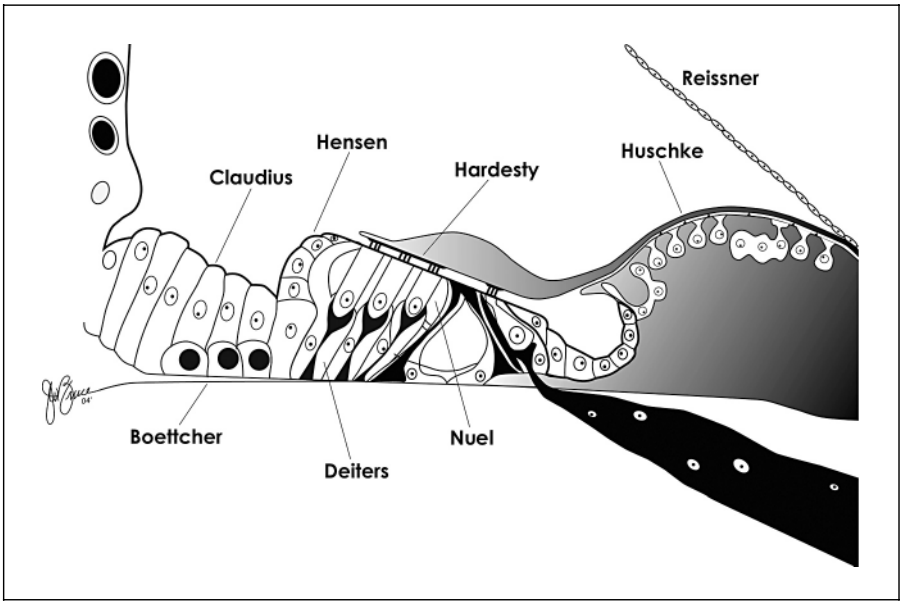

Fig. 1. Eponyms in the cochlea. *Böttcher's cells* are found between the Claudius cells and the basilar membrane so that their apical surfaces are never in contact with endolymph. *Claudius' cells* are cuboidal cells that rest on the basilar membrane and fill the distance between the Deiters cells and the lateral wall. *Deiters' cells* span from the basilar membrane to the reticular lamina and are closely associated with the outer hair cells. *Hardesty's membrane* is the layer of the tectoria closest to the reticular lamina and overlying the outer hair cell region. *Hensen's cells* are high columnar cells that are directly adjacent to the third row of Deiters' cells. *Huschke's teeth* are the tooth-shaped ridges on the spiral limbus that are in contact with the tectoria and separated by interdental cells. *Nuel's spaces* are the fluid-filled spaces between the outer pillar cells and adjacent hair cells and, by extension, the spaces between the outer hair cells. *Reissner's membrane* is composed of two cell layers and separates the scala media from the scala vestibuli. *Rosenthal's canal* (following the modiolus) is not shown. The section of the tectorial membrane above the inner hair cell is called *Hensen's stripe*. The definitions of cell types were mostly taken from Slepecky [1996].

with due respect for the master, noting that Scarpa's representation of the spindle 'does not completely agree with nature'. He then describes a 'Kanal' (canalis spiralis modioli) that follows the modiolus and observes that 'all nerve fibers that penetrate through the perforations [of the tractus spiralis foraminulentus] reach this canal and then distribute themselves as thin fibers on the spiral plate. Fibers destined for the first turn ascend close to the inner tubular lamella. Those for the second turn are guided through this canal to the tubular substance of the associated spiral lamella, etc.' Rosenthal does not illustrate his report. While this must have been the first detailed account of the canal, others before him may have given partial descriptions. Samuel Thomas Soemmerring may have illustrated the inferior half of the spiral canal as early as 1806 [quoted after Moralee, 1996].

Rosenthal has probably suffered more than most other inner-ear anatomists from posthumously mistaken identity. His discovery has on occasion been ascribed to Isidore Rosenthal [Critchley, 1978; Koenigsberg, 1989], a German physiologist (1836–1915) whose date of birth postdates the original publication. Several biographies modify his name to Friedrich Christof Rosenthal, and different encyclopedias list his year of birth as 1779 or 1780.

Friedrich Christian Rosenthal was born in Greifswald, Germany, in 1780. He wrote his dissertation in 1802 on the olfactory organ ('De organo olfactus quorundam animalium') at the University of Jena. After surgical training in Würzburg and Vienna, he returned to Greifswald in 1804 to settle down in private practice. However, under the continued influence of his mentor, Karl Asmund Rudolphi, he maintained an association with the university, completing his habilitation in 1807, again on the topic of olfaction. In 1810, he gave up his clinical practice for an appointment at the newly established University of Berlin. Following his stay in Berlin and a short interlude as an army medical officer during the revolt against the Napoleonic oppression, he returned to Greifswald and was made Professor of Physiology and Anatomy in 1820. He died there of tuberculosis in 1829.

Emil Huschke: 'Ueber die Gehörzähne, einen eigenthümlichen Apparat in der Schnecke des Vogelohrs', 1835

Huschke's scientific work centered around developmental issues. Not only his publications, but also the eponyms associated with him attest to a wide variety of interests. These include Huschke's foramen (on the tympanal plate), Huschke's valve (lacrimal duct), Huschke's cartilage (vomeronasal cartilage), Huschke's canal (union of the tubercules of the annulus tympanicus) and Huschke's ligament (in the stomach).

