

# Structural and Functional Organization of Sound-Generation and Sound-Perception Organs in Dolphins

Galina N. Solntseva<sup>1</sup>, Vyacheslav A. Rodionov<sup>2</sup>

<sup>1</sup> A. N. Severtsov Institute of Problem Ecology and Evolution, Russian Academy of Sciences 33, Leninsky Prospekt, Moscow, 119071 Russia; E-mail: g-solntseva@yandex.ru

<sup>2</sup> M. V. Lomonosov Moscow State University, Moscow, Russia

**Abstract:** A comparative morphological study of the sound-generation and sound-perception organs in dolphins was conducted. The exact conformity of the lateral edge of premaxillary sacs with the size and outer configuration of ventral valves having lip-shaped apophyses, the location of inferior vestibules and the entries to the nasofrontal and accessory sacs, and also some other peculiarities indicate that the complexity and fineness of organization of this part of air pathways are connected with sound – generation and are not necessary for breathing. The role of this complex in sound generation is also manifested by the fact, that the dolphins, which do not have it (river dolphin, porpoise), demonstrate much poorer sound repertoire, compared to the species, which possess it (white whale, bottlenose and common dolphins). In echolocating mammals, the substantial growth of the cochlea's sizes in comparison with the sizes of the vestibular apparatus, as well as other features in the structure of the cochlear canal and the cells of the organ of Corti serve as the cochlea's adaptations to the perception of frequencies of a wide range, including ultrasound (dolphins, bats). At the same time, the large cochlea and the extraordinarily small size of the vestibular apparatus in absolute hydrobionts, which possess varied orientation of hearing, can be considered to be the adaptation of the inner ear to aquatic life, as the hearing of aquatic mammals dominates among distant analyzers, thus providing the survival of these animals while dwelling in an aquatic environment.

**Key words:** epicranial air sacs, naris, nasofrontal sac, dorsal sac, sacssory sac, premaxillary sac, auditory organ

## Introduction

Cetaceans are one of the two orders of modern mammals fully adapted to aquatic living. However, besides common morphological features of all the order representatives, each of the two suborders has peculiarities in the structure of organs and systems. *Mysticeti* possess an olfactory analyzer and lack echolocation. At the same time, *Odontoceti* have lost the olfactory analyzer, but acquired an amazing echolocation capability. The well developed hearing of *Odontoceti* is complemented with a specialized system of sound-generation organs. The interaction of an excellent sound-receiver and fine sound-generation organs ensures odontocetes advanced abilities for orientation by the reflected echo-signal.

It is known that dolphins can dive to the depth of more than 300 m. At the same time, the collapse of their lungs occurs at the depth of 70 m. Because of this, dolphins, unlike other mammals, do not have enough air in their lungs and thus cannot use larynx for sound generation all of the time. The system of epicranial nasal passages is the only source that can provide sound generation in dolphins. This idea was first advanced by TOMILIN (1957) and then supported by numerous experimental data.

The goal of this research was to study the structural and functional organization of the sound-generation and sound-perception organs in Amazon River dolphin and oceanic odontocetes, and also to reveal

the homology of nasal area muscles between cetaceans and terrestrial mammals and to find general principles of functioning of the nasal system during breathing and sound generation.

## Material and Methods

We studied the anatomy of the system of epicranial air sacs and their connected musculature on representatives of the four odontoceti families: Amazon dolphin (*Inia geoffrensis* Blainville, 1817) from family Platanistidae; the common dolphin (*Delphinus delphis*, Lacepede, 1758), the spotted dolphin (*Stenella attenuata* Gray, 1846) and the bottlenose dolphin (*Tursiops truncatus* Montagu, 1821) from family Delphinidae; the common porpoise (*Phocoena phocoena* Linnaeus, 1758) from family Phocoenidae, and the white whale (*Delphinapterus leucas* Pallas, 1776) from family Monodontidae.

In some species (*Inia geoffrensis*, *Tursiops truncatus*, *Delphinus delphis*, *Delphinapterus leucas*) we also studied the anatomy and histology of the structures of the inner, middle and outer ear in ontogeny. We used 4-10% formalin and Wittmaack solution for fixation of the material. Celloidin sections with the thickness of 10-15  $\mu\text{m}$  were stained with haematoxylin-eosin by Mallory's method, and also impregnated with the salts of silver nitrate using the method of Kampas.

## Results and Discussion

Main structures of epicranial nasal passages

The formation of complex epicranial nasal passages having no analogues in other mammalian groups occurred synchronously with the fundamental transfiguration of the facial musculature. A number of studies covered the anatomy of these structures in different species of odontocetes. However, this research mostly presented a rather cursory description of the structures of air sacs and their musculature.

