Vestnik zoologii, **44**(3): e-1—e-18, 2010
DOI 10.2478/v10058-010-0013-y

UDC 591.485:591.3:599

MORPHOLOGY OF THE INNER EAR IN MAMMALS WITH DIFFERENT ECOLOGICAL PECULIARITIES IN ONTOGENY

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Received 3 August 2009
Accepted 7 September 2009

Morphology of the Inner Ear in Mammals with Different Ecological Peculiarities in Ontogeny. Solntseva G. N. — The inner ear is the first to form, as the core, phylogenetically most ancient formation of the peripheral auditory system both in phylogenesis and in ontogenesis. As the development of the inner ear continues, the other parts of the peripheral auditory system of different evolutionary age start to be formed, and the outer ear is the evolutionary youngest among them. All parts of the peripheral auditory system are multicomponent formations. As opposed to the outer and middle ears, which are characterized by different structural variations and a wide spectrum of adaptable transformations connected with the peculiarities of species ecology, the inner ear possesses a variety of functions in the repre-sentatives of different ecological groups and, therefore, keeps a similar structural organization. Usually, both in the cochlear and vestibular analyzers the topography, form and size of separate components vary. Basically, the anatomic formation of the structures of the inner ear finishes in the early prefetal period, while the cellular differentiation of the sensory epithelium of the cochlea, maculas and cristae in immature-born species continues up to the early stages of postnatal ontogenesis. In mature-born species (cetaceans, ungulates), the differentiation of the inner ear structures is complete by the moment of birth.

Key words: cochlea, vestibular apparatus, sacculus, utriculus, semicircular canals, utricular macula, saccular macula, crista ampullaris, receptor cells, organ of Corti.

Морфологические особенности онтогенеза внутреннего уха млекопитающих с различным образом жизни. Солнцева Г. Н. — Как в филогенезе, так и в онтогенезе прежде всего формируется внутреннее ухо как стержневое, филогенетически наиболее древнее образование периферического отдела слуховой системы. По мере развития внутреннего уха начинают формироваться другие звенья периферической слуховой системы разного эволюционного возраста, из которых филогенетически молодым является наружное ухо. В отличие от наружного и среднего уха, которые характеризуются самыми разнообразными структурными вариациями и широким спектром адаптационных преобразований, связанных с особенностями экологии вида, внутреннее ухо у представителей различных экологических групп при многообразии функций сохраняет однообразную структурную организацию. Как в кохлеарном, так и в вестибулярном анализаторах обычно варьируют топография, форма и размеры отдельных компонентов. Анатомическое формирование структур внутреннего уха в основном заканчивается в раннем предплодном периоде, в то время как клеточная дифференцировка чувствующего эпителия улитки, макул и крист у незрелорождающихся видов продолжается вплоть до ранних стадий постнатального онтогенеза. У зрелорождающихся видов (китообразные, копытные) дифференцировка структур внутреннего уха в основном завершается к моменту рождения.

Ключевые слова: улитка, вестибулярный аппарат, кортиев орган, саккулюс, утрикулюс, ампулярная криста, полукружные каналы, саккулярная макула, утрикулярная макула.

Introduction

The question on evolutionary origin of a labyrinth in vertebrates still remains open, despite the existing hypotheses explaining its evolution beginning from a lancelet up to mammals. A well-known hypothesis is that the labyrinth has appeared on the basis of the organs of a lateral line, which are openly located on the surface of an animal's body and have a direct contact with the environment. Complication of structures and functions of the lateral line organ has caused an appearance of a new structural formation — the vestibular apparatus. However, nobody among the researchers succeeded to trace how the evolution was progressing from an open labyrinth to a closed one, which is located deeply in the cranium.

The present research does not give a direct answer to this question, but it essentially contributes to its solution and is devoted to comparative analysis of an early embryogenesis of the vestibular and cochlear parts of the inner ear in terrestrial, semi-aquatic and aquatic mammals, since the sensory systems, in particular, brightly demonstrate the range of evolutionary and adaptive transformations, which have appeared in mammals during their transition from terrestrial to aquatic way of life.

The inner ear of mammals, in contrast to that of the lower vertebrates (amphibians, reptilians, birds) reveals the features of the progressive evolution which become apparent in the spiral torsion of the cochlea and the presence of the structurally complicated organ of Corti. Whereas the *lagena papilla* still remains in the representatives of the monotremats, the organ of Corti develops in the marsupials and in the placental animals.

The aim of the present research is to study the species and adaptive features of the cochlear and vestibular organs of mammals with different ecologies in pre- and postnatal ontogeny.

Material and methods

The following species of mammals (in postnatal ontogeny) were studied: Insectivora (*Talpa europaea* Linnaeus, 1758); Chiroptera (*Rhinolophus ferrumequinum* Schreber, 1774*)*; Rodentia (*Myicastor coypus* Molina, 1782*)*; Cetacea (Odontoceti: *Tursiops truncatus* Montagu, 1821*, Delphinus delphis* Lacepede, 1758*, Phocoena phocoena* Linnaeus, 1758*;* Mysticeti: *Balaenoptera acutorostrata* Lacepede, 1804*, Balaenoptera physalus* Lacepede, 1758); Carnivora (*Vulpes vulpes* Linnaeus, 1758*, Enhydra lutris* Linnaeus, 1758*, Mustela vison* Schreber, 1777); Pinnipedia (Otariidae: *Callorchinus ursinus* Linnaeus, 1758*, Eumetopias jubatus* Schreber, 1776; Phocidae: *Pagophilus groenlandicus* Erxleben, 1777, *Phoca vitulina* Linnaeus, 1758, *Phoca insularis* Belkin, 1967, *Erignathus barbatus* Erxleben, 1777, *Pusa hispida* Schreber, 1775, *Pusa caspica* Gmelin, 1788; Odobenidae: *Odobenus rosmarus divergens* Linnaeus, 1758).

For comparative ecological and embryological study were used the following species of mammals**:** terrestrial forms: Rodentia — laboratory rat (*Rattus norvegicus* Pallas, 1779), guinea pig (*Cavia porcellus* Linnaeus, 1758), Artiodactyla — pig (*Sus scrofa domestica* Linnaeus, 1758); semi-aquatic forms: Pinnipedia — Otariidae: Steller sea lion (*Eumetopias jubatus*); Phocidae: ringed seal (*Phoca hispida*), bearded seal (*Erignathus barbatus*); and Odobenidae: walrus (*Odobenus rosmarus divergens*); aquatic forms: Cetacea — Odontoceti: spotted dolphin (*Stenella attenuata* Gray, 1846), bottlenose dolphin (*Tursiops truncatus)*, common dolphin (*Delphinus delphis*), harbor porpoise (*Phocoena phocoena*), beluga (*Delphinapterus leucas* Pallas, 1776); Mysticeti: minke whale (*Balaenoptera acutorostrata*).

Specimens were fixed in 10% buffered formalin and Wittmaak fixative then dehydrated and treated in an increasing series of ethanol, embedded in celloidin, and sectioned at 10–15 micron thickness in a dorsoventral plane. The sections were stained with hematoxylin-eosin, according to the methods of Mallory and Kulchitsky, and impregnated with silver nitrate.

The duration of gestation and length of embryos an diverse stages of embryogenesis vary widely among mammals. To examine embryos of different species, I compared developing structures of the vestibular apparatus with the development of acoustic structures at the same stage of development. For convenience, I used the stages of development described in certain terrestrial species (Dyban et al., 1975).