Inspired by Scarpa's investigations of the bird labyrinth, Huschke first demonstrated the 'teeth' that bear his name at a congress in 1830, publishing his findings 5 years later [Huschke, 1835]. He describes the appearance and number of tooth-like extensions (dentes cartilagines, Knorpelzähne) in the ductus cochlearis in a number of bird species (fig. 2). Being a devotee of comparative anatomy, Huschke's investigations include goose, grebe, turkey, owl, falcon, raven, sparrow, robin, yellowhammer, tit, dipper, snipe, swallow, pigeon and plover. The equivalent mammalian Huschke's teeth are associated with the spiral limbus, where their protruding plates are in contact with the tectorial membrane, individually separated by the interdental cells. Although he is best known to us for the discovery of the 'teeth', Huschke must also receive credit for the first description of the basilar papilla (papilla spiralis acoustica) in 1824, long before Corti explored its fine structure.

Emil Huschke was born in Weimar, Germany, in 1797. He studied at the University of Jena where he received his doctorate in 1813 for a dissertation on respiratory organs. After a brief visit to Paris, he continued his career in Jena with a habilitation on facial features and expressions ('Über Physiognomie und Mimik'), followed in 1827 by an appointment as Professor of Anatomy and director of the Anatomical Institute. Huschke was very much influenced by the ideas of German Naturphilosophie seeking the connection between brain and soul ('Hirn und Seele'). He was also politically quite active and participated in the foundation of the Deutsche Burschenschaft, the student movement for German national unity and independence. He died in Jena in 1858 of meningitis.

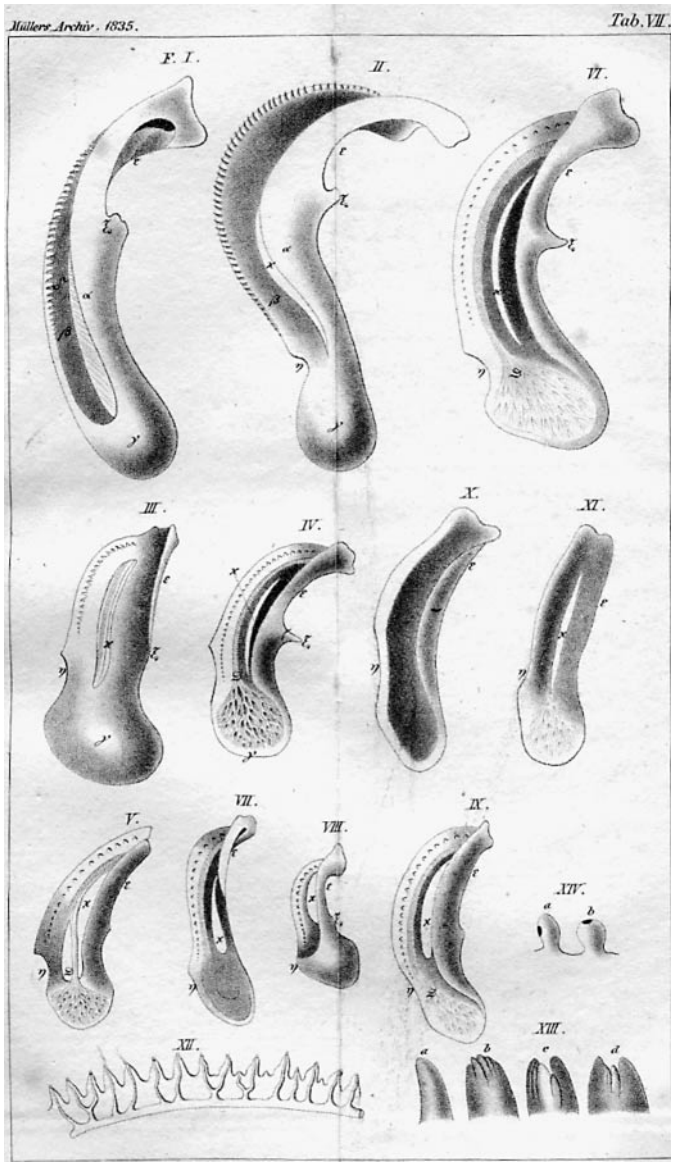

Fig. 2. Huschke's teeth. The plate from Huschke's publication depicts the tooth-like extensions in the ductus cochlearis of several bird species.

Ernst Reissner: 'Zur Kentniss der Schnecke im Gehörorgan der Säugethiere und des Menschen', 1854

Ernst Reissner followed Corti's investigations with more refined techniques, largely confirming Corti but also adding new details. He published his original studies on the development of the labyrinth in his dissertation for the medical degree at the University of Dorpat in 1851 under the title 'De auris internae formatione'.

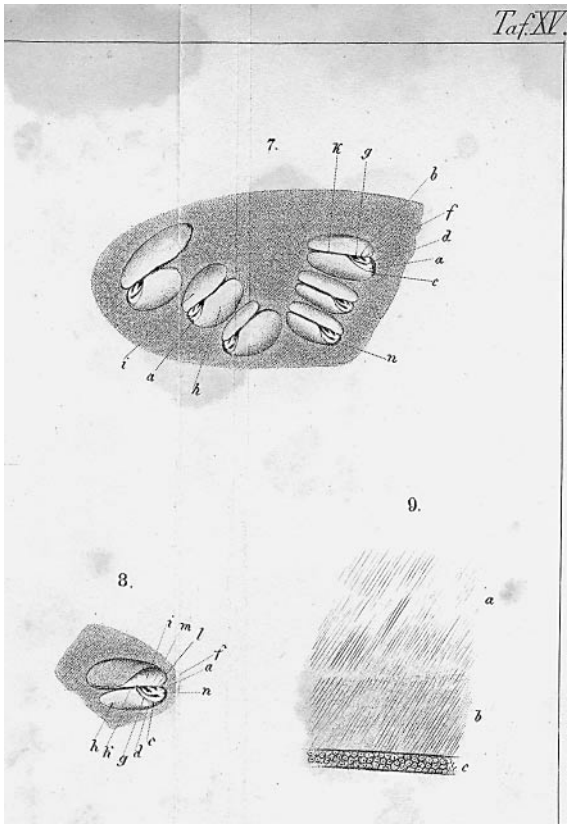

Fig. 3. Reissner's membrane. This section of the plate from Reissner's 1854 publication illustrates the partitioning of the cochlea.