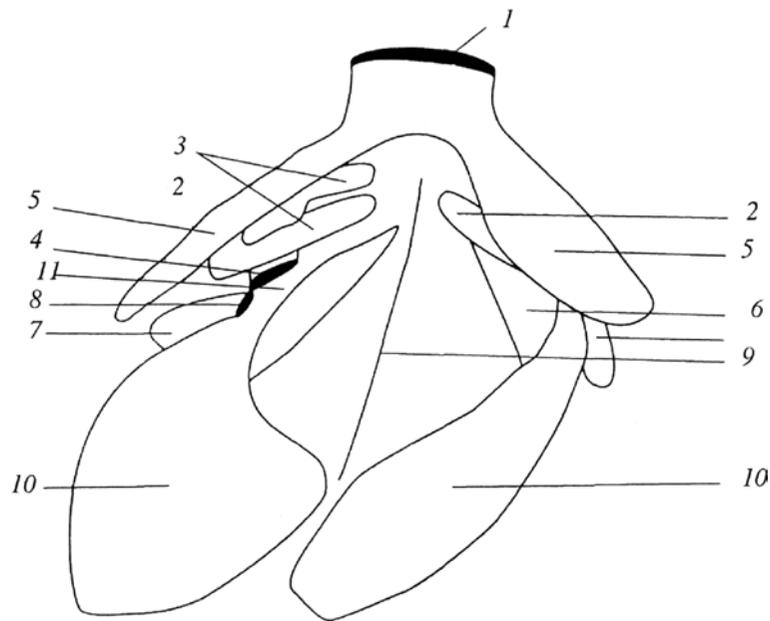
A more thorough study of the nasal area was conducted by LAWRENCE, SCHEVILL (1956) on *Tursiops truncatus*, *Stenella plagiodon*, *Delphinus delphis*, *Globicephala melaena* and *Lagenorhynchus acutus*. These authors described six layers of muscles: posteroexternus, intermedius, anteroexternus, posterointernus, anterointernus and profundus. Subsequent to HUBER (1934) they stated the homology of these muscles with the nasal part (pars nasalis) of maxillo-

nasolabial muscle (m. maxillonasolabialis). Besides the six muscle layers they described the nasal plug muscle, major and minor muscles of nasofrontal sac and also lateral and medial portions of melon muscle. As well as HUBER, LAWRENCE and SCHEVILL (1956) stated the homology of the latter with the labial part (pars labialis) of maxillonasolabial muscle.

MEAD (1975) conducted a comparative study on twenty species of toothed whales and accepted the classification of Lawrence and Schevill, but in contrast to them he regarded the anterointernus and the profundus as one muscle and described the diagonal membrane muscle. He gave a maladapted name (m. rostralis) to the labial part of m. maxillonasolabialis, earlier described by LAWRENCE, SCHEVILL (1956), and subdivided it into lateral and medial portions. Mead supposed that medial part of rostral muscle and anterointernus originated from pars nasalis, and its lateral part as well as four other layers – from pars labialis of m. maxillonasolabialis.

We have given a detailed description of nasal area peculiarities, including the musculature, for the bottlenose and Amazon dolphins (RODIONOV, MARKOV 1992, RODIONOV 1997), and also reported data on the location of several key points of air cavities in a three-dimensional coordinate system for the bottlenose dolphin (RODIONOV 2001). In addition, we have studied the homology of air sacs in several species of toothed whales (RODIONOV 1996). Given all this work has been previously presented, we do not present a circumstantial description of nasal structures and musculature, but here discuss only the most important distinctions revealed in the newly studied species of marine toothed whales (common dolphin, spotted dolphin, common porpoise, and white whale), and primarily treat the general features of organization of the processes of breathing and sound generation in dolphins.

We found 4 pairs of air sacs in the common and spotted dolphins as had been earlier reported for the bottlenose dolphin (Fig. 1). The topography of muscles and the degree of their development were similar to those investigated in the bottlenose dolphin. The similar structures of bigger size were also found in the white whale. However, the essential distinction of this species is that the diagonal membrane which goes down sharply from the nasal bones, in contrast to other dolphins, is not attached to the skull. It stretches inside the soft nasal passage and



**Fig. 1.** Epicranial air sacs of *Tursiops truncatus*.

1 – naris (blowhole); 2-4 – nasofrontal sac: 2 – anterior part, 3 – posterior part, 4 – its foramen; 5 – dorsal sac; 6 – diagonal membrane; 7-8 – accessory sac, 8 – its foramen; 9 – nasal septum; 10 – premaxillary sac; 11 – inferior vestibules.

osteal nasal passages and separates a small space between the skull and the membrane. The location of this membrane evidently enables the white whale, possessing rich vocal repertoire, additional abilities for sound generation.

In the porpoise, which does not whistle, the accessory sacs are lacking and the ventral walls of the closest to the surface dorsal sacs, in contrast to other dolphins, are not elastic and have numerous deep folds lying in the thick layer of dense connective tissue.

The toothed whales possess only one unpaired naris or blowhole. In the closed position it presents a semilunar cleft located broadwise related to the lengthwise axis of the body and turned with its convex side in caudal direction. In Delphinidae, the common porpoise and the white whale nares are located on the head asymmetrically with a shift towards the left side, and in Amazon dolphin this shift is pronounced stronger, than in other species. The naris lies on the highest point of head, but not at the edge of a muzzle, as in other mammals. Anterior and posterior sides of the naris are called lips. The posterior lip in all dolphins is stout and practically immobile. The anterior lip is thick, soft and flexible in all sea dolphins, but in the Amazon dolphin it is comparatively thin and stout. The naris opens as the anterior lip moves forward (into the melon). The valve

apparatus of the naris is usually called the blowhole valve. This structure should be expediently called the narial valve or the dorsal nasal valve (*valva nasalis dorsalis*), as it closes the outer part of the nasal passage (naris), whereas the ventral nasal valve closes the pear-shaped foramina.