Results

It is known that the inner ear, in which the cochlea and the vestibular apparatus are located, is placed in a petrous part (pyramid) of a temporal bone. Because of the complexity of its structure, it is also called a labyrinth. There are two labyrinths: osseous and membranaceous. The osseous labyrinth includes a cochlea, a vestibule and three semicircular canals. The vestibule looks like a cavity of an oval form. It is located between the cochlea and the semicircular canals. The membranaceous labyrinth is located inside the osseous labyrinth and its form usually repeats the form of a labyrinth, but is significantly smaller in size. The walls of a membranaceous labyrinth are formed by a dense connective tissue.

The inner ear of mammals, in contrast to that of the lower vertebrates (amphibians, reptilians, birds), reveals the features of the progressive evolution which become apparent in the spiral torsion of the cochlea and the presence of the structurally complicated organ of Corti. While the *lagena papilla* still remains in the representatives of the monotremats, the organ of Corti develops in the marsupials and in the placental animals.

The periotic bone in which the cochlea of mammals is located in the majority of mammals knits to the tympanic bone (rodents, carnivores, pinnipeds etc.). In the odontocetes, it only partially knits to the tympanic bone and it is located outside the tympanum.

In the inner ear, the principle of the cochlea's structure reveals similarities in almost all mammals. The number of the turns which form the cochlea can vary from 0.5 in monotremats to 4.5–5 turns in some rodents (fig. 1).

The increase of the number of cochlea's turns is explained by its morphological progress (Fleischer, 1973). However, in such echolocating animals as dolphins the cochlea is flat and forms 1.5–2.0 turns only, while in bats the number of its turns amounts to 3.5. Such variability in the number of cochlea's turns in echolocating forms proves that the cochlea's height caused by the turns' increase doesn't influence the perceptible frequency band.

Big cochlea is characteristic for all species of dolphins. The cochlear bones are localized in periotic, in the thickness of which a cochlea channel is extended. In Amazon river dolphin (*Inia geoffrensis*) a cochlea is half-covered with medial lobe of tympanic bone. In marine dolphins the cochlea is separated from the other bones and

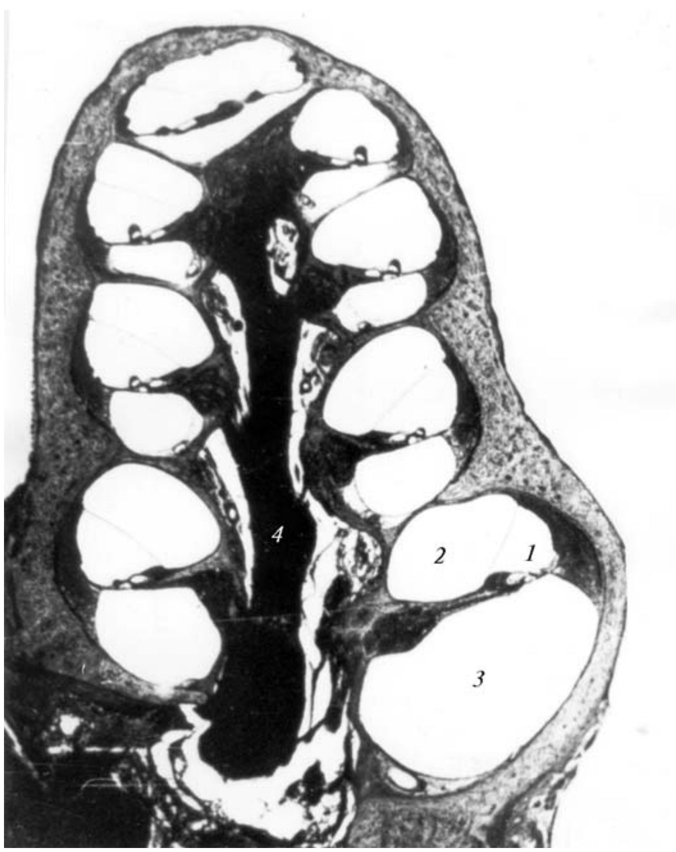

Fig. 1. The cochlea of *Myocastor coypus*. Slit through the cochlea axis. 4.5 turns of the cochlea are shown. Staining with hematoxylin-eosin. Magnification x25. *1* — cochlear canal; *2* — vestibular scala; *3* — tympanic scala; *4* — cochlear nerve.

Рис. 1. Улитка нутрии (*Myocastor coypus*). Поперечный разрез через ось улитки. Показаны 4,5 оборота улитки. Окраска гематоксилин-эозином. Увеличение x25. *1* — улитковый канал; *2* — вестибулярная лестница; *3* — барабанная лестница; *4* — кохлеарный нерв.

is an independent structure. Cochlear canal in river dolphin is weakly traced, and *crista transversalis* is almost twice as small as in marine dolphins, in which the *crista transversalis* is opened, and cochlear canal is well-traced.

In the majority of mammals the size of the cochlea's basal turn slightly differs from that of the turn which is located above. For the representatives of some genera the drastic enlarging of the cochlea's basal turn is typical (shrews, bats, odontocetes and pinnipeds).

The comparative analysis shows that in echolocating forms one of the important cochlea's adaptations, which provide high-frequency hearing: the increasing of the cochlea's basal turn. For example, the surface of the basal turn of dolphins is increased due to the "untwisting" of the cochlea up to 1.5–2.0 turns (fig. 2). The bat's cochlea reveals just the same, in spite of the fact that its promptness is increased up to 3.5.

During the comparison of the primary and the secondary osseous spiral laminas some peculiarities are revealed in the cochlea's basal and apical turns. The extension of the primary lamina along the cochlea's passage varies significantly less than such of the secondary lamina (Fleischer, 1973).

The structure of the primary osseous spiral lamina is dissimilar in different species. The vestibular and the tympanal osseous leaves which form the primary lamina can be thick and compact, as well as less developed. For example, in a man both leaves of the primary spiral lamina have a spongy structure, while in the *Loxodonta* a great loosening of the tympanal leaf is observed (Fleischer, 1973).

In the majority of mammals the secondary osseous spiral lamina is more developed in the cochlea's basal part than in the apical part, where it becomes thin.

In the Chiroptera and Odontocetes the secondary lamina occupies the whole cochlea's passage stretching from its basal to the apical turn. In the majority of mammals and in a man in the cochlea's basal part the secondary lamina is well-marked, and in the apical part it quickly disappears.

