

# Adaptive Features of the Middle Ear of Mammals in Ontogeny

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**Abstract:** The middle ear has been studied in many different species of mammals, showing morphological adaptations in the structures of the middle ear which are characteristic for species of different ecological habitats.

As a result, along with adaptive specializations in representatives of various ecological groups of mammals, the structure of the middle ear maintains a common basic structural pattern in most mammals; in species that are remote phylogenetically but similar in ecological specialization, parallelism in the structure of particular elements of the auditory ossicles are evident, as well as in the way these elements are joined together and attached to the middle ear cavity.

**Key words:** tympanic membrane, malleus, incus, stapes, musculus tensor tympani, musculus stapedius, bulla tympanica

## Introduction

The middle ear structure of mammals has attracted the attention of many scientists for a long time. At present there are numerous fundamental works devoted to comparative and anatomical studies of middle ear elements from mammalian species of many different orders (CLAUDIUS 1867, DORAN 1878, DENKER 1899, 1901, 1902, BONDY 1907, FREY 1911, CROWE *et al.* 1931, WASSIF 1948, 1950, YAMADA 1953, WEBSTER 1960, 1966, WERNER 1960, HENTZEN 1970, SOLNTSEVA 1975, 1995, 2006).

Based on the available literature and his own data, German researcher FLEISCHER (1973a, b) provided a comparative anatomical study of the middle ear in representatives of different orders of mammals. Fleischer's data, along with evidence from the other studies mentioned above as well as novel data presented here form the basis of this study.

During the process of evolution remarkable changes in auditory system development in a number of vertebrates have occurred. Morphological reorganization concern all the parts of peripheral auditory system and, first of all, outer and middle ear as

the earliest phylogenetic formations. For example, in the middle ear instead of one auditory ossicle (collella), inherent for lower vertebrates, three ossicles appear: malleus, incus and stapes. This system of the auditory ossicles has provided a special mechanical system for mammals which is capable to enhance a sound pressure upon an oval window membrane of the inner ear. From evolutionary point of view the transmission of the sound pressure from air to cochlea liquid is the most effective gear in mammals.

The main attention here is paid to marine mammals (cetaceans). This is the least studied order of mammals in this respect but is of great interest both because of the echolocation abilities of dolphins as well as for the way the aquatic environment influence how the adaptive features develop in the structures of the auditory system in aquatic mammalian species.

## Material and methods

The following species of mammals (in postnatal ontogeny) were studied: Insectivora (*Talpa europaea*

Linnaeus 1758), Chiroptera (*Rhinolophus ferrumequinum* Schreber 1774), Rodentia (*Mycastor 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: *Callorhinus 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 formes: Rodentia – laboratory rat (*Rattus norvegicus* Pallas 1779), guinea pig (*Cavia porcellus* Linnaeus 1758), Artiodactyla – pig (*Sus scrofa domestica* Linnaeus 1758), semi-aquatic formes: Pinnipedia – Otariidae: Steller sea lion (*Eumetopias jubatus*), Phocidae: ringed seal (*Phoca hispida*), bearded seal (*Erignathus barbatus*), and Odobenidae: walrus (*Odobenus rosmarus divergens*), aquatic formes: 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 ethanols, 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 lengths of embryos at different stages of embryogenesis vary widely among mammals. To examine embryos from different species, developing structures of the vestibular apparatus were compared with the development of acoustic structures at the same stage of development. For convenience, the stages of development described in certain terrestrial species by DYBAN *et al.* (1975) were used.

## Results

The peripheral part of the auditory system includes three components – outer, middle and inner ear. The outer and middle ear receive sounds from the environment and transmit them to the inner ear. A sound wave enters the outer ear, causing the tympanic membrane to vibrate. Through a chain of auditory ossicles, these vibrations are transmitted to the inner ear, where the mechanical...

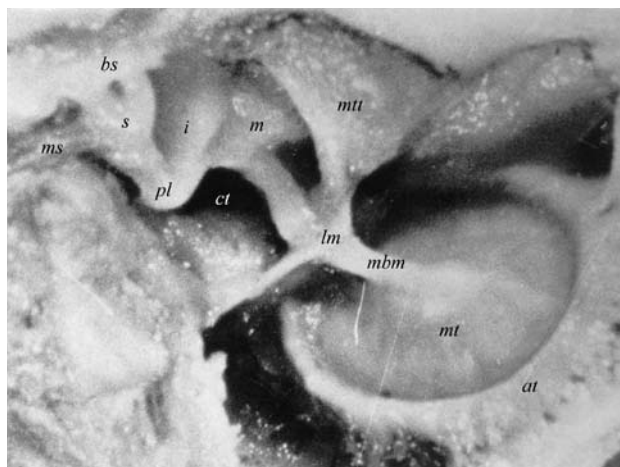
A combination of literature and original data allows for a comparative analysis of the structure and topography of the middle ear elements in mammals belonging to different orders.

The middle ear of mammals contains a tympanum (cavum tympani), which by means of an auditory tube is connected with the gullet cavity, tympanic membrane and a chain of the auditory ossicles (ossicula auditus): malleus, incus and stapes (Fig. 1). Ligaments and two muscles of the middle ear (m. tensor tympani, m. stapedius) are bound to the auditory ossicles. Muscles of the tympanum regulate the transition of auditory energy and preserve the inner ear from super-intensive sounds. Ligaments keep auditory ossicles in a definite position.

The tympanic bulla of mammals represents a tympano-periotic complex. The tympanic bone is composed of thin osseous walls, forming the tympanum, in which the elements of the middle ear are localized. The inner ear is situated in the periotic bone.

In mammals, a different extent of fusion of the periotic and tympanic bones and also for the tympanic bone with cranial bones, is noted. Similarly, in Carnivora, Rodentia and Pinnipedia (Otariidae) orders the tympanic bulla grows together with the cranial bones. In phocids it is detached and does not knit with them completely. In odontocetes the tympanic bulla is separated from the skull, to which it is hung up by means of a short ligament, while in mysticetes it grows together with cranial bones at more or less extent, but doesn't participate in the cranium formation, it is separated from cranium by the system of sinuses (YAMADA 1953).

The tympanic bulla of cetaceans is the most unique in its structural organization compared to other species of mammals. It consists of a tympano-periotic complex. The tympanic bone is composed of thin osseous walls, forming the tympanum, in which the elements of the middle ear are located. In



**Fig. 1.** Arrangement of the middle ear structures in the tympanum of the harp seal, *Pagophilus groenlandicus*. Anatomical preparation.

**mt** – tympanic membrane, **at** – tympanic ring, **mbm** – manubrium mallei, **m** – malleus, **lm** – ligamentum mallei, **i** – incus, **pl** – pr. lenticularis, **s** – stapes, **bs** – footplate of stapes, **ms** – m. stapedius, **mtt** – m. tensor tympani, **ct** – tympanum.

the family Delphinidae, the tympanic bulla is organized according to a common scheme.

The tympanic bulla of the river dolphin and in the marine species of dolphins is formed by tympanic and periotic bones, which, having joined together in the region of pr. posterior, pr. sigmoideus, and pr. tubarius, form a single tympano-periotic complex. In contrast to those of the marine species of dolphins, the tympanic bulla of the river dolphin is formed by thick osseous walls. The tympanic and periotic bones of these species are relatively closely attached to each other. The tympanic bone is massive, twice the size of periotic bone. It is pear-shaped and is divided into the medial and lateral lobes. The lateral lobe is more prominent compared to the median one. A cross furrow extends along the middle part of the lateral lobe, dividing this lobe into two equal parts. This feature is not found in any marine dolphin species.