All dolphins possess an unpaired dorsal nasal valve. It consists of connective tissue infiltrated with fat, and is threaded with numerous tendons, coming from fascicles of muscle fibers, which control its movements.

The naris leads to the unpaired common nasal passage (*meatus nasi communis*). The representatives of Delphinidae, the common porpoise and the white whale have compactly impacted folds on anterior and posterior walls of the common nasal passage at the level of the lower bound of the dorsal valve. These folds are usually named in literature ‘anterior’ and ‘posterior’ folds.

At a substantial depth from the surface of the derma the nasal passage is divided by a nasal septum (*septum nasi*) into the left and right osteal nasal passages (*meatus nasi osseus*), which cross the maxilla nearly vertically. In the sea dolphins the right nasal passage is much larger, than the left one. Each pear-shaped foramen and the adjoining ventral side of the common nasal passage is closed with the paired ventral nasal valve (*valve nasalis ventralis*). This

valve and its associated muscle are usually called, in the literature, the ‘plug’ and the ‘plug muscle’. The body of the valve consists from the fascicles of muscle fibers with embedments of fat between them. In *Stenella longirostris* these embedments of fat present the direct caudal continuation of the melon fat lens (CRANFORD 1988). In the Amazon dolphin both ventral valves possess such fat embedments, however they present not layers between muscle fibers, but the aggregations of fibrous-fat tissue in the dorso-caudal half of the plugs.

The analysis of the literature and our results show that the maximal number of paired sacs in toothed whales is 4. Our results indicate that the bottlenose, common, and spotted dolphins and the white whale possess 4 pairs of sacs, whereas the porpoise and Amazon dolphin have 3 pairs of sacs (the accessory sacs are lacking). The dorsal sacs lie in the closest proximity to the surface, just under skin and near the naris. They were found in all studied species, for the exception of *Hyperoodon* (Purves, PILLERI 1978).

The dorsal sacs are well developed. However, the position of the left and the right sacs and the construction of the dorsal valve differ between species. It is important to note, that in the species with rich acoustic repertoire (*Tursiops*, *Delphinapterus*, *Delphinus*) the valve closes tightly the outlet to the external opening – the naris, and separates the left and the right sacs, so they can be filled with air independently. Thus the dolphins are able to produce several signals simultaneously, while the air remains in the system of nasal pathways.

In contrast to this, in Amazon river dolphin the two sacs form one cavity. Due to the fact that there is only one sac, their independent work of two sacs is impossible. A comparatively thin and tough dorsal valve ‘overhangs’ the single dorsal sac. It doesn’t provide a tight closing of the naris and doesn’t prevent from air leakage during sound generation.

The nasofrontal sacs in the studied species, as well as in some of the other oceanic dolphins, were also found to have the anterior part, which lies in front of the nasal passage. Additionally, the comparatively narrow entrance to the nasofrontal sac is located over the outlet to the osteal nasal passage (above the pear-shaped foramina), which is durably separated from the sac due to the tight adjoining of ventral valve to the hind wall of the nasal passage.

In contrast to the sea dolphins, the Amazon dolphin does not possess the anterior part of the sac, and the posterior part of the sac is divided by a septum into the two nearly equal volumes located one above the other. The broad chink-shaped entrance to the sac presents, in this species, the direct dorsal continuation of the osteal passage and of posterior part of the premaxillary sac.

Premaxillary sacs in the sea dolphins are large and strongly asymmetric (the right one is 1.5 times as much as the left one). Their ventral walls adnate to premaxillary bone, and due to this factor, the sacs are immobile. In Amazon dolphin the sacs are small and are nearly equal in size. The rostral part of the sac’s ventral wall is not attached to the skull and thus can be slightly protracted forward by the muscle of the ventral valve (*m. nasolabialis profundus p. anterior medialis*). The accessory sacs are small sized and are shifted towards the lateral direction of the premaxillary sacs and the base of ligament. They open by a small chink into the special latero-caudal dilations of the premaxillary sacs, the so-called ‘inferior vestibules’. When the nasal channel is closed, the lateral dilations of ventral valves (‘plug lips’) lie inside these vestibules. Most of sea dolphins possess these sacs, though there are slight distinctions between species. In contrast, Amazon river dolphin doesn’t have accessory sacs, plug lips and vestibules.

The homology of air cavities and some other structures of nasal area found in dolphins with corresponding structures of other mammals have not been established. There is a supposition (AGARKOV *et al.* 1979) that the main three pairs of sacs (dorsal, nasofrontal and premaxillary) present the transformed nasal cavity of terrestrial mammals with its three nasal passages (upper, middle and lower). PURVES, PILLERY (1978) considered that the dorsal (vestibular) sacs are homologous to *vestibulum nasi* and the anterior part of the nasal tract in terrestrial mammals; the anterior and posterior parts of nasofrontal (tubular) sacs – to the frontal and ethmoid sinuses, and nasal ligament (*crus lateralis*) – to the lower nasal cartilages. However, there is a supposition (MURIE 1874), that dolphin air sacs are homologous to nasal diverticula of saiga antelope (*Saiga tatarica*).