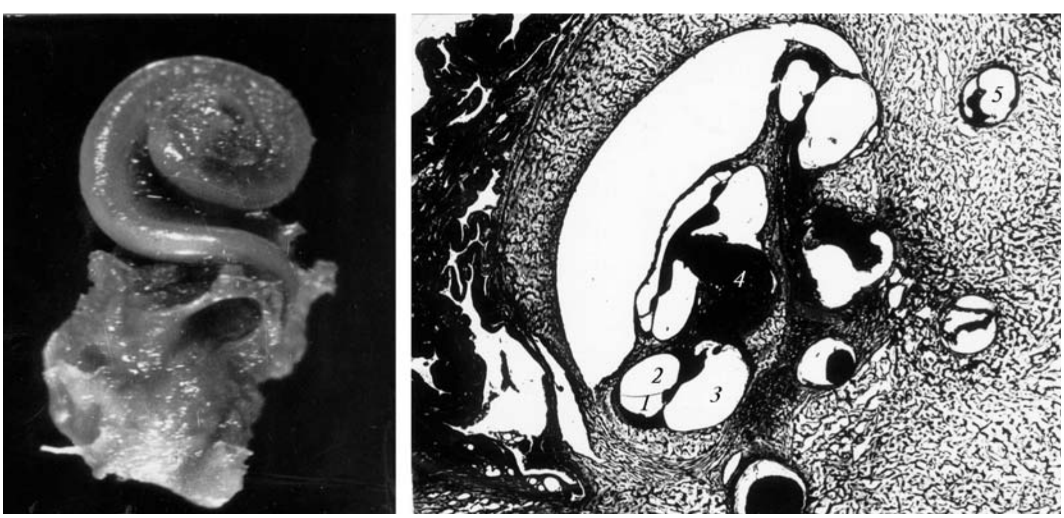

Fig. 2. The cochlea of *Delphinus delphis*. 1.5 turns of the cochlea are shown. Staining according to Kampas. Magnification x25. *a* — cochlea, anatomical preparation; *b* — histological preparation, slit through the axis of the cochlea. *1* — cochlear canal; *2* — vestibular scala; *3* — tympanic scala; *4* — cochlear nerve. 5 — semicircular canal

Рис. 2. Улитка обыкновенного дельфина. Показаны 1,5 оборота улитки. Окраска по Кампасу. Увеличение x25. *а* — улитка, анатомический препарат; *б* — гистологический препарат, продольный разрез через ось улитки. *1* — улитковый канал; *2* — вестибулярная лестница; *3* — барабанная лестница; *4* — кохлеарный нерв; *5* — полукружный канал.

The comparison of two spiral lamina's structure shows that the species which possess a thick secondary lamina have a well-developed primary lamina. It is basically typical in the forms with the narrow basilar membrane. In the forms with the underdeveloped secondary osseous lamina the distance between two laminas is bigger.

Another important peculiarity of the cochlea's structure in echolocating mammals is a well-developed secondary spiral bone lamella. The lesser a distance between primary and secondary spiral bone lamellas is, the narrower the width of the basilar membrane becomes, and the secondary spiral bone lamella turns out to be more developed, its rigidity is continuously and evenly decreasing from the cochlea's basal turn to the apical turn.

In all mammals the cochlea's basilar membrane heterogeneously widens along its length. For example, in a guinea pig the basilar membrane is wide in the cochlea's basal part, narrow in the medial part and widens again in the apical part. In the Odontocetes (porpoises) the diameter of the basilar membrane changes from the basal to the apical turn in 5.4 times (Kolmer, 1908) and in a Baird's beaked whale — in 10 times (Yamada, 1953).

In the majority of mammals the membrane is up to 29 micrometers thick. In bats and Odontocetes the basilar membrane is the narrowest and the thinnest. For example, in dolphins its thickness amounts to 6.5 μm.

The structure of the organ of Corti, as well as the quantity of its receptor elements, reveals similar features. Usually, the outer hair cells are located in three rows, the inner hair cells — in one row. The total number of the hair cells in a man amounts to 14 975, in a guinea pig — to 8939, in a cat — to 12 500, in a rabbit — to 7800, in a seal — to 17 972, in a ringed seal — to 21 792, in a bottlenose dolphin — to 17 384, in a pacific white-sided dolphin — 12 899 (Ramprashad et al., 1976).

Usually the number of the hair cells decreases in the direction from the basal to the cochlea's apical turn. Usually the volume of the nuclei of the organ of Corti hair cells increases in the same direction, as well as in the direction from the inner row of the outer hair cells to the periphery (Akimov, 1976).

In most mammals the structure of the organ of Corti reveals patterns of similarity. The number of receptor cells in echolocating and non-echolocating forms doesn't change. However, some researchers observed certain peculiarities in the structure of the organ of Corti bearing elements in dolphins and bats, in which these cells are enlarged in size and compactly located (Wever et al., 1971). The increasing number of the spiral ganglion's cells (3 times) and the enlargement of their size compared to a man testify in favour of the data concerning dolphins' and bats' high abilities to process acoustical information starting from the peripheral part of the auditory analyzer (Firbas, Welleschik, 1973).

The most interesting facts are revealed during the study of the inner ear's structure in mammals. First of all, this is the existence of two types of receptors belonging to a different evolutional age (outer and inner hair cells), which are spatially separated from each other (fig. 3). What is more, it has an extremely small number of the receptor cells and a sufficient stability in animals of the very variable hearing specializations. The auditory system of echolocating species and animals with low-frequency hearing possesses approximately equal quantities of the hair cells and the identical character of their distribution upon the basilar membrane.

According to our point of view, the fact that most mammals, even the species with extraordinarily broad hearing abilities, have relatively little number of receptors as well as auditory nerve's fibres, is connected with a temporary specificity of the acoustic signal's perception and processing. It is a consequent receipt of information that allows simultaneous use of comparatively little quantity of parallel canals in the periphery of the auditory system (Bogoslovskaya, Solntseva, 1979).