It appears, however, that even then a thesis was not the best way to disseminate information. Its publication did not have the impact that Reissner had expected, and his observations failed to enter anatomical treatises of the cochlea. He therefore published a summary of his thesis work in the *Archiv für Anatomie, Physiologie und Wissenschaftliche Medicin* [Reissner, 1854], stating rather frustratedly: 'Da aber die später erschienenen Abhandlungen von dem betreffenden Gegenstande gar Nichts erwähnen, fühlte ich mich veranlasst, meine Beobachtungen aufs Neue vorzunehmen' ('Since later treatises do not mention this object at all, I feel compelled to recheck my observations'). The object he is referring to is the 'Schneckenkanal' (canalis cochlearis), the third partition in the cochlea that he discovered and added to the already known scala tympani and scala vestibuli.

Describing the borders of the Schneckenkanal, he notes that the separation of the endolymphatic canal from the scala vestibuli has apparently been completely overlooked up to this point. This partition consists of a 'sehr zarten, structurlosen Lamelle, die mit Epithelialzellen ... bekleidet ist' (a very fragile unstructured lamella, which is covered with epithelial cells). Because it partitioned the canalis cochlearis from the scala vestibuli, the membrane was later referred to as 'vestibular membrane' until it received the Reissner eponym. The color engravings in Reissner's thesis are esthetically quite appealing, but we find the plates in the subsequent publication (fig. 3) more informative – although Claudius [1856] calls even these 'völlig unverständlich' (completely incomprehensible).

Ernst Reissner was born in the Latvian town of Riga (then under Russian rule) in 1824, received a medical degree at the University of Dorpat in 1851 and became Professor of Anatomy in 1855. Dorpat, now the University of Tartu in Estonia, was founded by the Swedish King Gustavus Adolphus in 1632 after the area had become part of the Swedish kingdom. Although a Russian university at the time of Reissner (and Böttcher), the language of instruction in Dorpat was German. Reissner published diverse anatomical studies, including studies on the hair of humans and mammals which his contemporaries considered as valuable as those on the ear. He retired from teaching in 1875 for health reasons, and died in 1878.

Friedrich Matthias Claudius: 'Bemerkungen über den Bau der häutigen Spiralleiste der Schnecke', 1851

Friedrich Matthias Claudius worked primarily on comparative anatomy during his tenure at the universities of Kiel and Marburg in Germany, focusing largely on the auditory organ. The discovery later associated with his name was described in a publication of 1856 [Claudius, 1856] in which he details his dissections of the cochlea of several mammals. He apologizes for the fragmentary nature of his studies but felt compelled to publish his incomplete observations to counteract the recent paper by Reissner [1854] which, in his words, places the progress achieved by Corti and Kölliker in jeopardy.

Aside from his rather brief but acerbic critique of Reissner, Claudius mostly devotes his publication to a parenchyma of largish, thin-walled cells which cover the surface of the zona pectinata (fig. 4). This fact was overlooked by Corti, who thought that there were only a few such cells because he did not use cross-sectional preparations. Claudius blames their great fragility ('grosse Zartheit') for the fact that these cells can only seldom be obtained in large numbers; in addition to great care, their