The musculature of the dolphin epicranial air sacs is well developed and differentiated. In spite of the distinctions in the structure of epicranial nasal passages, it was rather easy to reveal the corre-

spondence between concrete muscles in *Tursiops*, *Delphinus*, *Stenella*, *Phocoena*, *Delphinapterus* and *Inia*. The characteristic feature of nasal musculature in all dolphins are its multilayer structure, and presence of plain flabelliform muscles with broad terminal aponeuroses. These processes help to exert pressure on all the deeper lying structures. Each 'floor' is located one above the other. The air cavities possess musculature, which can change the dimensions of these cavities and squeeze out the air from them into the cavities of other 'floors'.

Our attempt to establish correspondence between the names for nasal area muscles, which we suggest for use in further investigations, and the names proposed by LAWRENCE, SCHEVILL (1956) and MEAD (1975), who gave the most circumstantial description of muscles. Other authors also use some different terms. For example, RAPP (1837) uses the name *m. nasalis* for all nasal musculature of *Phocoena*, which, evidently *m. maxillonasalis* + *m. maxillonasalis inferior* + *m. dilatator nasi* + *m. buconasolabialis* + *m. nasolabialis profundus p. anterior*. HUBER (1934) distinguishes in *Tursiops* two portions of maxillonasolabial muscle, which correspond to, or includes *pars labialis* – *m. nasolabialis profundus*; *pars nasalis*. All muscles enumerated above for *m. nasalis* were described by RAPP (1837) in *Lagenorhynchus*, *Grampus* and *Globicephalus*, and PURVES, PILLERY (1978) in *Platanista indi* and *Pseudorca crassidens* also distinguished *m. nasolabialis*, which corresponds to the muscle of ventral valve described by us – *m. nasolabialis profundus p. anterior medialis*.

PURVES, PILLERY (1978) suggested several other names of muscles, which corresponded to our names as follows: *m. nasolabialis* = *m. nasolabialis profundus* + *m. dilatator nasi*; *m. maxillonasalis* = *m. maxillonasalis* (all portions) + *m. maxillonasalis inferior*; *m. procerus nasi* = medial fibers of *m. maxillonasalis p. dorsalis* + medial fibers of *p. intermedia*.

### Functioning of the nasal system during breathing

In cetaceans the nasal openings open by the action of musculature and close passively, according to the bounce and elasticity of surrounding tissues. The toothed whales also possess the mechanism of passive nasal passage closing. The dolphin nares open due to the contraction of the muscles (*m. nasolabialis profundus p. anterior lateralis* et *p. anterior medialis*,

*m. maxillonasalis p. intermedia profundus*), which pull forward (inside the melon) the unpaired dorsal valve, paired ventral valves and anterior wall of the nasal passage. This creates overpressure inside the melon. Elastic melon structures reserve the energy of dilatation and return the valves to the initial position (i.e. close the nasal passage) after the relaxation of muscles.

Though all researchers have rejected the idea of the existence of the muscle system serving the purpose of nasal passage closing in the dolphins, the active co-approach of the nasal passage walls is also possible. It is achieved by contraction of the powerful deep nasolabial muscle (*m. nasolabialis profundus*), which encircles the melon with its tendons (Fig. 2). This muscle presses the melon to the skull and compresses the semifluid fat inside it, which transfers the pressure to the anterior wall of the nasal passage and forces it towards the skull. The bands of fat, stretching from the fatty 'lens' of the melon inward the ventral valves, expand the valves and press them into the pear-shaped openings.

Besides, *m. maxillonasalis*, the *p. intermedia lateralis dorsalis* pinches the nasal passage at its part between the dorsal and nasofrontal sacs. Dolphins have another possibility for active nasal passage closure. It is realized through the active work of a well developed *m. dilatator nasi* (Fig. 3, 4) muscle in the area of pear-shaped openings. During the contraction, the dilatator, which enclasps the ventral valves, forces them into the pear-shaped openings. This provides an active and effective occluding of lower part of the joint (soft) nasal passage. Thus, in dolphins the nose dilatator executes the function of locking instead of opening the nose.

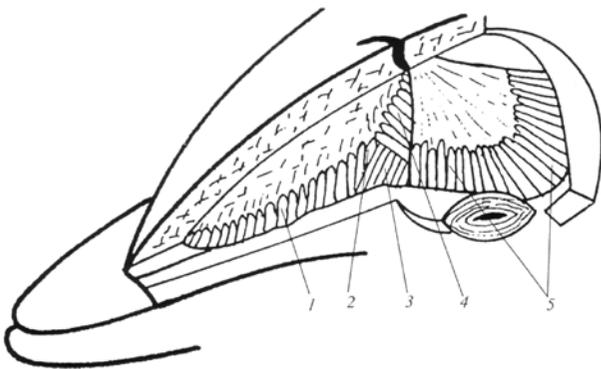
The radiological investigations on bottlenose, common and spotted dolphins indicate that the air sacs are not involved in the act of breathing (DORMER 1979).

### Functioning of the nasal system during sound generation

It is important to note that the dolphins do not possess musculature that provides an active pumping of air into the nasal system (we mean only epicranial muscles). Though some amount of air remains in the nasal system after act of breathing, its operative condition can only be provided by a discharge of air from the lungs through the larynx and osteal nasal passages. The data of radiological studies (NORRIS *et al.* 1971,



**Fig. 2.** Nasal muscles of *Tursiops truncatus*  
1-3 – m. maxillonasalis: 1 – p. dorsalis, 2 – p. intermedia lateralis dorsalis, 3 – p. i.I. ventralis; 4-5 – m. nasolabialis: 4 – p. anterior, 5 – p. lateralis.