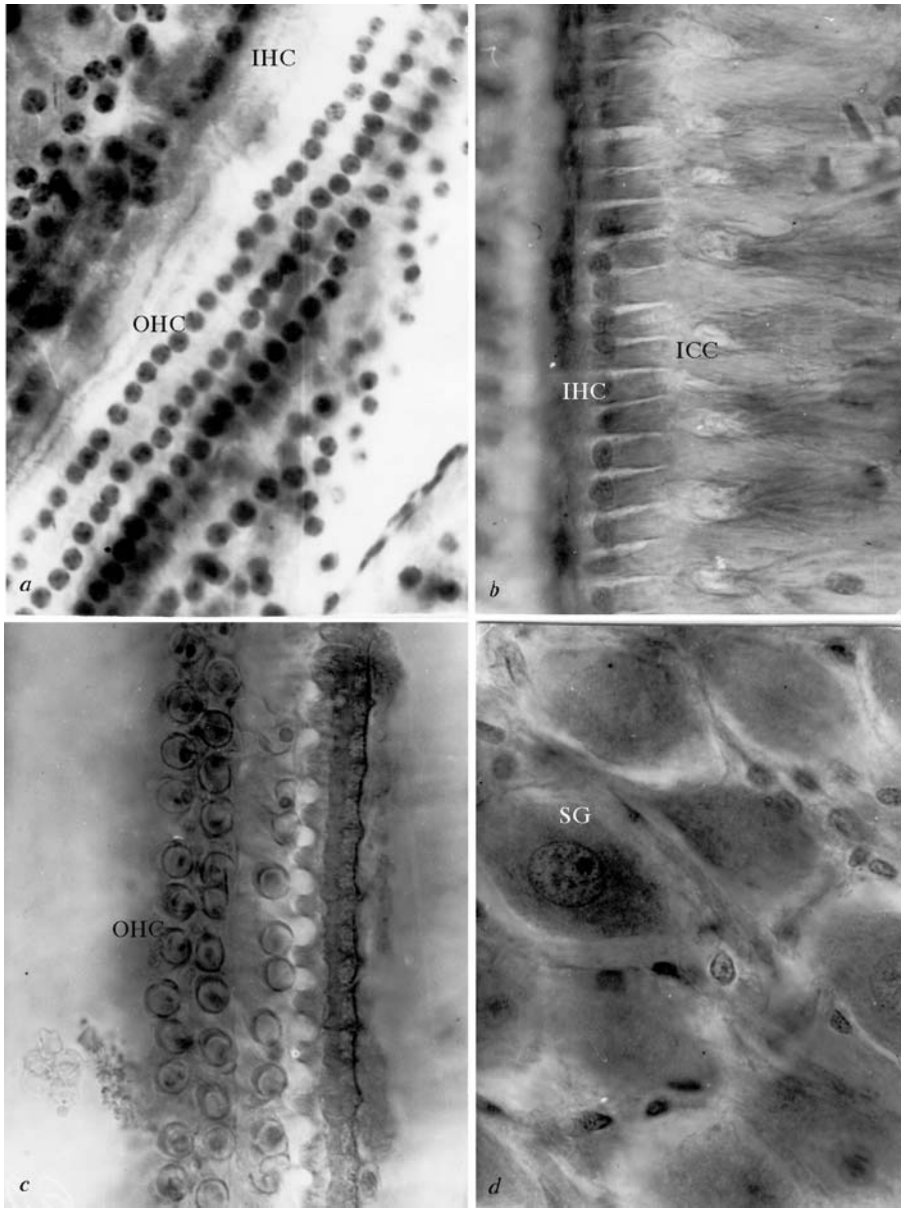

Fig. 3. The organ of Corti of *Delphinus delphis*. Slit through the cochlea axis at the level of the basal turn. Staining with hematoxylin-eosin (immersion objective 90, ocular 7). *a* — general view; *b*, *c*, *d* — cells of the organ of Corti. IHC — inner hair cells; OHC — outer hair cells; ICC — inner columnar cells; SG — cells of spiral ganglion.

Рис. 3. Кортиев орган обыкновенного дельфина. Продольный разрез через ось улитки на уровне базального оборота. Окраска гематоксилин-эозином (об. им. 90, ок. 7). *a* — общий вид; *b*, *c*, *d* — клетки кортиева органа OHC — наружные волосковые клетки; IHC — внутренние волосковые клетки; ICC — внутренние клетки-столбы; SG — клетки спирального ганглия.

Due to two partitions, the cochlea's tunnel is divided into three independent canals (canals of cochlea): tympanic, vestibular and middle, or cochlear. The first two canals are filled with a perilymph and communicate with each other through an opening on the cochlea's top — *helicotrema*. The middle canal is filled with an endolymph and ends blindly, widening in the cochlea's apical part and spirally repeating the number of the turns which form the cochlea. On the cross-sections the cochlear canal has three walls: inferior, superior and external.

The inferior wall is the continuation of the spiral lamina, which starts from modiolus and consists of two layers. The spiral ganglion's dendrites pass between them in the radial canals. The upper layer of the osseous lamina turns into a spiral limb and the lower one — into a basilar membrane. The inferior wall of the cochlear canal divides the spiral canal into vestibular (*scala vestibuli*) and tympanic (*scala tympani*) scalae of the cochlea. On the cochlea's top the osseous lamina ends with a peculiar curve in the form of a hook (*hamulus cochleae*).

The superior wall of the cochlea's canal is formed by the Reisner's membrane, which isolates it from the vestibular canal of the cochlea. The external wall is the thickest and covers the upper part of the spiral ligament; it takes part in the endolymph production, which fills the cochlear canal (*ductus cochlearis*).

The Reissner's membrane looks like a thin membrane which, from the cochlear canal's side, is covered with a flat polygonal epithelium, and from the vestibular canal's side it is covered with a thin endothelium of a mesenchymal origin. The layer is formed by thin elastic fibers. During the basilar membrane's oscillations and the perilymph's displacements in the vestibular canal the oscillations of the Reissner's membrane occur, which, in their turn, are transmitted to the cochlear canal's endolymph. The basilar membrane (*membrana basilaris*) forms the inferior wall of the cochlear canal. The organ of Corti is situated on its surface. From the side of the tympanic canal the surface of the basilar membrane is covered with the same endothelium, under which blood vessels are situated. The basilar membrane passes through the whole cochlear canal in the form of a connective-tissue spiral. The inner edge of the basilar membrane begins from the upper leaf of the osseous spiral lamina of *habenula perforata*, and the external one is fastened in the area of *lamina spiralis ossea*. The basilar membrane is subdivided into two zones: inner and outer. In the inner zone the tunnel, inner and outer hair cells of the organ of Corti are located, and in the outer zone there are mainly the Hensen's cells.

At the basis of the outer cells-columns the inner zone turns into the outer zone. The collagen fibers which form the structure of the basilar membrane are the shortest at the cochlea's basis and while moving to the apical part they greatly lengthen and widen. The width of the basilar membrane depends on the distance between primary and secondary osseous spiral laminas. The secondary osseous spiral lamina (*lamina spiralis ossea secundaria*) is connected with the vestibular fibres of the basilar membrane. It was experimentally shown that the flexible basilar membrane and the rigid osseous spiral lamina form the oscillating system of the cochlea.

The organ of Corti is located on the vestibular surface of the basilar membrane; from its inner side the organ of Corti is adjoined by a connective-tissue structure — a vestibular, or spiral, labium, which passes on the inner spiral incisure.

The tectorial membrane starts from the spiral labium and is located above the elements of the organ of Corti in the form of a jelly-like lamina and stretches spirally along the organ of Corti.

In the tectorial membrane the following structures are discerned: the axial part, which adjoins to the top of the epithelial cells of the spiral labium, the middle part, which is freely located above the organ of Corti, and the external part, which, as it is supposed, is connected with the Hensen's cells (Titova, 1968).

The organ of Corti of mammals is formed by supporting and receptor elements. The supporting elements are represented by inner frontier cells, inner cells- phalanxes, inner and outer cells-columns and Deuters's, Hensen's, Claudius's supporting cells.

The inner frontier cells border upon the inner side of the inner hair cells and form 1–2 rows of elements. With their tops they adjoin to the tops of the inner cells-phalanxes. The narrow and flat head of the inner frontier cells is tightly connected with the structural elements of the reticular membrane. The basal part of the cell is located in the area of *habenula perforata*. The nucleus is located in the basal part of the cell.

The inner cells-phalanxes form one row. Their upper end is connected with the reticular membrane and has the form of a phalanx, with the help of which the inner hair cells are separated from each other. The middle part of the inner cell-phalanx is flattened out and narrowed. The external side of the inner hair cells is adjacent to the cell's body. The basal part of the cell is located in the area of *habenula perforata*, as well as the inner frontier cells. Between these cells the dendrites of the spiral ganglion are located. The nucleus lies in the basal part of the cell. Between the inner cells-phalanxes and the frontier cells there is an isolated intercellular cavity, in the apical part of which the inner hair cells are located (Titova, 1968).

The outer and the inner cells-columns adjoin to each other by their tops and form a three-cornered tunnel which is filled with an endolymph. This tunnel spirally passes through the whole the organ of Corti. With the help of their basis the cells-columns contact with the basilar membrane. The cells-columns are located at the sharp angle facing each other; as a result their tops adjoin to each other. At that the outer cells-columns form the bigger angle of inclination than the inner cells-columns.

In the place of their contact the cells-columns form a peculiar arch (*arcus spiralis*). The apical part of the inner cells-columns forms a head lamina. In the aggregate these laminas enable the formation of the space between the inner hair cells and the first row of the outer hair cells. In the area of the contact with the inner hair cells the head laminas have inner incisures. The outer cells-columns adjoin to the head lamina of the inner cells-columns from below and give outward from themselves long oar-like processes, which contact with each other and thus isolate the lateral sides of the first row of the outer hair cells from each other, as well as the second row of the outer hair cells from the first row. The number of the inner cells-columns exceeds the number of the outer cells-columns. For example, in a man the number of the inner cells-columns amounts to 5600, and the number of the outer cells-columns amounts to 3850.