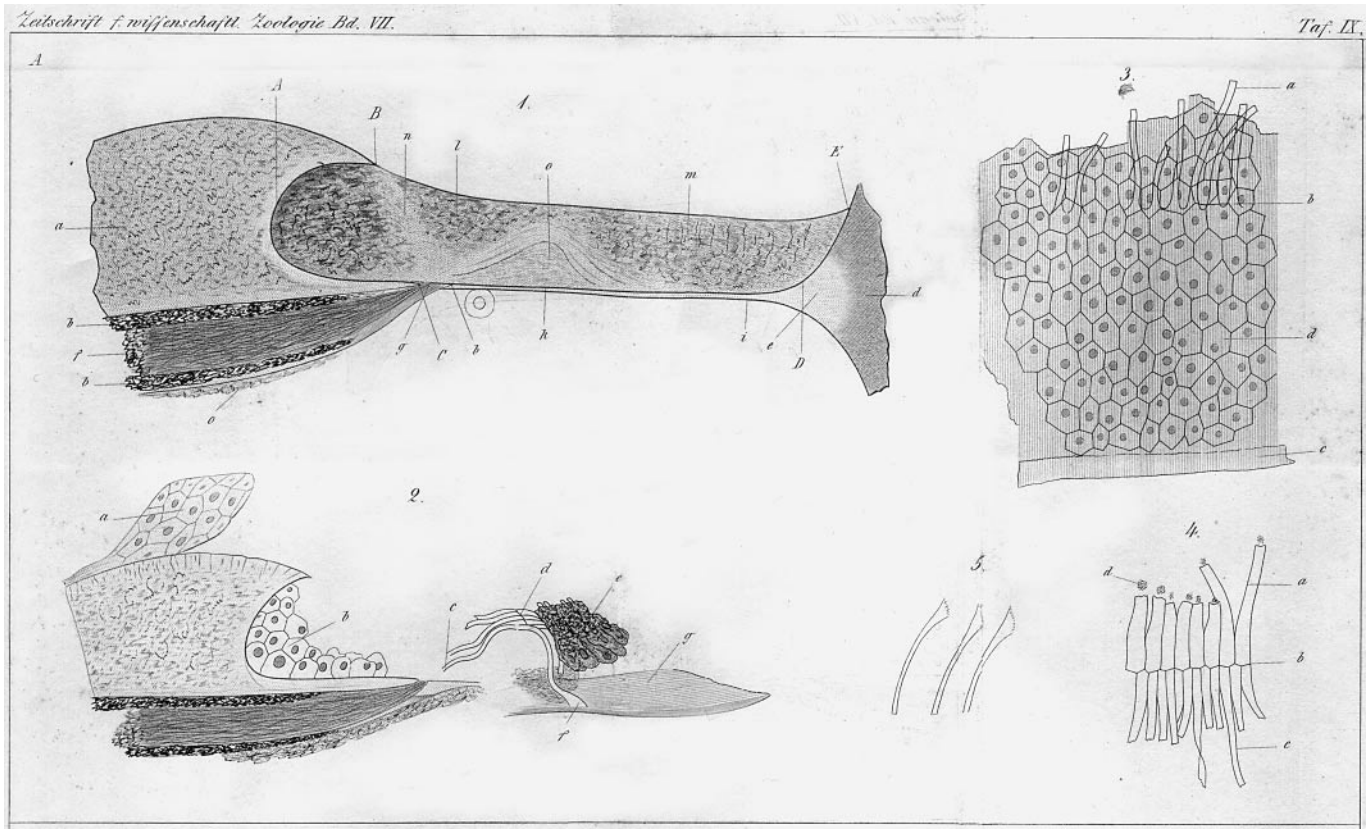

Fig. 4. Claudius' cells. The plate from Claudius' publication records his investigations of different cell types of the cochlea.

preparation – so he admits – requires some luck. He observes correctly that cell size changes little in the various regions of the cochlea, from the beginning of the spiral to the hamulus, the apex of the cochlea. The number of layers, however, depends on the height of the sulcus and is therefore greater near the base than the hamulus.

Friedrich Claudius was born in Lübeck, Germany, in 1822. He signs his publications as 'M. Claudius'; the initial refers to his middle name, Matthias, given to him in honor of his grandfather and also the name of his uncle, the famed German poet Matthias Claudius. Following studies in Jena, Göttingen and Kiel, Claudius received his doctorate in 1844 in Göttingen. He volunteered as physician in the army of Schleswig-Holstein from 1848 to 1850 and was appointed to the zoological museum at Kiel in 1849 and as docent for anatomy in 1854. In 1859 he became professor and director of the Institute for Anatomy at the University of Marburg where he taught microscopic anatomy and established a collection of morphological specimens of the inner ear. He fell severely ill in 1862 and was relieved of his duties in 1867. He died in Kiel in 1869.

Arthur Böttcher: 'Weitere Beiträge zur Anatomie der Schnecke', 1859

Arthur Böttcher contributed numerous studies on the fine structure of the reticular lamina and the nerves of the organ of Corti. He originally described the cells that eventually would bear his name in his dissertation at the University of Dorpat, 'Observationes microscopicae de ratione qua nervus cochleae mammalium terminator' [1856]. However – just like Reissner – he felt compelled to reiterate his observations in a journal article [Böttcher, 1859].

In this article, Böttcher primarily addresses several points of contention in contemporary cochlear anatomy, for example, the question of whether Corti's cells (hair cells) are continuations of the nerve fibers or independent structures akin to the Pacinian corpuscles. But he also challenges his colleague at Dorpat, Reissner, by stating that he looked for the 'Schneckenkanal' and the membrane that Reissner had described, and pointedly declaring that he himself did not see it.

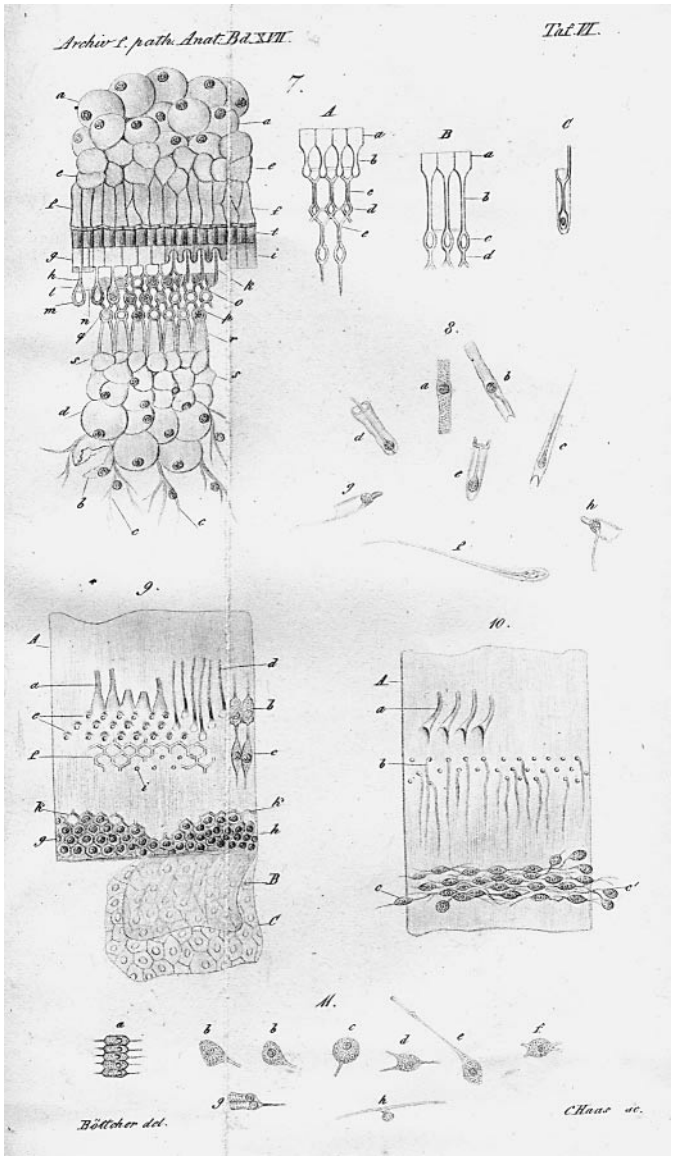

Fig. 5. Böttcher's cells. The plates in Böttcher's 1859 publication show drawings of different cell types of the cochlea, including single hair cells and the cells later named 'Böttcher's cells' (upper left).