**Fig. 3.** Some nasal area structures of *Tursiops truncatus*.  
1 – diagonal membrane; 2 – nasal ligament; 3 – nasal septum; 4 – pear-shaped foramen; 5 – premaxillary sac.

DORMER 1979) indicate that, before phonation, the larynx is pulled backward and downward by contraction of muscles, thus it frees the volume, which it occupies in the nasopharyngeal cavity. The edge of the pharyngeal tube stays half-opened and a small amount of air comes through the larynx from the lungs to the nasopharyngeal cavity and osteal passages. After that the larynx closes and stays closed during the whole process of sound generation. All further activity occurs at the upper levels and without participation of the intercostal muscles and the diaphragm.

It is known that the work of the sound-generation system can be provided only by unequal pressures of the different parts of the air cavities, i.e. by forcing the air from one volume to the other. The air

must pass from a region with high pressure to a region of lower pressure. According to earlier obtained data, the rapid increase of air pressure in osteal nasal passages occurs before sound generation in the bottlenose dolphin, the white whale and the porpoise (RIDGWAY, CARDER 1988). The link between the left and right passages is sustained via the nasopharyngeal cavity. Due to this link, equal air pressure is registered in both passages. At the same time the filling with air of the premaxillary sacs, stretching from below out of the high-pressure area, occurs through the front edge of the pear-shaped openings (NORRIS *et al.* 1971, DORMER 1979). In the bottlenose dolphin, the air pressure in the premaxillary sacs keeps up at the same level as in the osteal nares throughout the whole phonation. This indicates that premaxillary sacs, osteal passages and nasopharyngeal cavity function as a complex in which the premaxillary sacs play the role of a buffer which controls the air pumping to the upper levels of the nasal system.

However, the autonomous work of sacs relative to the osteal passages is also possible. It was shown that during the generation of echolocation pulses the air pressure in the osteal nares did not change, though pressure increased in the soft part of the nasal passage (DARGOLZ *et al.* 1981). Consequently, during pulse generation bottlenose dolphins can manage to produce pulses with the amount of air which is contained in the system of the epicranial cavities.

In all sea dolphins the left and the right halves of the system of epicranial air passages can work independently and with the same capacity. In the right osteal nasal passage the 'inner' whistle (mew) sounds following the echolocation process but not heard outward were registered. These sounds have a different structure compared to communicative whistles. Such sounds were not registered in the left osteal passage. The concrete data on the location of the source of sound generation are still lacking. It was shown, though on the small amount of data, that the dorsal sacs participate in the production of whistle sounds, but are not involved in generation of echolocation pulses. Sounds are not generated in the hind halves of nasofrontal sacs, located between the skull and the nasal passage. Evidently, the source of all dolphin sounds is located in a section of nasal passages between the premaxillary and dorsal sacs.

The exact conformity of the lateral edge of premaxillary sacs with the size and outer configuration of ventral valves having lip-shaped apophyses, the

location of inferior vestibules and the entries to the nasofrontal and accessory sacs, and also some other peculiarities indicate that the complexity and fineness of organization of this part of the air pathways are connected with sound generation and are not necessary for breathing. The role of this complex in sound generation is also manifested by the fact, that the dolphins, which do not have it such as Amazon river dolphin and the harbour porpoise, demonstrate a much reduced sound repertoire, compared to other species, which do possess it such as the white whale, bottlenose dolphin and the common dolphin.

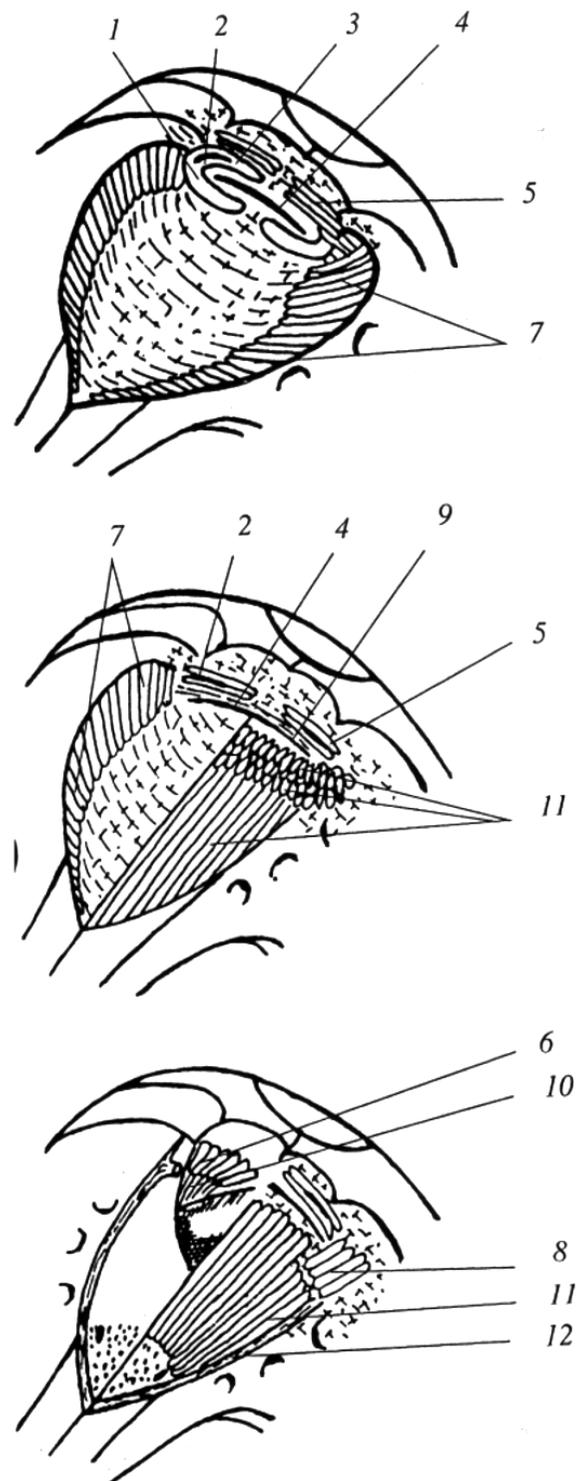
All air sacs, as well as all parts of air passages, have their own musculature which can change the dimensions and configuration of sacs, increase or decrease air pressure in them, regulate the force of compression of pathways' walls, strain the diagonal membrane and nasal ligament and also execute many other actions (RODIONOV, MARKOV 1992, RODIONOV 1996, 1997).