The supporting cells-columns locating on the basilar membrane stretch it and, together with the other supporting elements, transmit the basilar membrane's oscillations to the receptor cells.

The Deiters's cells are located on the basilar membrane; usually they form three rows and lie close to the inner cells-columns. These cells are the supporting cells for the outer hair cells. The Deiters's cells have a polygonal cylindrical form with a big rounded nucleus which is located in the basal part of the cell. In its upper part the Deiters's cell forms a phalanx-shaped incisure — the upper head, which, together with other laminas, phalanxes and outgrowths of the cells-columns takes part in the formation of the reticular membrane. Also, from the Deiters's cell the lower head begins, the bowl-shaped bottom of which gives support to the basis of the outer hair cell.

The Hensen's cells, in contrast to the Deiters's cells, are not connected to the reticular membrane's structures. They adjoin to the Deiters's cells and form a wide row fastening to the basal part of the basilar membrane. The nucleus is big and rounded. It is supposed, that the transportation of the nutrients to the hair cells and to the Deiters's cells from the vascular stria is provided with the help of the Hensen's cells (Titova, 1968).

The Claudius's cells are located behind the Hensen's cells and have a cubical form with distinct intercellular borders. It is supposed, that the functional role of the Claudius's cells, as well as the role of the Hensen's cells, is a trophic one.

The outer (OHC) and the inner (IHC) hair cells are the receptor elements of the organ of Corti. According to the Retzius's assessment (Retzius, 1884), there are about 12000 outer and 3500 inner hair cells in a man's cochlea — slightly less than in the cochlea of a cat and a guinea-pig. The inner hair cells (IHC) lie in one row with an inclination from modiolus and the outer hair cells (OHC), which are isolated from IHC by the tunnel, lie in three rows with an inclination to the opposite side. In different turns of the cochlea the OHC slightly differ in shape, while the IHC's shape is invariable in all cochlea's turns.

The height of the cylindrical OHC's increases in the direction from the basal to the apical turn (20 and 50 μ, accordingly) and their diameter is practically invariable (5 μ). The OHC's stability is provided by the system of the Deiters's supporting cells and the space between them, which is filled with a liquid (Nuel's space). The receptor pole of the hair cells is formed by a cuticular lamina and sensitive flagellums.

The flagellums are represented by peculiar rigid rods which in their narrowest part, a neck, near the cuticular membrane, have the diameter of about 0.05 μ, and in the rest part — about 0.2 μ. The fine structure of the flagellums is known: there is a bundle of fibrils inside, which is 30–40 A thick (collateral line of fishes). The flagellum's membrane is the part of the receptor cell's membrane and each of the flagellums is fixed on the cuticular lamina with the help of a peculiar rootlet.

Each OHC is provided with 100–120 flagellums which are located in three parallel rows in the form of the letter W, the top of which is turned towards modiolus. The flagellum's length in the cochlea's basal part amounts approximately to 2 μ and increases towards the top up to 6 μ. In a guinea-pig, a cat, a rat and a man the flagellums of the middle and modiolus row are shorter than those of the distant row; as the investigations with the application of the electron microscope showed, the flagellums only touch the tectorial membrane, at that the longest of them can be pressed in it.

The OHC contains a lot of organelles: mitochondrions, ribosomes and some specific inclusions. The mitochondrions are concentrated in the subapical and the basal part of the cell, as well as along the cell walls. Cytoplasmic membranes form flat cisterns which are parallel to the cell walls; the nucleus is located close to the OHC's basis.

Directly behind the nucleus the central part of the cell's cylinder contains also numerous microtubules and vesicles — features, which are typical for the presynaptic endings.

The inner hair cells (IHC) turned out to be less specialized elements as compared with the OHC. The basic differences from the latter are: a pear-shaped form, location of the filaments, distribution of the cytoplasmic organelles and the type of contact with nerve endings. Besides, the IHC's body is totally surrounded by the supporting elements. Sensory filaments, as it is in the OHC, are situated in three rows in the form of the greatly flattened letter W, the number of the filaments in average amounts to 60, and in the apical turn they are longer than in the basal one. The distribution of the mitochondrions in the IHC's body is not as irregular as it is in the OHC; the nucleus is located in the center of the cell. In the upper, relative to the nucleus, cytoplasm's part numerous Golgi vacuoles can be met, under the nucleus the membranes of the granular endoplasmic reticulum can be found, as well as mitochondrions. The smooth endoplasmic reticulum is concentrated in the subapical part mainly, where it has the form of small tubules and cisterns. The receptor-neuronal contacts are not limited by the basal part of the cell only, but are irregularly located in the area of the lower two thirds of the cell. The basal part of the IHC is quite often irregularly shaped with numerous and noticeable outgrowths.

The most interesting facts are revealed during the study of the inner ear's structure in mammals. First of all, this is the existence of two types of receptors belonging to a different evolutional age (outer and inner hair cells), which are spatially separated from each other. What is more, it has an extremely small number of the receptor cells and a sufficient stability in animals of the very variable hearing specializations. The auditory system of echolocating species and animals with low-frequency hearing possesses approximately equal quantities of the hair cells and the identical character of their distribution upon the basilar membrane.

According to our point of view, the fact that most mammals, even the species with extraordinarily broad hearing abilities, have relatively little number of receptors as well as auditory nerve's fibres, is connected with a temporary specificity of the acoustic signal's perception and processing. This is a consequent receipt of information that allows simultaneous use of comparatively little quantity of parallel canals in the periphery of the auditory system (Bogoslovskaya, Solntseva, 1979).

The neurons which innervate the auditory receptor cells form a spiral ganglion: a nerve-knot of the VIII pair's acoustic part of the craniocerebral nerves. The ganglion fills the Rosental's canal in the cochlea's axis and repeats the number of its spiral turns. The ganglionic neuron has, as a rule, a much widened body with two processes: peripheral and central. The body is covered with a special, complicatedly constructed myelinated membrane or capsule.

The peripheral process (dendrite) penetrates to the Corti's organ through an aperture in *habenula perforata*; cat has 2500 of such apertures (Spoendlin, 1972). The dendrite is covered with a myelin (medullated) membrane which disappears only at the entrance of the *habenula*'s aperture. In the terms of electrophysiology the peripheral process as well as the central one is an axon since the place of the myelin membrane's termination is morphologically similar to the Ranvie's interception (Engstrom, Wersall, 1958) and according to the existent conceptions this is exactly the area, which is analogous to the initial neuron's segment, where the action potential is generated. The central processes (axons) form the auditory nerve, which fibres, combined with vestibular ones, enter the CNS in the area of the medulla's and pons's boundary (Bogoslovskaya, Solntseva, 1979).

There is no consensus of opinion in the literature about how many types of cells can be distinguished among the spiral ganglion's neurons. Depending on methods and purposes of investigation so many different criterions were used that the obtained results, in spite of their fundamental character, are very hard to coordinate between each other. We believe that it is very important to quote here the basic points of view on this question.

The oldest and the most generally accepted discerning of the ganglionic cells is their division into two types according to their peripheral processes' distribution. The neurons with the radial distribution of dendrites innervate the inner hair cells (IHC) only, at that every neuron contacts with one or two IHC only, but at the same time each of these cells interacts with many neurons. Such "radial" cells form the overwhelming majority of the spiral ganglion's neurons and carry out the projection of the cochlea to the cerebral centers according to the principle "point to point". The cells of the second type have dendrites which go spirally for the major space of the cochlea turn's passage and contact with a great amount of the outer hair cells (OHC) which, in their turn, are connected with the spiral dendrites of many neurons (Smith, Sjostrand, 1961).