In marine species of dolphins, the tympanic bulla is formed by more thin and rather fragile osseous walls. The tympanic and periotic bones appear to be isolated from each other and are approximately equal in size. The tympanic bone has a lengthened form with well-developed medial and lateral lobes. This is especially evident when comparing the dorsal and parasagittal surfaces of the tympanic bulla in river and marine species of dolphin.

A comparison of the ventral surface of tympanic

bullae in river and marine species of dolphins shows that in river dolphins, the periotic bone is more wide and short and has a smoothed surface. In marine species it is lengthened and has a ribbed surface, which is stretched along the whole length of the periotic bone.

In river dolphins, a sigmoid process is well developed; it is thickened, lengthened, separated from the other structures, and it is twice the size of this process in marine species of dolphins. The medium and posterior processes of the periotic bone of river dolphins are developed less than those of marine species of dolphins, in which they are massive and broad. The anterior process in a river dolphin is sharp, while in marine species it has a spade-shaped form with smooth and rounded edges. The posterior process of the periotic bone in river dolphin is smooth and is not defined, while in the marine dolphins this process is hypertrophied, and has a few small and thin thorns on the top. A deepening for the attachment of m. stapedius of the middle ear in river dolphin is oval and profound; in marine species, it is wider, not profound and has no distinct borders. There is an elliptic foramen on the posterior surface of the tympanic bulla of all three species studied. It is rounded in the river dolphin and oval (and almost two times larger) in the marine species of dolphins. In all species of Delphinidae, a tubarius arm (an additional ossicle) is located in the area of the anterior surfaces of the tympanic bulla. This arm is equally well developed in the river and marine species of dolphins.

The tympanic bulla in dolphins is surrounded by a system of sinuses, which have an osseous base and are covered by a mucous membrane, which includes multiple protein glands. There are some suppositions that sinuses are the result of the tympanum overgrowth (BOENNINGHAUS 1903).

The isolation of tympanic bulla from the skull bones is provided by the sinuses, which surround the tympanic bulla from every quarter and are filled with fat emulsion foam. The foam consists of the smallest air bells which are good sound insulators, and, as a result, all acoustic oscillations which come from the skull bones do not reach the inner ear. To the cochlea, the only way is left – through the outer ear and the system of the auditory ossicles (FRASER, PURVES 1960, SOLNTSEVA 1995). Thanks to this separate sound reception by each of the auditory receivers,

dolphins are able to hear binaurally which allows them to determine the direction to a sound source (KELLOGG 1958). In addition, the tympanic bulla in odontocetes can perform slight movements relative to the skull with the help of muscles; as a result, the stereophonic (volumetric) reception of the reflected echo signals may be provided.

Through the sinus system, an adipose tension is stretched down to the lower mandible, through the pterygoid sinus and reaching the lateral side of the tympanic bulla. This connection of tympanic bulla with the lower mandible is expressed at a different degree in various species and is named as a sound crater or canal (BOENNINGHAUS 1903). The odontocete sinuses have been speculated to fill roles of compensation for specific gravity (DENKER 1902) and pressure regulators in the middle ear (KELLOGG 1928).

The tympanic bone in mysticetes forms a heavy compact tympanic bulla, which knits with periotic bone only in two points. As for odontocetes, in mysticetes the tympanic bulla does not participate in the formation of the skull wall, from which it is separated by the system of sinuses. The sinuses of mysticetes are constructed in a simpler way than in odontocetes. The system of sinuses is composed of the pterygoid and peribullar sinuses (BOENNINGHAUS 1903).

The tympanum is located between the external auditory meatus and the inner ear labyrinth, and is separated from these formations by thin membranes. Six walls are discernible in the tympanum: an anterior wall, where the orifice of the Eustachian tube is situated; a posterior wall, having a foramen leading into antrum mastoideum; medial, upper, and lateral walls, formed by the tympanic membrane; and a bottom wall. The medial wall is formed by a labyrinth capsule and separates the middle ear from the inner ear. This wall contains the oval and round windows. The upper wall has a form of an osseous partition.

In most mammals, the tympanum is covered by a thin mucous membrane due to a number of permeating blood vessels. In forms living in aquatic environment, the mucous membrane of the tympanum is strongly thickened because of the abundant blood vessels that penetrate its medium layer.

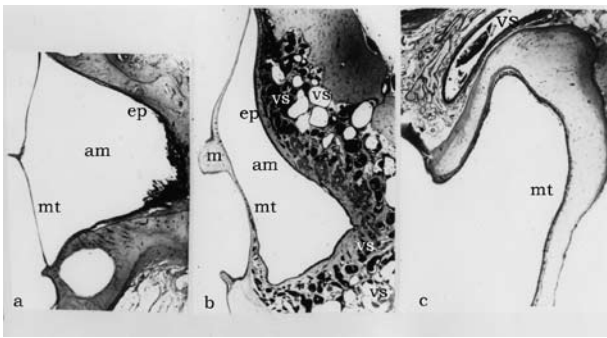
In several semi-aquatic (sea otter, pinnipeds) and aquatic (cetaceans) forms venous sinuses are located in the walls of the tympanum, concentrated mainly in the osseous part of the external auditory

meatus (SOLNTSEVA 1988 b). In cetaceans most of the tympanum is filled with a cavernous plexus, consisting of a dense net of blood vessels. The venous sinuses are located in the area of the tympanic membrane (Solntseva 2006).

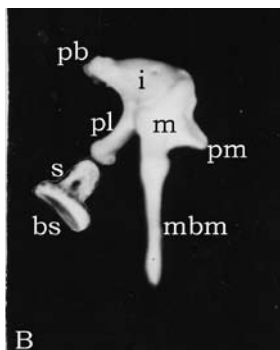
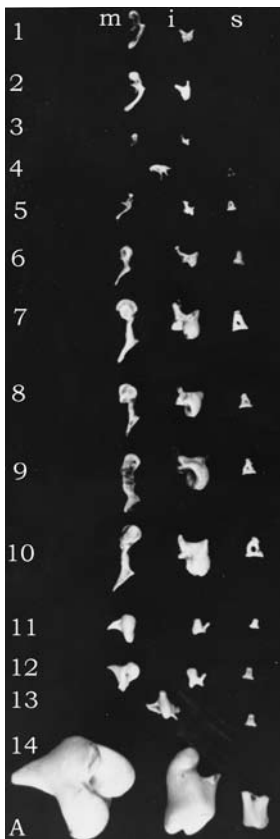
Several types of tympani are evident in different species (SIMKIN 1977). A spherical type is inherent to the species that use ultrasound in orientation and echolocation (forest and home mice, jerboa, red field voles, bats, cetaceans, pinnipeds). A spongy type of tympanum occurs in the species that live in the conditions of a dense environment (subterranean and aquatic forms) or inhabit solid and rocky substrates (gray field voles, steppe lemmings, pika, weasels, stoats, ermines). A chamber type of tympanum is inherent to ground squirrels and dormice. The tympanum of this type is divided by thin osseous partitions into a row of open-ended chambers. The coarse-cellular type is similar to the chamber type and is found in squirrels, chipmunks, marmots and martens. The tympanum is partitioned with poorly defined osseous ribs.