The independent work of the right and left parts of the joint (soft) nasal passage, and well-developed and well-differentiated facial musculature substantially extend the potential of the dolphin sound-generation system. It was shown that dolphins can simultaneously use 2, 3 and even 4 generators of sound producing whistle and pulse signals in different combinations (LILLY, MILLER 1961, BUSNEL *et al.* 1971, MARKOV, OSTROVSKAYA 1990).

### The sound-perception apparatus of dolphins

The study of the auditory organs of marine mammals (Pinnipedia, Cetacea), which appear to represent completely different lineages of placental animals, started more than three centuries ago. However, these works were anatomical and fragmentary in nature. Such an approach to the study of the auditory organs created difficulties in understanding the location of the auditory apparatus as a whole. This inevitably led to incorrect interpretations of the mechanism of acoustic signal reception under water. In order to examine the structure of auditory reception in marine mammals (Cetacea) in detail, a comparative morphological study of the outer, middle and inner ears was necessary in mammals belonging to various ecological groups (SOLNTSEVA 1990, 1992, 1995, 1999).

Thanks to these studies an understanding of the process of functional division for the frequency selectivity between the peripheral and central auditory systems made marked progress. It turned out that



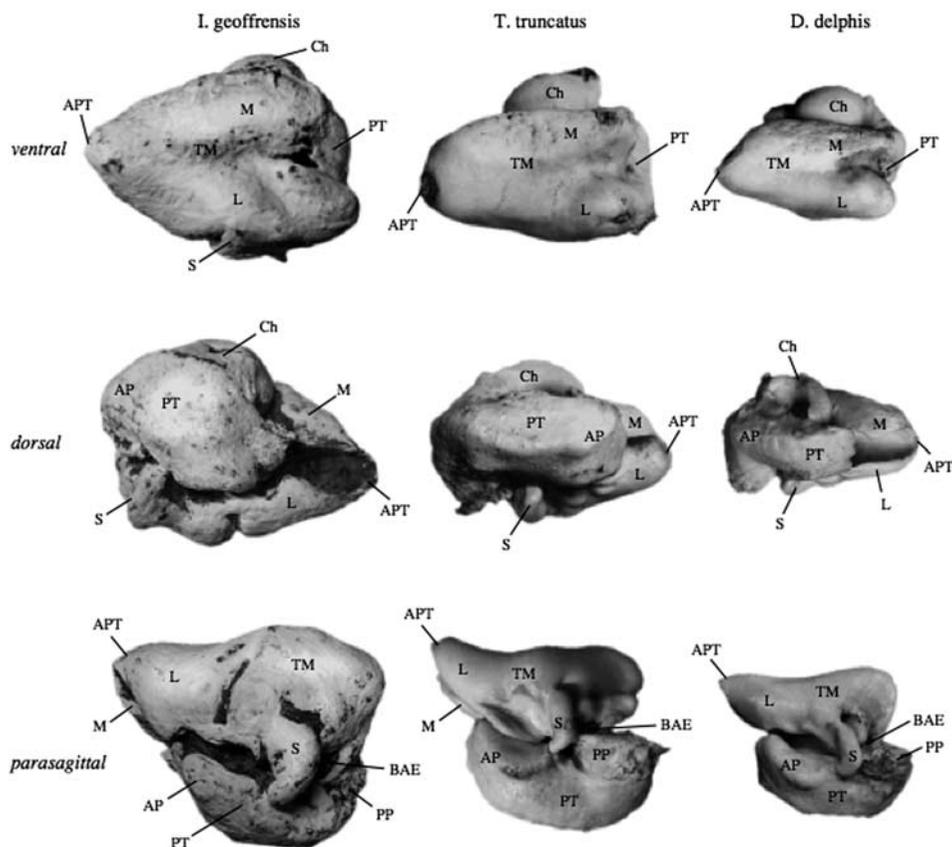
**Fig. 4.** Deep nasal area muscles of *Tursiops truncatus*. A – on the right the dorsal wall of the nasofrontal sac is removed; B – on the left the nasofrontal sacs and m. dilatator are removed; C – on the right side m. dilatator nasi and nasal ligament are removed. 1-3 – nasofrontal sac: 1 – anterior part, 2 – its foramen, 3 – posterior part; 4 – nasal passage; 5-6 m. buccinasolabialis: 5 – p. anterior, 6 – p. posterior; 7-8 – m. dilatator nasi: 8 – p. profundus; 9 – nasal ligament; 10-12 – m. nasolabialis profundus p. anterior medialis; 11 – its lateral aponeurosis, 12 – its roughness on the premaxillary bone.