Thereby, two or three (and may be more) neuron types exist in the spiral ganglion of mammals. However, during the analysis of the different authors' data it remains unclear, how are the cell's types marked out on the basis of different structural criterions, correlate with each other, since none of them coincide completely with another by the quantitative indices. The correspondence between the morphological types of the spiral ganglion's cells and the characteristics of their reactions and the responses of the auditory nerve's fibres which were electrophysiologically registered is not specified up to now (Bogoslovskaya, Solntseva, 1979).

Such characteristics as the neurons number, their size, the distribution density along the cochlea's turns and the correlation with the hair cell's number are important indices of the spiral ganglion general structural organization and the auditory function's intensity. Unfortunately, because of the difficulties with the material processing the data have been so far obtained only for several mammalian species.

In mammals of a different hearing specialization the difference in the ganglionic neurons number is much more significant than in the receptors number. Man and dolphins, for example, possess approximately equal quantity of the hair cells while the spiral neurons number increases in echolocating forms in 2–3 times. On average the neuron's relation to the receptor cells amounts to 4–5.5 : 1 in dolphins, 3 : 1 in a seal and a cat, and 2 : 1 in a man. For the bat from the *Vespertilionidae* family it is found to be 6 : 1 (Firbas, Wellenschick, 1973). However, this correlation is inconstant along the whole of the cochlea's length and usually gradually decreases from 6 : 1 in the basal turn to 3 : 1 in the apical end of the organ of Corti.

The auditory nerve represents a complex fibrous system which consists of several components. Its main part is formed out of the axons or the central processes of the spiral ganglion's cells. They transmit the specific information to the primary acoustic centers, which are located in the CNS (Echandia, 1967). After leaving the cell's body the axon passes inside the Rosenthal's canal where it is usually impossible to track it at a long distance among other processes. Sometimes in young animals the axon is subdivided into several branches, which are not observed in the adult individuals.

It was shown that the fibres from the apical turn are passing in the center of the nerve, but beginning from the basal part they are located on the periphery of the nerve trunk (Sando, 1965).

Consequently, the comparatively-morphological analysis of the mammals' cochlea shows that there are two types of its structure. The first structural type can be found in the mammals whose habitat conditions are not connected with the usage of ultrasonic orientation. The following features are typical for this type: less developed cochlea's basal turn, wide and thick basilar membrane, large distance between the primary and the secondary osseous spiral laminas, weak development of the secondary lamina and its disappearance in the cochlea's apical turns.

The second structural type of the cochlea is present in the species which use ultrasonic orientation and echolocation (shrews, rats, bats, fur seals, dolphins). For this type the following features are typical: noticeable enlarging of the cochlea's basal turn, narrow and thin basilar membrane, small distance between the spiral laminas and well developed secondary osseous spiral lamina.

The vestibular apparatus of the investigated species consists of the system of membranaceous saccules and closed among themselves canals, which are filled with endolymph. This system is referred to as a membranaceous labyrinth, which includes a round sacculus, an oval utriculus, and also three semicircular canals located in three mutually perpendicular planes. In each of the semicircular canals, there are widenings (ampullae), which form connections with utriculus. In ampullae, the receptor structures — ampullar cristae — are located. The receptor structures of sacculus and utriculus are represented by the auditory spots (maculae): saccular macula, located on the lateral wall of sacculus, utricular macula, located at the basis of utriculus, and *macula neglecta*, which is located in the inner ear on the medial wall of utriculus, but in many species of mammals it is absent. In terrestrial, semi-aquatic and aquatic mammals all structures of the membranaceous labyrinth differ among themselves in their location in the inner ear, as well as in their size and form. However, for all species the presence in maculae of the otolithic membrane of a gelatinous consistence is typical, as well as the presence of the gelatinous cupula on the tops of the auditory cristae. Macula is the receptor formation, consisting of the sensory cells, which are covered with the otolithic membrane with small crystals — otoconias, plunged into the otolithic membrane.

The auditory cristae have the similar structure, but opposed to the maculas, the surface layer of the cristae' receptor epithelium is covered with a gelatinous cupula.

Other receptor formation of the inner ear is *papilla basilaris*, which in higher reptilians and birds develops into the auditory organ (*papilla acustica basilaris*) and in mammals — into the organ of Corti, which is located in the closed cochlear canal, involuted into a spiral cochlea.

Relative to each other, the receptor spots of the saccular and utricular maculae form a right angle. There is an assumption that there are no basic distinctions in the structure of these maculas (Burlet, de, 1934), however, the electron-microscopic researches have shown, that the sensory epithelium of the organ of equilibrium consists of the receptor hair cells of two types. The cells of the first type have a jug-like form and the cells of the second type — a cylindrical form; more significant distinctions between both types of the sensory cells are revealed in the connection with the features of their innervation (Wersall et al., 1965). Studies of other authors have shown that during the evolution the receptor cells of the first type have appeared in the inner ear of mammals in connection with the change of position of the animal's body in a gravitational field after their coming out on land (Titova, 1968).

As the comparative analysis of the inner ear's development has shown, in most of mammals at the stage of 20 pairs of somites (forelimb bud, stage 13), an acoustic vesicle develops.

Both in terrestrial mammals, pinnipeds and cetaceans at the 14–15th stages of development, the acoustic vesicle is divided into the superior and inferior saccules. From the inferior saccule, the sacculus and a cochlear canal are formed, and, from the superior saccule, the utriculus and semicircular canals develop. Both parts are surrounded by a condensed mesenchyme. The wall of the acoustic vesicle consists of a single-layered epithelium. The epithelial thickening of the medial wall of the acoustic vesicle is an anlage of terminal organs of a labyrinth — *macula communis*. Macula and the acoustic vesicle increase in size and are simultaneously divided into superior and inferior parts. By means of an epithelial bridge, these parts are temporarily connected with each other. Further, the epithelial bridge is replaced by an indifferent epithelium and two neuroepithelial spots are formed, one of which is located in pars superior and the other — in pars inferior. The anlage of terminal organs is located in *pars superior* and gives rise to the development of macula utriculi and ampullar cristae of the anterior vertical and horizontal semicircular canals. The anlage of terminal organs in *pars inferior* forms a process inward and backward in the ampulla of the posterior vertical semicircular canal, forming the ampullar crista.

The other part of this anlage grows in length and is divided into two anlages: a small top and a big bottom. Out of the top anlage, the saccular macula is formed; the bottom anlage develops further, forming the anlage of Corti's organ.

At the 16th stage, the cochlear canal twists spirally, forming a lower, or basal turn of the cochlea, which is surrounded with an aural capsule, consisting of a condensed mesenchyme. At the given stage, the formation of the cochlea in terrestrial and semi-aquatic species maintains behind the formation of the equilibrium organ.

In most investigated species the semicircular canals are very narrow in diameter. Sacculus and utriculus are of a small size and have a roundish or an oval form.

At the same stage of development, in representatives of different ecological groups, the sites of the upper part of the wall of the superior saccule thicken, and flat recesses are formed from them; their opposite walls adjoin each other. Later on, these places of the adhesion resolve and, from the external parts of the recesses, the semicircular canals are formed. The inferior and posterior vertical semicircular canals develop from a common anlage, their back ends fall into the middle part of utriculus. The other ends of the semicircular canals fall directly into utriculus, as a result of what the widenings (ampullae) are formed.