The middle ear is separated from the outer ear by a tympanic membrane, stretched onto a tympanic ring (anulus tympanicus) (Fig. 2). The tympanic membrane is formed by three layers. Its basis is composed of radially and circularly directed connective-tissue fibers, which grow together with the periosteum of the malleus handle (manubrium mallei), set into the tympanic membrane. From inside, the tympanic membrane is covered by a mucous membrane (stratum mucosum), formed by a pavement epithelium; from the surface, the tympanic membrane is covered by a lacking hair, glands and papillary layer tegument (stratum cutaneum). The tympanic membrane has the shape of a cone with the top directed into the tympanum. A stretched part (pars tensa) and a small, unstretched part (pars flacida), which is more flexible due to the lack of the basis, are discernible on the tympanic membrane.

In most mammals the tympanic membrane is round in shape, slightly stretched into a cone and very thin. A significantly thickened tympanic membrane occurs in semi-aquatic and aquatic species (Fig. 2). The tympanic membrane of dolphins is not connected directly to the handle of the malleus, as it usually appears in most mammals. They are connected by a triangular ligament fixed asymmetrically to the tympanic membrane, which is round and thick.



**Fig. 2.** The tympanic membrane of the different species of mammals. Histological preparations. Staining with hematoxylin-eosin. Increase 25x. **a** – nutria, *Myocastor coypus*, **b** – harp seal, *Pagophilus groenlandicus*, **c** – bottlenose dolphin, *Tursiops truncatus*. **mt** – tympanic membrane, **am** – external auditory meatus, **ep** – epidermis, **m** – malleus, **vs** – venous sinuses.



**Fig. 3.** The auditory ossicles of various mammal species (**a**). Vertical direction – names of auditory ossicles (m – malleus, i – incus, s – stapes), horizontal direction – animal species. Increase 1.2 x.

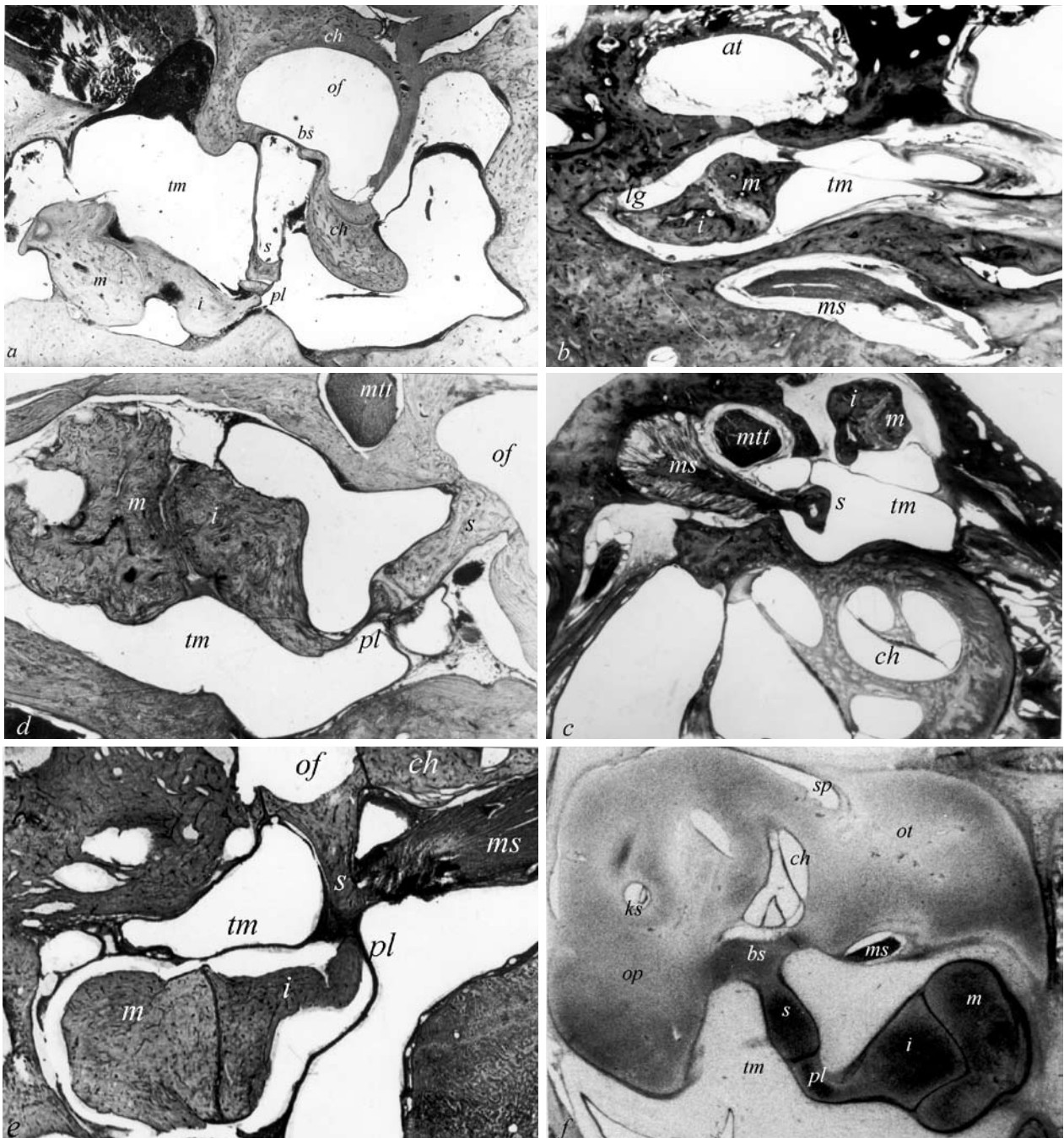
1 – common fox (*Vulpes vulpes*); 2 – common dog (*Canis familiaris*); 3 – american mink (*Mustela vison*); 4 – nutria (*Myocastor coypus*); 5 – sea otter (*Enhydra lutris*); 6 – Steller sea lion (*Eumetopias jubatus*); 7 – harp seal (*Pagophilus groenlandicus*); 8 – Caspian seal (*Pusa caspica*); 9 – Largha seal (*Phoca vitulina*); 10 – insular seal (*Phoca insularis*); 11 – common dolphin (*Delphinus delphis*); 12 – bottlenose dolphin (*Tursiops truncatus*); 13 – harbour porpoise (*Phocoena phocoena*); malleus missing, or fused with incus? 14 – fin whale (*Balaenoptera physalus*); **b** – chain of auditory ossicles of the northern fur seal, *Callorhinus ursinus*. Knitting of the malleus and incus in the area of incudo-malleal articulation is shown.

In mysticetes, the tympanic membrane consists of two parts: a fiberless ‘glovish outgrowth’, protruding into the cavity of the external auditory meatus, and its deviating fibrous ligament, which is attached to a cylindrical handle of malleus. The fibrous ligament of mysticetes is analogous to the triangular ligament of odontocetes. The tympanic membrane of the right whales in its structure and form occupies an intermediary position between that of the family Balaenopteridae and that of the suborder Odontoceti (FRASER, PURVES 1960).

A reduced tympanic membrane surface is evident in the forms capable of echolocation or ultrasound orientation (shrews, bats, some species of pinnipeds, cetaceans).

The tympanic membrane of both river and marine dolphin species is considerably modified compared to those of terrestrial and semi-aquatic species. It is rounded, convex, and very thick and is not directly joined to manubrium mallei. They are connected through an elastic triangular ligament asymmetrically attached to tympanic membrane. The tympanic membrane-ligament forms an additional lever in the chain of ossicles, which considerably increases the coefficient of acoustic pressure transmission through the middle ear underwater. The elasticity of the tympanic membrane allows it to transmit a wide range of sound signals, including ultrasounds. At the same time, the dolphin tympanic membrane may be thickened and elastic for another reason: these structural peculiarities protect it against damage caused by rapid changes in pressure upon rapid diving to large depths, especially in marine species.