some functions, previously ascribed to 'brain levels', may be instead carried out by sound-transmission and sound-reception apparatuses. Thus, the differentiation of biologically important frequencies in echolocation species takes place even at the level of outer, middle and inner ears. These findings led to the evaluation of the role of the peripheral auditory system in acoustic information processing in a wide range of species, possessing low-, middle- and high-frequency hearing (BOGOSLOVSKAYA, SOLNTSEVA 1979).

Experimentally, by means of conditioned reflex, behavioural and electro-physiological methods of research, it was established that the upper range of auditory perception in dolphins reaches 120-140 kHz with the frequency of best sensitivity equal to 60-70 kHz (SCHEVILL, LAWRENCE 1953, BULLOCK *et al.* 1968, BELKOVICH, DUBROVSKY 1976). Data on the frequency range of hearing of Amazon river dolphin are contradictory. Amazon river dolphin is assumed to perceive acoustic signals with frequencies as low

as 15 kHz (EVANS, AWBREY 1988). According to experimental data reported by other researchers, the range of acoustic perception of Amazon river dolphin is 1-105 kHz, the range of the highest sensitivity being 20-60 kHz. (NACHTIGALL 1986).

In the representatives of Delphinidae family, the auricle is completely reduced. The external auditory meatus begins with a small hole, located at the distance of several centimeters (up to 4 cm) behind the eye. It has a form of a bent double tube, whose lumen diameter and shape change sharply all along. Curves divide the auditory meatus into three parts. The first and the third ones are placed horizontally relative to the tympanic bulla, and the second one is going down almost vertically, deviating medially. Heading out of hypoderm in a distal part, the auditory meatus cavity is overgrown with epithelial cells. The proximal part in a straightened form represents a cone of irregular form with an oval basis (Fig. 5). This part of the auditory meatus is surrounded by an open-ended



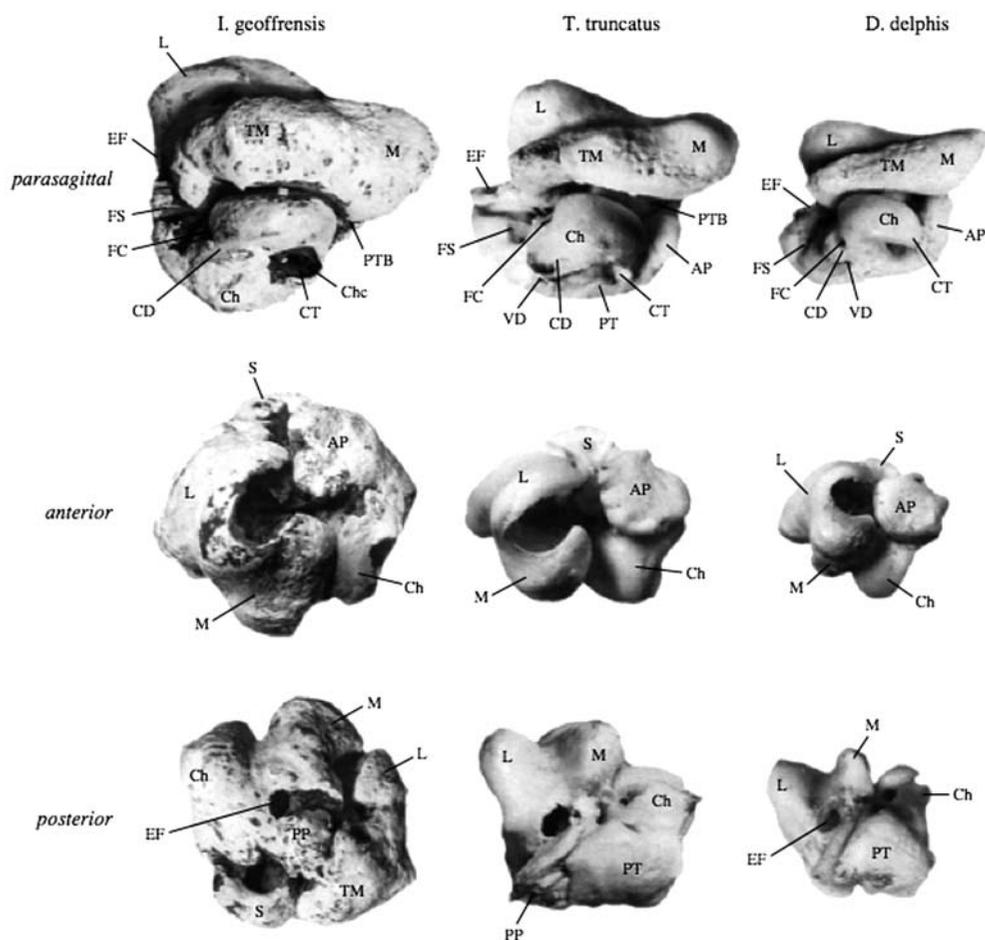
**Fig. 5.** The ventral, dorsal, and parasagittal projections of the bulla tympanica of three dolphin species (*I. geoffrensis*, *T. truncatus*, and *D. delphis*). Designations (here and in Fig. 6). PT – os perioticum; AP – anterior process of the os perioticum; Ch – cochlear bone; Chc – cochlear canal; TM – os tympanicum; S – sigmoid process; BAE – bony part of external auditory meatus; L – lateral lobe of os tympanicum; M – medial lobe of os tympanicum; PTB – pr. tubarius; EF – elliptic foramen; FS – fossa for m. stapedius; FC – cochlear foramen; CD – external division of cochlear duct; VD – external division of vestibular duct; CT – crista transversalis; SL – sulcus lateralis; APT – anterior process of os tympanicum; PP – posterior process of os perioticum.