In describing his microscopic preparation (fig. 5), he mentions that, beginning with the upper surface, directly under the tectorial membrane, and working downward, one comes upon a layer of cells, which Corti, Claudius and he had noted earlier (and only in passing) as epithelial cells. They are round and pale, but not always uniform in size. They are also difficult or almost impossible to isolate, because of connections between their delicate membranous walls. Böttcher devotes little more than one of the 37 pages of his paper to these cells, considering them only an incidental observation in the course of his attempt to discover and describe the location of the true endings of the cochlear nerve fibers. Nevertheless, he is now convinced that they differ in many ways from epithelial cells and are more closely related to the organ of Corti than has been realized before.

Like Reissner, Arthur Böttcher was a product of the University of Dorpat. He was born in 1831 in the Latvian (then Russian) province of Kurzeme, began his studies in 1851 and received his doctorate in 1856, just 5 years after Reissner, for studies on the nerve supply to the cochlea. Following brief stints in Berlin, Paris and Vienna, he returned to Dorpat, where he advanced to Professor of General Pathology and Pathological Anatomy in 1862. He died in 1889 after 12 years of severe illness.

Böttcher's name is frequently spelled 'Boettcher'. This is, for a change, not an Anglicization of his name, but a common variant of German spelling. While his 1859 article gives his name as 'Boettcher' and is frequently cited as such, contemporary bibliographical references, for example the 'Album Academicum' of his alma mater [Hasselblatt and Otto, 1889], list him as Böttcher. Since 'ö' or 'oe' did not matter much at the time, they should not matter to us now.

Otto Deiters: 'Untersuchungen über die Lamina spiralis membranacea', 1860

Otto Deiters is probably most familiar to the scientific community through his work on the central nervous system and, in particular, the nucleus vestibularis lateralis that later received his name. Deiters' career was cut short by his untimely death, and much of his work was edited and published posthumously by Max Schultze, professor of anatomy at the University of Bonn, where Deiters had spent most of his academic career.

The cochlear cells that now bear his name are described in a chapter entitled 'Die specifischen Zellen der Lamina spiralis' in Otto Deiters' monograph *Untersuchungen über die Lamina spiralis membranacea* [Deiters, 1860]. Differences in terminology do not make for easy reading, because what he calls 'die Cortischen Zellen' are our hair cells, and what he calls his 'Haarzellen' are what we designate in his honor as Deiters' cells. In his figures the latter, thanks presumably to destructive histological artifacts, have only short cell bodies and long extensions that make contact with the basilar membrane below and the base of an outer hair cell above, as well as with the

lamina reticularis. He pictures this important relationship in elegant detail (fig. 6) and recognizes that the phalangeal processes do not follow a straight line. He emphasizes that they progress at an oblique angle from their point of contact at the base of one hair cell and make contact with a different hair cell at the reticular lamina. Incidentally, he often calls attention to the presence of Claudius cells in his specimens.

Otto Deiters was born in Bonn, Germany, in 1834, where he received his medical degree in 1856 for a dissertation on the growth of muscle fibers ('De incremento musculorum: Observationes anatomico-physiologicae'). After a brief stay in Berlin with Virchow, he returned to Bonn for his habilitation and was appointed lecturer in anatomy while practicing as a physician in internal medicine. Family financial problems after his father's death made it necessary for him to open a private clinical practice, a major burden in addition to his commitment to his university appointment, lectures and his much beloved anatomical work. The result was that his own health became so impaired that he died in 1863, only 29 years old, the victim of typhus apparently acquired on what was intended to be a journey of convalescence.