The morphological variations of the auditory ossicles of mammals are more complicated than in representatives of other classes of terrestrial vertebrates (Fig. 4 a, b, c, d, e, f). The malleus is differentiated into the head of the malleus (capitulum mallei), neck of the malleus (collum mallei) and handle of the malleus. The head of malleus bears an articular surface for a junction with incus. At the medial side of the handle of malleus, near its neck, a small muscular arm (pr. muscularis) is located, which serves for the fastening of a tensor muscle of the tympanic membrane. At the dorsal edge of the handle of the malleus, a short arm (pr. brevis) is fastened; and at the dorsal edge of the neck of the malleus, a long arm (pr. longus), which is reduced in most mammals to a small, sharp pr. gracilis, is connected with the



**Fig. 4.** Histological preparations of middle ear in various species of mammals. Staining with hematoxylin-eosin. Magnification 25 x.

**a** – fox, *Vulpes vulpes*, **b, c** – northern fur seal, *Callorhinus ursinus*, **d** – harp seal, *Pagophilus groenlandicus*, **e** – bottlenose dolphin, *Tursiops truncatus*, **f** – beluga, *Delphinapterus leucas*'s embryo (embryo length is 250 mm). The auditory ossicles arrangement in the cavity of the middle ear is shown; the malleus and the incus are connected with each other at the right angle, what disables them to perform independent from each other movements. **M** – malleus, **I** – incus, **s** – stapes, **pl** – pr. lenticularis, **bs** – footplate of stapes, **tm** – tympanum, **ch** – cochlea, **op** – periotic bone, **ot** – tympanic bone, **sp** – peribullar sinus, **ks** – semicircular canal, **at** – tympanic ring, **ms** – m. stapedius, **mtt** – m. tensor tympani, **of** – fenestra ovalis, **lg** – ligamentum of short arm of incus.

help of a ligament within the tympanum's wall. In other species, the long arm is large in size and connects rigidly with the wall of the tympanum. The m. tensor tympani is attached to the handle of malleus,

under whose contraction the tympanic membrane is pulled inside and, through a system of auditory ossicles, presses the stapes into an oval window. The malleus is fixed in a definite position with the help

of three ligaments: a fore bundle that reaches fissura Glasseri and gets attached to the pr. anterior of malleus; a ligament located in the area opposite the neck of malleus; and an axial ligament representing the axis, around which malleus rotates.

The incus has a body and two components: the long arm (*crus longum*) and the short arm (*crus breve*). The long arm is stretched parallel to the handle of the malleus. Its lower end is curved, forming a junction with the stapes with the help of a lenticular arm. The short arm is located in the deepening of the osseous tympanum, where it is bound by a ligament.

The stapes is composed of a body formed by two crura, of the head (*capitulum stapedis*) and a footplate (*basis stapedis*). The head of the stapes is connected with the long arm of the incus. The crura form an inter-ear area. The footplate of the stapes is oval and is kept in an oval window of the inner ear with the help of a ring-shaped ligament. *M. stapedius* is attached to the head of the stapes, lying in the area of the posterior wall of the tympanum.

Although the organization of the principle auditory ossicles is similar in all mammals, characteristic structural traits are revealed in different ecological groups (Fig. 3). Structural variation is apparent with changes in size, element form and weight ratio of the auditory ossicles, as well as in the form of their junction and attachment to the tympanum. In different orders, an accretion of malleus and incus is noted (*nutria*, fur seal). In most mammals, the long arm of malleus grows together with the wall of the tympanum, and its form is significantly varied. In some insectivores and bats, *pars transversalis* of the malleus is well developed. The incus is small, articular surface in the area of incudomalleal articulation is diminished and the muscular arm is located at the occipital part of the *pars transversalis*.

In different members of the orders Rodentia, Perissodactyla and Carnivora, the long arm of malleus is diminished or completely reduced (the genera *Cricetus*, *Rattus*, *Tapirus*, *Vulpes*). Also in these forms, a well-defined *pars transversalis* of the malleus and a shortened articular surface between malleus and incus are inherent (Fig. 4a). A well-developed *pars transversalis* of malleus and an enlarged incus are characteristic for cetaceans, in which great rigidity in junction between the malleus and incus is revealed. The handle of malleus in cetaceans is reduced to a round prominence in odontocetes and to a conical process

in mysticetes. An enlarged handle in the suborder Odontoceti, in contrast to the suborder Mysticeti, occurs due to the muscular arm (YAMADA 1953).

In some members of orders Artiodactyla and Carnivora, *pars transversalis* of malleus is reduced, but the surface of incudo-malleal articulation and the size of incus are enlarged (*Martes*, *Sus*). The incus reveals variations in different mammals both in structure and size of the body and in topography of its processes. In most mammals, the long and short arms are located at an angle to incus body. In Phocidae, they are located almost parallel to each other. A sharply thickened and elongated long arm of incus is evident in cetaceans. In mysticetes, the short arm is almost reduced, depriving the incus from support on the wall of the tympanic bone and indicating that, in mysticetes, the incus can function in a slightly different way than in odontocetes (YAMADA 1953).

The structure of the stapes varies significantly among species. In order Monotremata, the stapes is not differentiated into crura and appears in the form of a column. A noticeable narrowed stapes is inherent to mole and, especially, genus *Heliophobius* (Fleischer 1973a, b). Differentiation of the stapes is absent from odontocetes and, as a result, the stapes attains the form of a rounded cone (Fig. 4d). The stapes of mysticetes is differentiated into crura, and the space between them is covered with an osseous plate. In dolphins, the head of the stapes, lacking a noticeable neck, goes into the stalk of an oval form, which is broadened at the base and is precisely adjusted to the oval window (YAMADA 1953). Such a location of the stapes base in the oval window provided grounds for several researchers to speculate falsely about the growth of the stapes in the oval window of the dolphin's inner ear (BOENNINGHAUS 1903). In pinnipeds and sea-otters, the compact and heavy stapes shows strongly thickened crura, which form a small area between them. In otariids (Northern fur seal, Steller sea lion), some differentiation of the stapes into the crura is evident in the complete absence of an area between the crura. In all small mammals, the stapes is fragile and light (*Suncus*, *Crocidura*, *Chiroptera*, *Microtus*, *Spalax*), and in most mammals, the stapes is hollow. The base of the stapes may be flat, concave or oval. Species of the genera *Thylogale*, *Heliophobius* and *Loxodonta* have a stapes with a flat base. A concave base is inherent to the genera *Nyctalus* and *Tapirus*. A prominent base is characteristic of *Cynocephalus*,

*Microtus*, *Mustela* and *Procavia*. The shape and size of the base of the stapes can also vary. In the orders Monotremata, Chiroptera and Cetacea (Odontoceti), the base of the stapes is round in shape. The elliptical contour is inherent to the stapes base of some members of Insectivora, Primates, Rodentia and Perissodactyla.