At the 17th stage of development, the lumens of the semicircular canals, as well as the size of sacculus, utriculus and the auditory cristae increase. In otariids, as well as in terrestrial species, the initial cellular differentiation of the sensory epithelium into receptor and supporting cells is marked in the utricular macula. In odontocetes and mysticetes the earlier differentiation of the sensory epithelium is marked in saccular macula, while in phocids and in a walrus the cellular differentiation is marked neither in saccular macula, nor in utricular macula.

At the given stage of development, in all investigated species, the cochlear apparatus is represented by a cochlear canal of a slit-like form, whose basis, formed by a columnar epithelium, and a roof, consisting of cells of a cuboidal epithelium, are well-discernable.

In terrestrial species, otariids and in a walrus, the size of the vestibular apparatus surpasses the size of the cochlear part of the inner ear twice, the lumens of the semicircular canals are wide, utriculus has an oval form and sacculus has a roundish form (fig. 4). In phocids, the size of the cochlear and vestibular parts of the inner ear reveals similar size, while the form and size of sacculus, utriculus and semicircular canals keeps similarity with terrestrial species. In cetaceans, the vestibular apparatus is extraordinary small. The connection between utriculus and sacculus is carried out by means of a narrow canal (*ductus utriculosaccularis*), which opens into *ductus endolymphaticus.* Utriculus is connected with sacculus by means of a sacculo-endolymphatic canal. In the cochlear part of the inner ear, the medial turn of the cochlea is formed. Structures of the cochlear canal are not formed; the cellular differentiation of Corti's organ is absent.

In all studied species of mammals, at the 18th stage of development, an increase in the size of structures of the vestibular apparatus occurs proportionally to the growth of a prefetus. In otariids, as well as in the species, whose way of life is in a greater degree connected with the stay on a firm substratum, the increase of size of all structures of the vestibular apparatus occurs proportionally to the increase of the cochlea's size. In absolute hydrobionts (cetaceans), the increase of the cochlea's size considerably outstrips the growth of structures of the organ of equilibrium. The receptor spot of the utricular macula acquires the more horizontal position in relation to the receptor spot of the saccular macula, which lies almost vertically. As a result, both spots form a right angle relative to each other. Maculas represent the receptor formations covered by a columnar epithelium. Each of them carries a strongly specific function.

In cetaceans and pinnipeds, as well as in terrestrial species, in the formed ampullae of the semicircular canals, the ampullar cristae are located; their receptor epithelium according to its structure is similar to the receptor epithelium of maculae. Above the surface of the sensory epithelium, the otolithic membrane, which in aquatic species is much thinner than in terrestrial and semiaquatic mammals, is located. In cetaceans, the ampullar crista is big and occupies a significant part of the ampullar space of the semicircular canals. The receptor epithelium covers the whole surface of the crista. At the given stage, contrary to the anterior and posterior vertical semicircular canals, the formation of the horizontal semicircular canal continues in all studied species. In humans, the growth of the horizontal and posterior vertical semicircular canals comes to an end by the 7th month of the prenatal life, while the growth of the anterior vertical semicircular canal — only by the moment of birth. The author connects it with the fact that in comparison with the posterior vertical and horizontal semicircular canals, the anterior vertical semicircular canal is vitally important to the developing fetus, as this structure takes part in the fixation of a body in a vertical position.

Fig. 4. Histotopography of the peripheral part of the auditory system in dorsoventral sections of prefetal heads of *Sus scrofa domestica*, stages 18,19. The cochlea is formed, as in definitive forms; an anatomical formation of the vestibular apparatus is completed. *1* — cochlear canal; *2* — scala vestibuli; *3* — scala tympani; *4* — cochlea; *5* — cochlear nerve; *6* — auditory capsule; *7* — sacculus; *8* — utriculus; *9* — semicircular canal; *10* — musculus stapedius; *11* — stapes; *12* — incus; *13* — malleus; *14* — membrane tympani; *15* — external auditory meatus; *16* — cerebrum.

Рис. 4. Гистотопография периферического отдела слуховой системы в дорсовентральных срезах головы у предплодов домашней свиньи (*Sus scrofa domestica*), стадии 18–19. Улитка сформирована, как и у дефинитивных форм; закончилось анатомическое формирование вестибулярного аппарата. *1* — улитковый канал; *2* — вестибулярная лестница; *3* — барабанная лестница; *4* — улитка; *5* — кохлеарный нерв; *6* — ушная капсула; *7* — саккулюс; *8* — утрикулюс; *9* — полукружный канал; *10* — стременная мышца; *11* — стремя; *12* — наковальня; *13* — молоточек; *14* — барабанная перепонка; *15* — наружный слуховой проход; *16* — мозг.

The differentiation of the sensory epithelium of maculas and cristae is marked in all investigated animals. In a walrus, the initial cellular differentiation is observed in the utricular macula, as well as in terrestrial species. Phocids are characterized by the simultaneous differentiation of the sensory epithelium in the utricular and saccular maculae. In cetaceans, the initial cellular differentiation of the sensory epithelium is marked only in one site of the saccular macula.

At the given stage, the formation of the cochlea finishes with the formation of the last apical turn. In representatives of odontocetes (*Stenella attenuata*, *Delphinapterus leucas*), the height of the cochlea amounts to 2.0 turns; in pinnipeds (*Eumetopias jubatus*, *Erignathus barbatus*, *Pusa hispida*, *Odobenus rosmarus divergens*) and in representatives of mysticetes (*Balaenoptera acutorostrata*) — 2.5 turns. In terrestrial species (*Sus scrofa domestica*, *Rattus norvegicus*), the cochlea is formed by 3 turns and in bats (*Rhinolophus ferrumequinum*) — by 3.5 turns. In some terrestrial mammals, the height of the cochlea reaches 4.5 turns (*Cavia porcellus*). The elements of the cochlear canal are not formed and the cells of Corti's organ are at the same stage of differentiation in all turns of the cochlea. From the columnar epithelium of the cochlear canal, two thickenings are formed: axial and lateral; from them the structures of the cochlear canal and the cells of the organ of Corti develop.

At the 19th stage of development, in saccular macula, the differentiation of the sensory epithelium into receptor and supporting cells occurs simultaneously in several sites of maculas and cristae, spreading over the most part of their surface. The structure of the cells, which, as well as the cells of the organ of Corti, form a mosaic distribution pattern, is well-discernable. The neurons of the vestibular ganglion contain big nuclei of an oval form with expressed nucleoli. The size of all structures of the organ of equilibrium is considerably increased. In otariids and in a walrus, as well as in terrestrial mammals, the size of utriculus surpasses the size of sacculus. In cetaceans, the utriculus and sacculus are similar in size with that in phocids.

In cochlea, formation of the elements of the cochlear canal is marked (fig. 5). The flattening of the cells of a cuboidal epithelium and the loosening of connective tissue, adjacent to this epithelium, occurs. In this place, the tympanic and vestibular scalae are formed. The Reissner's membrane is formed. The differentiation of the cells of the organ of Corti begins in the basal turn of cochlea from the moment when the cells of a columnar epithelium start to move apart, and is spread gradually over the turns located above. As a result, in all turns of the cochlea a different degree of anatomic and cellular differentiation is observed.