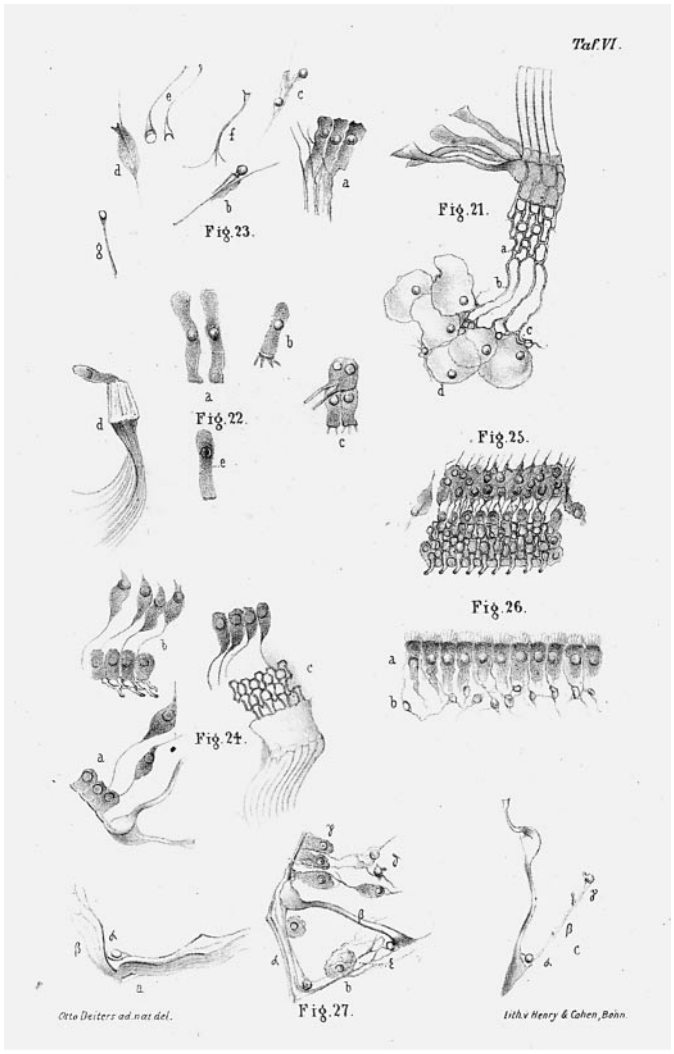

Fig. 6. Deiters' cells. One of the plates from Deiters' publication contains various depictions of hair cells and their attachment to Deiters' cells.

Victor Hensen: 'Zur Morphologie der Schnecke des Menschen und der Säugethiere', 1863

Christian Andreas Viktor Hensen is considered by many to be the father of modern oceanography. At the University of Kiel, Germany, he devoted much of his later career to marine biology and ecology, studying in great detail fish populations and 'plankton', a term that he coined. He also furthered oceanography politically, becoming a member of the Prussian House of Representatives in 1867, where he succeeded in creating a 'Royal Prussian Commission for the Exploration of the Oceans'. Between 1871 and 1889, he led five major marine biological expeditions in the Baltic, the North Sea and the Atlantic.

Oceanography, however, was not his major assignment at the university. As professor of physiology, he devoted himself to the physiology of sensory organs and in particular, vision, hearing and balance. The cochlear cells that are named for him first appear in his 1863 paper [Hensen, 1863; fig. 7], the product of a meticulous study conducted over several years in which he covers just about every aspect of cochlear anatomy. There he points out that, although Corti described the structures he found as lying flat on the basilar membrane, Huschke's spiral papilla rises arch-like to a height of almost 0.2 mm. Böttcher and Deiters, who did not work much with cross-sections, position the Claudius cells right next to the hair cells. Hensen corrects this view by including a new type of elongated cells with their upper ends connected to the phalanges of the reticular lamina. He calls them simply 'Stützzellen' (supporting cells), and they are now known as Hensen's cells.

Hensen was mostly working with specimens from cattle, horses and humans, none of which show 'Hensen's bodies', those droplets of an oily liquid that stain dark by osmic acid and which are so prominent in the upper turns