The auditory ossicles in dolphins have specific structural features, joint location and the way of fixation in the tympanum (Fig. 5). In the river dolphin, ossicles are larger than in the marine dolphins; however, they are very similar to each other in the structural organization. In both the river dolphin and the marine dolphins, malleus has a small head with two faces located at a right angle for junction with incus. The neck of malleus is poorly developed. The manubrium malleus is reduced to a small rounded formation. Pr. gracilis of malleus has the shape of a triangle with a sharp vertex fused with the tympanic bone, which is not the case with most terrestrial species, in which the junction of this process with the tympanic bone is elastic (via a ligament). This allows the malleus to oscillate independently of the incus. In dolphins, malleus and incus are joined together rigidly, at a right angle; as a result, they function as a single structure. The incus of river dolphin is more massive than that of marine species. Pr. longum of the incus of all three species is hypertrophied, and the pr. breve is a thin osseous structure; however, both processes

are of the same length. The stapes of all three species is small, its head is poorly developed and is shaped as a smoothed cone. The body of the stapes is not differentiated into arcs, as is the case with most mammals, as has the form of a plug. The head of the stapes is joined to pr. lenticularis of incus, which is well developed. The base of the stapes is rounded and tightly fits in the oval foramen of the inner ear.

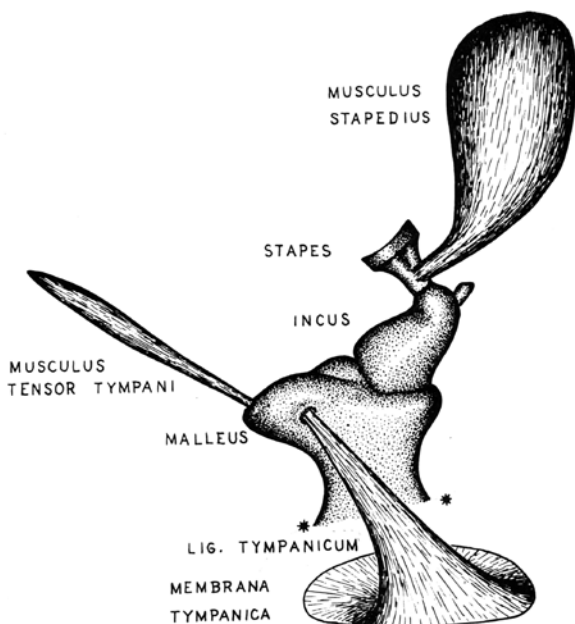
### Prenatal development of the middle ear of mammals

Here a comparative embryological description of the peripheral auditory system is presented, to our knowledge for first time. This was carried out on representatives of terrestrial, semi-aquatic and aquatic mammals with unique embryonic collections of cetaceans and pinnipeds and has allowed for the study the structural organization of the outer, middle and inner ears in representatives of various ecological groups in more detail, and also to determine stages of formation of morphological adaptations and other basic structures revealed by us early (SOLNTSEVA 1993, 1999).

The pair anlage of a membranaceous labyrinth is marked at the stage of two-three pairs of somites (WILSON 1914). Further along, at the stage of six to nine pairs of somites, the auditory placode is formed (KAPPERS 1941), and at the stage of 14 to 15 pairs of somites, the auditory pit is formed, from which an acoustic vesicle develops at the stage of 20 pairs of somites (forelimb bud, stage 13) (TITOVA 1968). At the same stage, in all investigated species, the bud of the auditory ossicles in the form of a mesenchymal condensation was found.

The middle ear of mammals is formed by a protrusion of the first pharyngeal recess, the endoderm of which will be transformed into a common tube-tympanic protrusion. It has already been mentioned that in all investigated species, the bud of the auditory ossicles appears at the 13th stage in the form of a condensation of a mesenchyme and is located separately from the temporal pyramid bud. At the 16th stage, in the buds of the auditory ossicles, their contours, which are connected among themselves continuously, become visible. At this stage, the tympanum is represented by a narrow, blind canal, which is located below the bud of the auditory ossicles. The bud of a tympanic membrane is marked.

At the 17th stages, each of the buds of the auditory ossicles is represented by an already independ-



**Fig. 5.** Scheme of the structure and connection of the middle ear elements of the bottlenose dolphin, *Tursiops truncatus* (Fleischer, 1973).

ent formation; their base is formed by the immature precartilaginous tissue. Malleus has a small size. Compared to malleus, incus is large. The stapes is differentiated into crura; bottom lamina is of an oval form. The size of the tympanum is increased. The tympanic membrane is thick and very friable. At the same stage, the tympanic membrane acquires a three-layer structure and is located almost horizontally on the lateral wall, forming one of the tympanic bone sides.

At the 18th stage, the process of cartilaginitization starts in the center of each bud of the auditory ossicles and spreads gradually to their periphery. The auditory ossicles are surrounded by perichondrium, which consists of small flat cells – chondroblasts. Due to the perichondrium, the places of

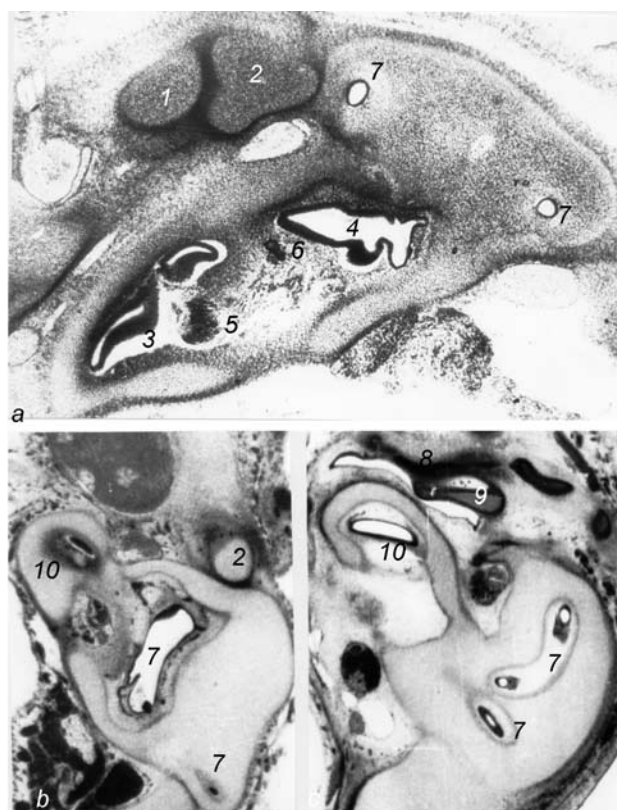
junction of the auditory ossicles are well noticeable. At the same stage, the formation of the features connected with interposition of the auditory ossicles is marked (Fig. 6-12). The auditory ossicles change position due to their turning around the sagittal and frontal axes of the animal's body. The stapes is located more caudally in relation to malleus and incus. As a result of the turning, the bottom lamina of the stapes appears to be located caudally. The auditory ossicles are increased in size. In malleus, a head, a neck and a handle are well-expressed. In incus, a body and both processes are formed. In the stapes, there is no differentiation into crura; therefore the stapes acquires the form of a smoothed cone. The basis of the auditory ossicles is formed by a mature precartilaginous tissue. Further, the replacement of the mature precartilaginous tissue by the embryonic hyaline cartilage occurs. The process of cartilaginitization of the auditory ossicles starts in the center of each bud and spreads gradually to their periphery (SOLNTSEVA 1983).

In odontocetes and mysticetes, in early prefetal period, the tympanic membranes-ligaments reveal similarity in the structure at the similar stages of development (Fig. 11, 12), whereas in the fetal period their structure acquires the species-specific features (SOLNTSEVA 1992).