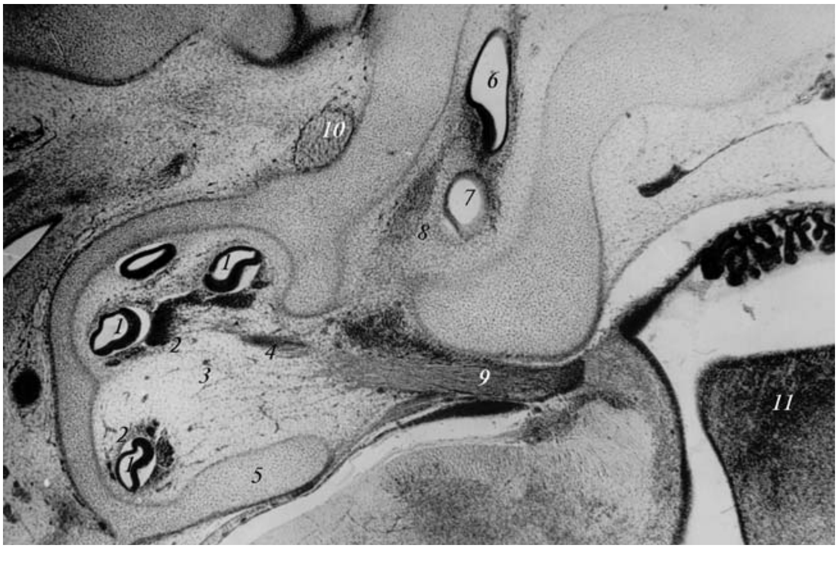

Fig. 5. Histotopography of the peripheral part of the auditory system in dorsoventral sections of the head of a prefetal *Eumetopias jubatus*, stages 18, 19. An initial differentiation of the elements of the cochlear canal is marked in the cochlea. *1* — cochlear canal; *2* — cochlear ganglion; *3* — cochlea; *4* — cochlear nerve; *5* — auditory capsule; *6* — sacculus; *7* — utriculus; *8* — vestibular nerve; *9* — acoustic nerve; *10* — musculus stapedius; *11* — cerebrum.

Рис. 5. Гистотопография периферического отдела слуховой системы в дорсовентральных срезах головы у предплода сивуча (*Eumetopias jubatus*), стадии 18, 19. В улитке отмечена начальная дифференцировка элементов улиткового хода. *1* — улитковый канал; *2* — кохлеарный ганглий; *3* — улитка; *4* — кохлеарный нерв; *5* — ушная капсула; *6* — саккулюс; *7* — утрикулюс; *8* — вестибулярный нерв; *9* — слуховой нерв; *10* — стременная мышца; *11* — мозг.

In otariids and in a walrus, at the 20th stage of development, the vestibular apparatus is twice bigger than the cochlear part, as well as it is in terrestrial mammals; in phocids their size reveals similarities. In cetaceans, the vestibular apparatus is twice smaller than the cochlea. The cellular differentiation of the sensory epithelium of maculae, cristae and the organ of Corti continues. The cochlear and vestibular branches of the auditory nerve are formed.

In the cochlear canal, a spiral limb, a vascular stria and a tectorial membrane are formed. The differentiation of the cells of the organ of Corti continues. The size of the cochlea is increased. At the given stage, the basic process of anatomic formation of the structures of the inner ear has ended.

Discussion

Both in phylogenesis and in ontogenesis the inner ear is the first to form, as it is the core, phylogenetically most ancient formation of the peripheral auditory system. As the development of the inner ear continues, the other parts of the peripheral auditory system of different evolutionary age start to be formed, the most evolutionary young among them is the outer ear.

The comparative analysis of development of the auditory and vestibular structures in representatives of terrestrial, semi-aquatic and aquatic mammals has shown that the formation of these structures occurs in an early prefetal period and is extended in time that is caused by the presence of the heterochrony in the development of the inner ear (Solntseva, 1999, 2002).

In representatives of different ecological groups, in an early embryogenesis, the auditory and vestibular structures are simultaneously separated from each other and reveal similar features in structure. In most of mammals, in the first half of an early prefetal period (stages 13–15), both auditory and vestibular formations have common features in structure. Specific features in the structural organization of the hearing and equilibrium organs are formed in the second half of an early prefetal period (stages 16–20) at similar stages of development and in a certain sequence. Basically, in immature-born species, the anatomic formation of structures of the inner ear comes to an end in an early prefetal period, while the cellular differentiation of the sensory epithelium of the cochlea, maculae and cristae continues up to the early stages of a postnatal ontogenesis. In mature-born species (cetaceans), the differentiation of structures of the inner ear finishes by the moment of birth.

In studied groups of mammals, the features, which are connected with the stages of differentiation of the sensory epithelium of maculae and cristae into the receptor and supporting cells, are revealed. In terrestrial and semi-aquatic mammals (otariids, a walrus), whose way of life to a greater degree is connected with the stay on a firm substratum, the initial cellular differentiation of the sensory epithelium occurs in the utricular macula that indicates the important role of the organ of gravitation in the vital activity of these mammals. The simultaneous cellular differentiation of the sensory epithelium in the saccular and utricular maculae, as well as the similarity of size of the cochlear and vestibular parts of the inner ear in phocids allow for assumption that for these species the organs of gravitation and vibration are equally vitally important. Each of these organs is adapted for functioning in the habitat with certain physical properties. In absolute hydrobionts (cetaceans), the initial cellular differentiation of the saccular macula indicates that in aquatic mammals the organ of vibration carries out a more important function in comparison with the organ of gravitation.

All parts of the peripheral auditory system are multicomponent formations. As against the outer and middle ear, which are characterized by very diverse structural variations and a wide spectrum of the adaptable transformations connected with peculiarities of the species ecology, the inner ear in representatives of different ecological groups, in spite of the variety of functions, keeps a monotonous structural organization. Usually, both in the cochlear and vestibular analyzers the topography, form and size of separate components vary.

In the echolocating mammals, the substantial growth of the cochlea's size in comparison with the size of the vestibular apparatus, as well as other features in the structure of the cochlear canal and the cells of Corti's organ's, serves as the adaptation of the cochlea to the perception of frequencies of a wide range, including ultrasounds (dolphins, bats). At the same time, a huge cochlea and extraordinary small size of the vestibular apparatus in absolute hydrobionts with a various orientation of hearing can serve as the adaptations of the inner ear to aqueous medium, as hearing in the aquatic mammals dominates among distant analyzers, thus providing the survival of these animals in conditions of constant dwelling in aquatic environment.

Comparative study of the peripheral auditory system's development allowed to reveal the general regularities of its formation in ontogenesis of representatives of various ecological groups: (1) in most mammals at the early stages of development (st. 13–16), the peripheral auditory system has common basic features in structure; (2) species-specific features in the structural organization of the peripheral auditory system are formed in the early prefetal period, depending on the frequency tuning of the auditory system in each species; (3) these structural features are caused by habitat peculiarities and develop in parallel from the homologous anlages of the peripheral auditory system in phylogenetically distant and close forms; (4) in mammals, the morphological features of the peripheral auditory system, which were formed in an early prefetal period, continue to develop in a fetal period and during the whole period of a postnatal development.

This work was supported by the International Science Foundation (Project NF 3000). Embryos of cetaceans and pinnipeds were obtained from colleagues at several institutes of the Russian Ministry of Fish Industry (Moscow, Vladivostok, Kaliningrad, Archangelsk, Astrachan). The unique collection of Stenella attenuata was passed to me by the well-know American researcher of marine mammals, Dr. William F. Perrin (La Jolla, USA). I am grateful to all colleagues for providing the embryological material.

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