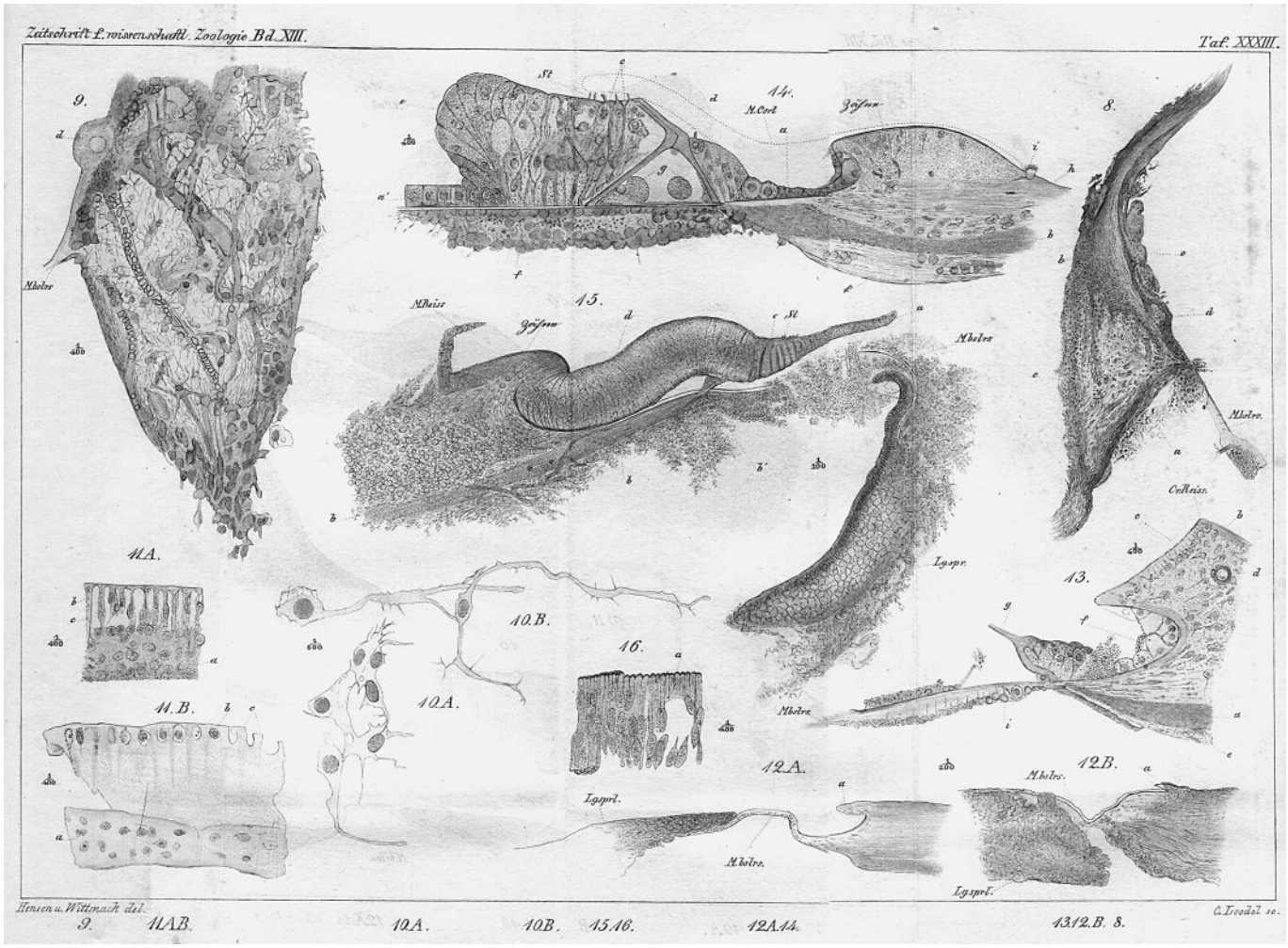

Fig. 7. Hensen's cells. Two plates in Böttcher's publication provide details of many cochlear structures including the shape and position of 'Hensen's cells' (No. 14).

of the guinea pig's cochlea. Hensen also receives credit for describing what became known as 'Hensen's stripe', the section of the tectoria forming the membrane's contact with the stereocilia of the inner hair cells.

Viktor Hensen was born in Kiel, Germany, in 1835 and studied medicine first at Würzburg, then Berlin and finally at Kiel, where he received his doctorate in 1859 for a thesis on epilepsy and urinary secretions. His studies on the structure and function of the auditory organ made him famous in his early years and led to his appointments at the University of Kiel as Associate Professor of Physiology in 1864 and full professor in 1868. He died in 1924.

Jean-Pierre Nuel: 'Beitrag zur Kenntniss der Säugethierschnecke', 1872

Nuel's primary area of expertise was ophthalmology, and he wrote articles and books on basic aspects of vision and practical guides to surgery. He conducted his studies of the organ of Corti as a student during a summer semester (1871) in the anatomical institute in Bonn, Germany, and published the description of his dissections 1 year later [Nuel, 1872].

His publication, as he emphasizes in the introduction, concerns two main aspects of cochlear anatomy, the fibers of the membrana basilaris and the course of the nerve fibers in the canalis cochlearis. For the bulk of his paper, he goes into detailed descriptions on these two subjects,

taking issue mostly with Böttcher's work which he considers, at least in part, decidedly incorrect ('entschieden unrichtig'). Finally, he turns his attention to the relationship between hair cells and Deiters' cells. The precise relationship between these two cell types, although described by Deiters 10 years earlier, was still a matter of dispute. Nuel grants the Deiters cells more independence ('Selbstständigkeit') than earlier authors and reiterates that the conical structures (i.e. phalanges) of Deiters' cells traverse at an angle reaching the reticular lamina approximately 2 hair cells to the side. His drawings emphasize the spaces between pillar cells and hair cells and also imply spaces between the phalanges of the Deiters cells and the hair cells (fig. 8). However, Nuel uses this sketch to draw the reader's attention to the bundles of appendages ('Büschel von Anhängen') on the Corti cells which he prefers to call little rods ('Stäbchen') rather than hairs. He had seen these untold times in the best-preserved preparations, and he thus postulates that these are indeed natural and preformed structures and not artifacts as Böttcher had stated. What later became the spaces of Nuel were not a major topic of discussion in his paper. A monograph in 1878 ('Recherches microscopiques sur l'anatomie du limaçon des mammifères') further details Nuel's studies of the inner ear.

Nuel was born in the small town of Tétange in Luxembourg in 1847 as the third of 11 children. He received his medical degree in Ghent in 1870 and was licensed in Luxemburg in surgery and in gynecology. Although he first took up private practice, he continued his studies at Utrecht, Vienna and Bonn, eventually turning his attention to ophthalmology. He held a professorship in opthalmology in Louvain in Belgium from 1877 to 1880, moved to Ghent in 1880 for a professorship in physiology and finally in 1885 to Liège to hold the chair in Ophthalmology and Physiology of Sensory Organs. He died in 1920 in Liège.