The formation of a cavernous plexus is marked at the 18-19th stages (Fig. 11). The development of the venous and peribullar sinuses occurs a little bit later, beginning from the 21st stage of development. The replacement of the cartilaginous tissue by osseous tissue is marked at the 20th stage in the form of separate centers of ossification in integumentary bones of a cranium, tympanic and petiotic bones. The initial ossification of the auditory ossicles is marked at the 21st stage. The process of formation of the ear muscles and a ring-shaped ligament of the stapes has ended. The aural capsule is formed by a slightly differentiated cartilage.

At 19th stage, in the middle ear, formation of tympanum and cartilaginitization of the auditory ossicles continues. In different species, the replacement of the mature precartilaginous tissue by a primary cartilaginous tissue occurs non-simultaneously.

In the grey rat, the basis of the auditory ossicles is still formed by a mature precartilaginous tissue at this stage. In a guinea pig, the cartilaginitization of malleus has finished, while in incus and stapes, this

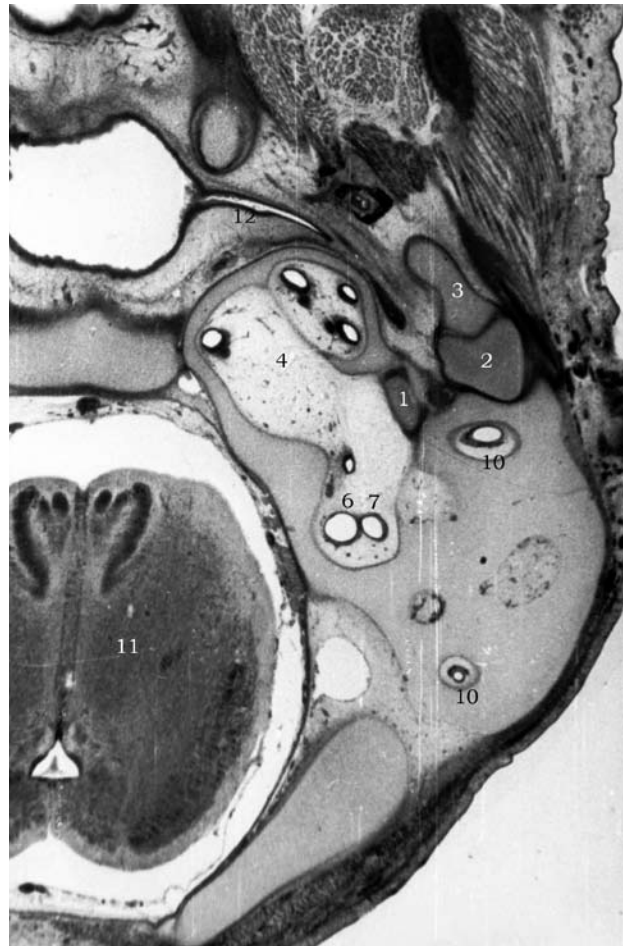


**Fig. 6.** Histotopography of the peripheral auditory system in dorsoventral sections of prefetal heads of the walrus, *Odobenus rosmarus divergens*. a – stages 15; subdivision into cochlear and vestibular parts; auditory ossicles with distinct borders; b – stage 16; a horizontal semicircular canal with a broad lumen; c – stages 16, 17; the manubrium mallei is joined to the tympanic membrane in the tympanum. 1 – malleus, 2 – incus, 3 – cochlear canal, 4 – vesibular apparatus, 5 – cochlear branch of n. acousticus, 6 – vestibular branch of n. acousticus, 7 – semicircular canal, 8 – tympanic membrane, 9 – manubrium mallei, 10 – cochlea.



**Fig. 7.** Histotopography of the peripheral auditory system in dorsoventral sections of prefetal heads of domestic swine *Sus scrofa domestica*, stages 18-19. The manubrium of the malleus is connected to the tympanic membrane along its entire length, as in other terrestrial species. Labels of figures 7-12: 1 – stapes, 2 – incus, 3 – malleus, 4 – cochlea, 5 – cochlear branch of n. acousticus, 6 – utriculus, 7 – sacculus, 8 – tympanic membrane, 9 – external auditory meatus, 10 – semicircular canal, 11 – cerebrum, 12 – auditory tube, 13 – tympanum, 14 – venous sinuses, 15 – m. tensor tympani, 16 – m. stapedius, 17 – ampulla of semicircular canal, 18 – vestibular branch of n. acousticus, 19 – n. acousticus, 20 – vestibular apparatus, 21 – cavernous plexus, 22 – ligamentum mallei.

process has just begun. In a domestic pig, only malleus is cartilaginous. In bats, as well as in rats, the auditory ossicles are formed by a mature precartilaginous tissue. In pinnipeds, the maturation of the auditory ossicles occurs non-simultaneously. First, the malleus matures, then the body of incus, while the lenticular processes of incus and stapes are formed by a mature precartilaginous tissue. In cetaceans, on the contrary, stapes and incus mature first, whereas in malleus, the process of cartilagification only begins. However, by the 20th stage, the replacement of



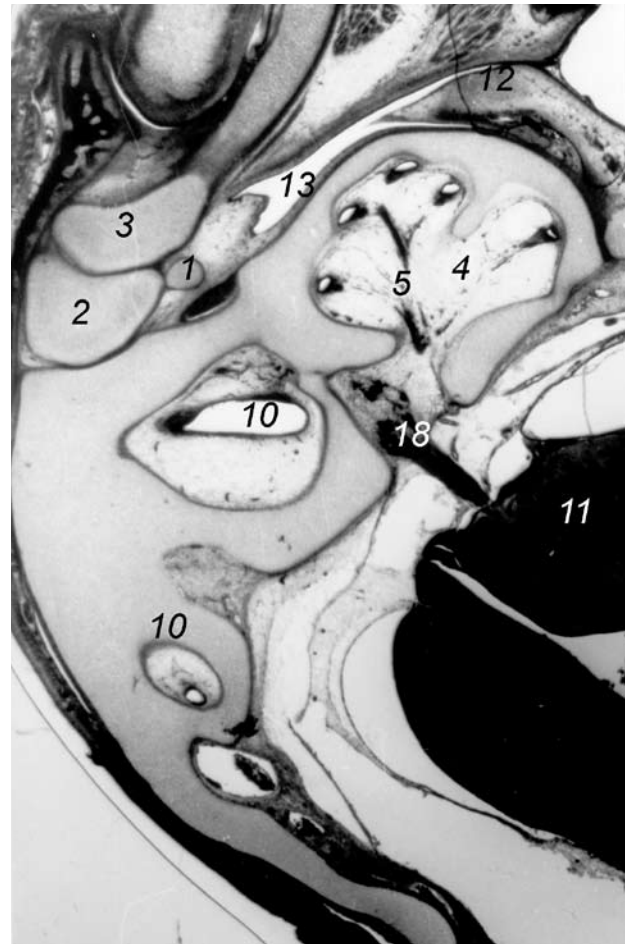
**Fig. 8.** Histotopography of the peripheral auditory system in dorsoventral sections of prefetal heads of the Steller sea lion *Eumetopias jubatus*, stages 18-19. At the same stages, the formation of the features connected with interposition of the auditory ossicles is marked. The auditory ossicles change position due to their turning around the sagittal and frontal axes of the animal's body.

the mature precartilaginous tissue by an embryonic cartilage has been completed.

At the 20 stages, in the middle ear of odontocetes, the formation of a cavernous plexus is marked. In prefetal pinnipeds and cetaceans, in the osseous part of the auditory meatus, the formation of the venous sinuses is marked. The development of the peribullar sinuses located between the cranial wall and tympanic bulla is typical for cetaceans only. In odontocetes (white whale), the separation of the tympanic bulla from the cranium is noticeable.



**Fig. 9.** Histotopography of the peripheral auditory system in dorsoventral sections of prefetal heads of the bearded seal, *Erignathus barbatus*, stages 18-19. The auditory ossicles are massive; the malleus and incus are joined at a right angle.



**Fig. 10.** Histotopography of the peripheral auditory system in dorsoventral sections of prefetal heads of the walrus, *Odobenus rosmarus divergens*, stage 18-19. The auditory ossicles are increased in size; the basis of the auditory ossicles is formed by a mature precartilaginous tissue.

At the 20th stage, the second half of an early prefetal period comes to an end. The basic process of formation of the middle ear has finished (SOLNTSEVA 1990, 1992, 1993).

## Discussion

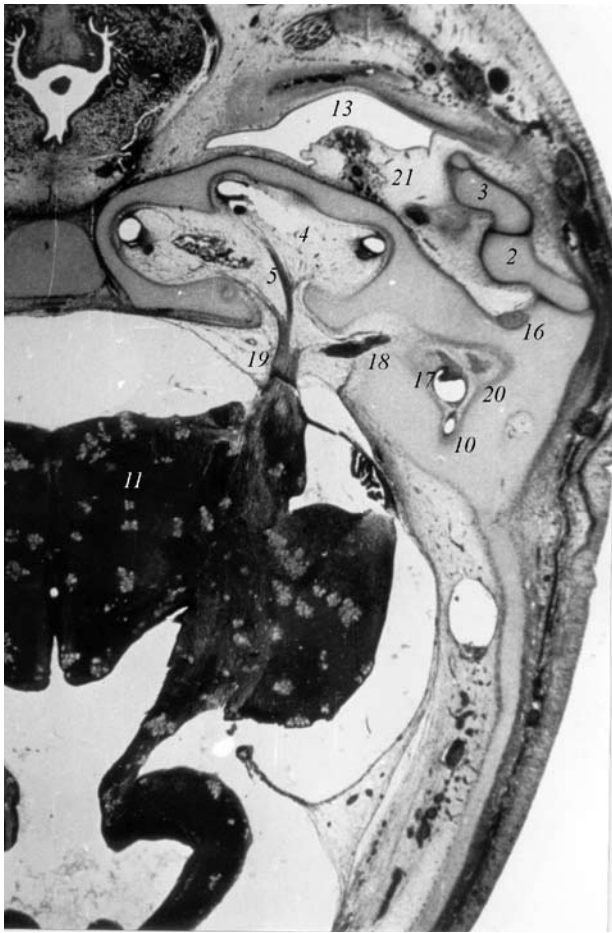
All parts of the peripheral auditory system of mammals are multicomponent formations. As opposed to the outer and middle ears, which are characterized by different structural variations and a wide spectrum of adaptable transformations connected with the peculiarities of species ecology, in the representatives of different ecological groups, the inner ear possesses a variety of functions and therefore keeps a similar structural organization.

The middle ear of different species of mammals is characterized by different degree of fusion of tym-

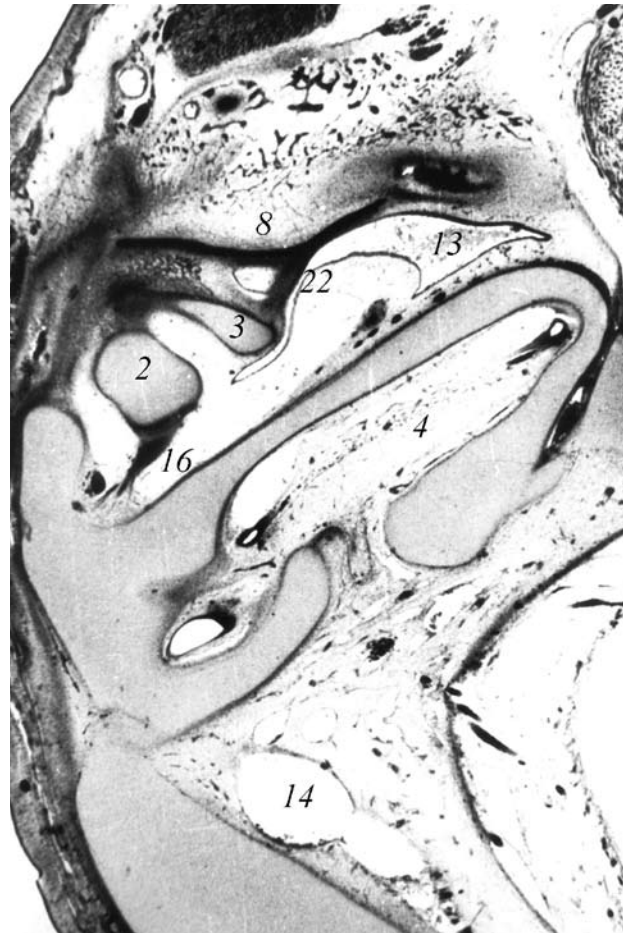
panic bulla and skull bones (FRASER, PURVES 1960). The tympanic bulla in most species fuses with the skull bones and takes part in the formation of the skull wall. It is known that such fusion can provide osseous sound conduction (KUNZE, KIETZ 1949).

Under the influence of acoustic oscillations, the movements of skull bones are transmitted to the osseous labyrinth of the inner ear through the perilymph. This does not occur in some species of bats, rodents (PYE 1968, FLEISCHER 1973 a, b) and odontocetes, due to the fact that the tympanic bulla is acoustically isolated from the skull bones by being flexibly connected to it by means of connective tissue. As a result of this, both ears become the independent receivers and are able to provide the basis for determining directional information of acoustic signals.

The isolation of the tympanic bulla from the skull bones is provided by the sinuses, which sur-



**Fig. 11.** Histotopography of the peripheral auditory system in dorsoventral sections of prefetal heads of *Stenella attenuata*, stages 18-19. The malleus and incus are joined to each other rectangularly, as in the definitive forms; in the tympanum, the formation of a cavernous plexus characteristic of only cetaceans is marked.



**Fig. 12.** Histotopography of the peripheral auditory system in dorsoventral sections of prefetal heads of *Balaenoptera acutorostrata*, stages 18-19. The foci of ossification in the os tympanic are formed; a thick ligament joins a thickened tympanic membrane to the manubrium mallei.

round the tympanic bulla from every quarter and are filled with fat emulsion foam. The foam consists of small air bubbles which efficient isolate for acoustic signals and, as a result, acoustic oscillations from the skull bones do not reach the inner ear. The only way left for sound to reach the cochlea is through the outer ear and the auditory ossicles (FRASER, PURVES 1960, SOLNTSEVA 1995). Thanks to this separate sound reception (i.e., by each of the auditory receivers), dolphins are characterized by the so-called binaural effect which allows them to determine the direction to a sounding object (KELLOGG 1958). In addition, the tympanic bulla in odontocetes can perform slight movements relative to the skull with the help of muscles; as a result, the stereophonic (volumetric) reception of the reflected echo signals is provided.