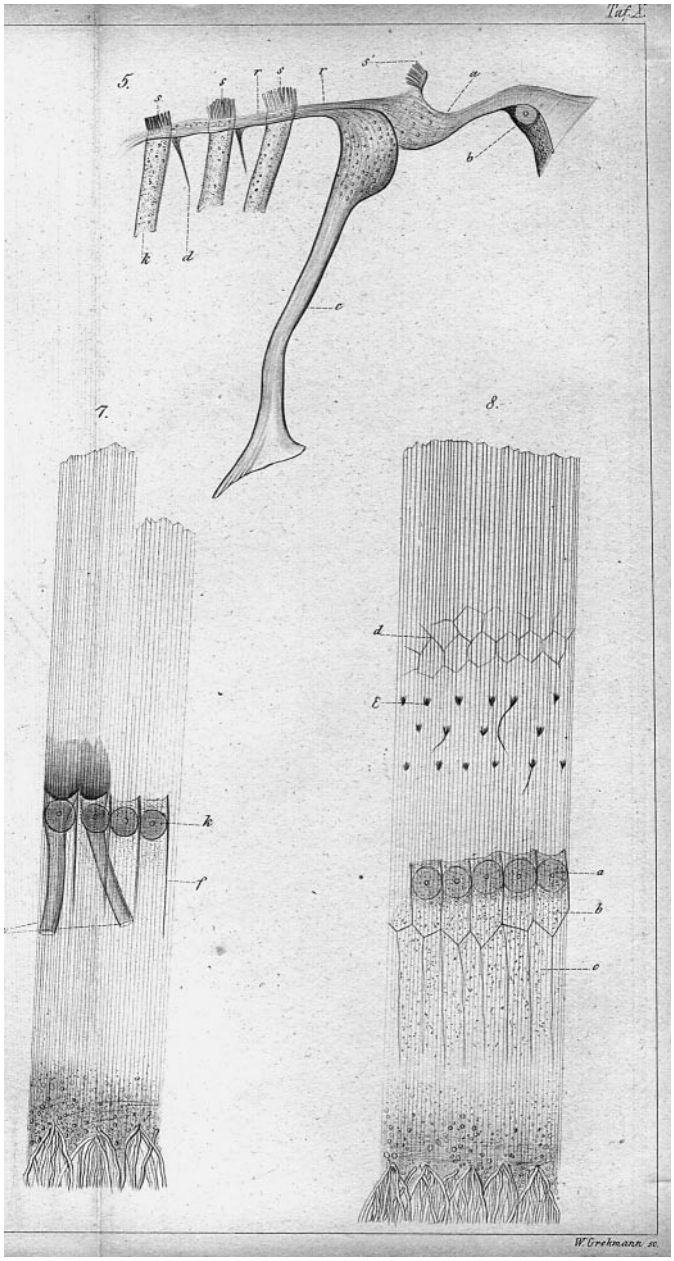

Fig. 8. Nuel's spaces. In this section of his plate (No. 5c), Nuel's drawing emphasizes the spacing between outer hair cells and pillars.

Irving Hardesty: 'On the Nature of the Tectorial Membrane and Its Probable Role in the Anatomy of Hearing', 1908

Hardesty devoted his scientific studies mostly to the fine structure of the tectorial membrane. He was particularly concerned about shrinkage artifacts introduced by the acids and alcohols included in most fixatives used at the time.

Hardesty began his studies on the tectoria [1908] with attempts at obtaining frozen sections (not very successfully) and determining the ideal way for the preservation of the membrane. He finally settled on 'Zenker's fluid', which contains potassium bichromate, mercury bichloride and acetic acid, 'all of which have decalcifying action and none of which, combined, seemed to cause shrinkage or distortion of the tectorial membrane'. In such preparations, mostly from fetal and young pigs, he makes detailed

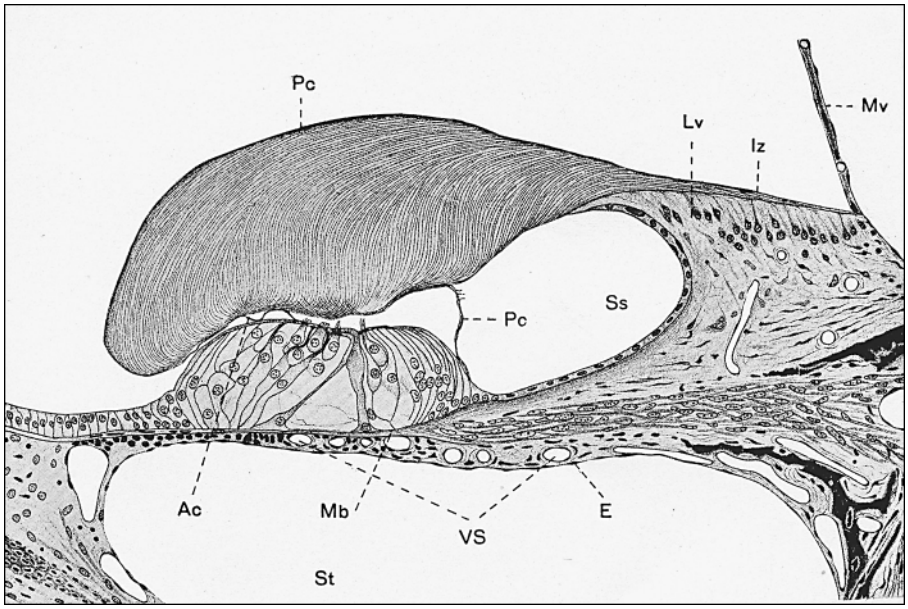

Fig. 9. Hardesty's membrane. This figure from Hardesty's paper details the relationship of the tectoria with the underlying tissues. The accessory structure 'Ac' became known as 'Hardesty's membrane'.

measurements and anatomical observations, including the novel finding of an 'accessory membrane' (fig. 9) which he summarizes as follows: 'A thin, exceedingly delicate, accessory tectorial membrane is described lying along the under surface of the outer zone of the main body to which its outer edge is lightly attached. It varies in width somewhat as does the main body and its fibers extend toward Hensen's stripe, but only extend over the outer series of hair cells.'

While we remember Hardesty for his membrane, we certainly do not remember him for the theoretical considerations that he derived from his anatomical studies. In the same paper, he states as his last point: 'The theories in which the basilar membrane is considered the vibrating mechanism in the cochlea are considered untenable, and an application of the telephone theory to the tectorial membrane as the vibrating mechanism is suggested on the basis of its logical position, its extent, shape, proportions, consistency and structure, and the probable character of the transformed and transferred sound waves in the endolymph of the cochlea.'

Hardesty was born in Beaufort, N.C., USA, in 1866. He received a PhD at the University of Chicago in 1899 and wrote his article while an associate professor at the University of California. He later worked at Tulane University and was President of the New Orleans Academy of Science. He died in New Orleans in 1944.

Acknowledgements

Information on the anatomists of the inner ear from earlier literature was helpful in preparing this article. Unfortunately, most of these sources remain incomplete in covering the eponyms of the cochlea, and some of them, surprisingly, contain biographical, bibliographical or anatomical errors. While we do not wish to claim that the information presented here is without flaw, we were fortunate to have access to the original literature. Biographical information was gleaned from various encyclopedias, obituaries, family histories and university archives. The authors are greatly indebted to Ms. Amy Chatfield for her skillful and relentless pursuit of all sources and resources.

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