In non-echolocation mammals, the structure of the middle ear reveals patterns of similarity, although the structure of the tympanum and auditory ossicles varies drastically. For this type of the middle ear structure, the following is typical: knitting of the tympanic bulla with the skull bones, thinning and sharpening of the long arm of malleus down to its reduction and changing to *pr. gracilis*, which is flexibly connected with the tympanum's wall, as well as an extension of the articular surface in the area of the incudo-malleal connection. Thanks to the anatomical reorganization of the external auditory meatus and peculiarities of their location, the main principle of the sound transmission in the middle ear in different habitats remains (SOLNTSEVA 1985a, b, 1986).

The structure of the tympanic membrane in dif-

ferent mammals is particularly worthy of notice. In terrestrial, aerial and subterranean forms, the tympanic membrane is very thin, soft, rounded and slightly elongated to a cone shape. This structure of the tympanic membrane is revealed in some semi-aquatic species (mink, nutria). In aquatic mammals, the tympanic membrane is thickened, and its shape can remain round or oval (Fig. 3). However, in one representative of semi-aquatic species, a Northern fur seal, *Callorhinus ursinus*, the tympanic membrane is thin, but its size is greatly decreased and it is rigidly fixed on the tympanic annulus. This increases its elasticity and provides conditions for the transmission of the frequencies of broad-band frequencies, including ultrasounds (SOLNTSEVA, 1987 b).

The tympanic membrane of cetaceans is greatly modified. The tympanic membrane of mysticetes represents the 'membranous outgrowth' with the fibrous ligament outgoing, from which it fastens to the reduced handle of the malleus (SOLNTSEVA 1988 a).

The tympanic membrane of odontocetes is greatly thickened, rigid and does not have a direct connection with the malleus's handle. This connection is instead carried out by means of the triangular ligament, which asymmetrically fastens to the tympanic membrane. The tympanic membrane and the ligament form the additional lever that is very important for increasing the sound pressure transmission by the middle ear under water (SOLNTSEVA 1990).

On the way of adaptation to the aquatic way of life, the rigidity of incudo-malleal articulation increases (sea otter, pinnipeds). Parallelism in the structure and connection of auditory ossicles can be noticed in phylogenetically distant species (nutria, fur seal), in which the knitting of two ossicles in the area of incudomalleal articulation occurs (Solntseva 1987a). Such rigidity in the articulation of auditory ossicles in aquatic and echolocating species provides the possibility of an unhampered sound signal transmission to the inner ear as it decreases the sound energy loss in articulations and joints, thus creating optimal conditions for sound conduction. In contrast to the pendulous system of the auditory ossicles of terrestrial forms, in aquatic and echolocating species, an elastic vibrating system is evident, which is able to return to its original previous position after the transmission of a sound wave (SIMKIN 1977).

There are various structural variations in the structure of auditory ossicles in different species of

mammals. However, in the row reflecting the way of adaptation to the aquatic way of life, a clear tendency is found, which includes the thickening and shortening of malleus's handle in sea otters and pinnipeds, and its complete reduction in cetaceans. As similarly there is the lengthening and thickening of the malleus's thin process. In the structure of incus, attention is paid to the lengthening and thickening of the long process. In the structure of the stapes, the inter-crura opening in dolphins decreases down to its complete disappearance.

The auditory ossicles show interspecific variability, which becomes apparent in the modifications of size and forms of the auditory ossicles themselves and their processes as well, in the weight ratio of the auditory ossicles, as well as the way of their fastening in the tympanum. The similar type of structure of the middle ear elements can be found in mammals with a high-frequency hearing (shrews, bats, rats, cetaceans, fur seal). In spite of external differences of the auditory ossicles of these animals, they possess a morphological similarity, which becomes apparent in lengthening, thickening and modification of the malleus's long process, its rigid connection with the tympanum's wall, and in the increasing of the rigidity in the area of the incudomalleal articulation.

For maximum transmission of the energy of an incoming signal, it is necessary for specific acoustic resistance of an environment to be coordinated with specific acoustic resistance of the auditory receiver. Such coordination is achieved with the help of variations in the structure of the transmissive apparatus of the middle ear depending on the environment where transmission of acoustic information occurs. For the optimal reception of sound signals in aqueous medium, the sound receiver should possess a high modulus of elasticity, which is provided by the rigidity of auditory ossicles's conjunction with each other and their fastening in the tympanum. For example, the Northern fur seal's malleus and incus form a united incudomalleal complex as both ossicles are fixedly joined with each other and function as a single unit. The broadening in ultrasonic range causes the increase of resonance frequency of natural oscillations of the auditory ossicles as well as the increase of the tympanic membrane's elasticity (SOLNTSEVA 1990, 1995).

In addition to sound conduction, the middle ear of mammals carries out a precautionary function by decreasing the energy of the incoming signal to the

inner ear. This function is enabled by the contraction of the middle ear muscles – m. tensor tympani and m. stapedius – which are well developed in echolocating species (dolphins, bats). By means of the tympanic membrane's and the auditory ossicles's tension, the muscles of the middle ear create conditions for ultrasound conduction; relaxation of these muscles preserves the cochlea from super-intensive signals. It is assumed that the muscles of the middle ear are able to provide tuning of the auditory system to certain frequencies (BLAIR 1964).

The comparative morphological analysis of the middle ear of the river dolphin and marine species of dolphins has demonstrated that this organ has a common general structure characteristic of all representatives of the family Delphinidae and has some species-specific structural features related to ecological characteristics.

The upper limit of acoustic perception, as well as the highest-sensitivity frequency, in the river dolphin is considerably lower than in the marine species; therefore, the structure of the tympanic bulla of *Inia geoffrensis* has some specific features, which are apparently related to the ecological specificity of this species, namely, the functioning of the organ of hearing in a highly noisy and littered environment. By the littered environment, I mean that the water is mixed with air bubbles and silt and sand particles, which considerably deteriorates echolocation in the river by interfering with the perception of reflected echo signals. Therefore, the echolocation signals may decay over longer distances. This may be one of the reasons why the echolocation receiver of the river dolphin may operate at relatively short distances, with a highest-sensitivity frequency of about 20-60 kHz.

The specific structural characteristics of the tympanic bulla of marine species of dolphins may be regarded as morphological adaptations that can improve the reception of echolocation signals by the acoustic receiver at both short and long distances under the ocean conditions, with a highest-sensitivity frequency of 65-70 kHz.

Therefore, turning to aquatic way of life, following adaptations of the middle ear's structure are revealed: (1) modification of relative size and forms of particular elements of auditory ossicles: thickening of malleus's handle down to its complete reduction in cetaceans; lengthening of incus's long process and decreasing of the inter-crua opening down to its complete reduction in odontocetes; (2) significant increase of the rigidity in incudo-malleal articulation; (3) modification of weight ratio in the system of auditory ossicles; (4) drastic thickening of mucous membrane covering the tympanum due to the increase in amount of blood vessels in its middle layer; (5) relative thickening of tympanic membrane especially in cetaceans due to development of connective tissue's elements; (6) development of venous sinuses which are concentrated near tympanic membrane and in the walls which form tympanum; (7) development of cavernous plexus which is typical to cetaceans only.

Comparative studies of middle ear's development presented here revealed 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 middle ear has common basic features in structure; (2) species-specific features in the structural organization of the middle ear are formed in the early prefetal period (according to periodization of Schmidt 1968), depending on the frequency tuning of auditory system in each species; (3) these structural features are caused by habitat peculiarities and develop in parallel from the homologous rudiments of the middle ear in phylogenetically distant and close forms; (4) in mammals, the morphological features of the middle ear, which were formed in an early prefetal period, continue to develop in a fetal period and during the early period of a postnatal development.

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