cartilaginous tube of a horseshoe-shaped form, which is homologated with cartilaginous curl of the terrestrial mammals' auricle. Well-developed muscles of the outer ear are attached to the proximal part of the auditory meatus: *m. auricularis externus*, *m. zygomaticoauricularis*, *m. occipitoauricularis*, and are located along the auditory meatus (BOENNINGHAUS 1903).

The tympanic bulla of cetaceans is the most unique in its structural organization compared to other species of mammals (Fig. 5, 6). It represents a tympano-periotic complex. The tympanic bone is composed by 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. The tympanic and periotic bones are partially knitted with each other in the area of the posterior, sigmoid and tubarius (additional ossicle) arms (KASUYA 1973). In river dolphin (*Inia geoffrensis*), apart from the marine species of dolphins (*Tursiops truncatus*, *Delphinus delphis*, *Phocoena phocoena*, *Stenella attenuata*), the tympanic bulla is formed by thick os-

seous walls. The tympanic and periotic bones in river dolphins relatively bear against each other giving an impression of an entire structure. The tympanic bone is massive, with a pear-shaped form, its size exceeds the size of the periotic bone twice. The tympanic bone is divided into medial and lateral lobes. Lateral lobe is more prominent compared to the medial one. Along the medial part of the lateral lobe a cross furrow extends, which divides this lobe into two equal parts, which apparently does not occur in the marine species of dolphins.

In the marine species of dolphins the tympanic bulla is formed by more thin and rather fragile osseous walls. Localization of tympanic and periotic bones has such a pattern, that it creates an impression of isolation of these ossicles from each other. Their size is approximately equal. The tympanic bone has a lengthened form with well-defined medial and lateral lobes. That is especially evident in comparison of the dorsal surface of tympanic bulla in river and marine species of dolphins.



**Fig. 6.** The parasagittal, anterior, and posterior projections of bulla tympanica of three dolphin species (*I. geoffrensis*, *T. truncatus*, and *D. delphis*).

A comparison of the ventral surface of the tympanic bulla in river and marine species of dolphins shows, that in the river dolphin the periotic bone is more wide and short and with a smoothed surface. In marine species the os perioticum is lengthened, has a ribbing on its surface that is stretched along the whole length of the periotic bone.

In the river dolphin a sigmoid process is well developed, it is thickened, lengthened, separated from the other structures, and its size twice exceeds the size of this process in marine species of dolphins. Anterior and posterior processes of the os perioticum in the river dolphin are less developed than in marine species, in which these processes are massive and broad. The anterior process in a river dolphin is sharp. In marine species it has a spade-shaped form with smooth and rounded edges. The posterior process of the os perioticum in the river dolphin is smoothed and is not defined, while in the marine dolphins this process is hypertrophied, and is supplied with a few small and thin thorns on the top. A deepening for the m. stapedius of the middle ear in the river dolphin is oval and profound, in marine species it is more wide, not profound and does not have distinct borders.

In the area of the anterior surfaces of tympanic bulla in all species of dolphins a tubarius arm (additional ossicle) is found. This tubarius arm is equally well-developed in the river and marine species of dolphins.

The isolation of the 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 bubbles 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, 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 object making sound (KELLOG 1958). Besides, the tympanic bulla in *Odontoceti* can perform slight movements relative to the skull with the help of muscles; due to this the stereophonic (volumetric) reception of the reflected echo signals is provided.

The auditory ossicles of the dolphin species have specific features in structure, arrangement, junction, and the type of fixation in the tympanum.

In the Amazon river dolphin (*Inia geoffrensis*), the ossicles are larger than in the Black Sea dolphins (*Tursiops truncatus*, *Delphinus delphis*); however, they are very similar to each other in the structural organization. In both Amazon river dolphin and Black Sea dolphins, the malleus has a small head with two faces located at a right angle for junction with the incus. The neck of the malleus is poorly developed. The whole malleus is composed of a compact and cylindrical pars transversalis. The incudomalleal articulation has two completely smooth articular surfaces, which are slightly prominent in the malleus and a bit concave in the incus. The manubrium mallei is reduced to a small rounded formation. The pr. gracilis of the malleus has the shape of a triangle with a sharp vertex fused with the os tympanicum, which is not the case with most terrestrial species, in which the junction of this process with the os tympanicum is elastic (via a ligament). This allows the malleus to oscillate independently of the incus. In the dolphin, the malleus and the incus are joined together rigidly, at a right angle; as a result, they function as a single structure. The incus of the Amazon river dolphin is more massive than that of the Black Sea species. The pr. longum of the incus of all three species is hypertrophied. The pr. breve is well-defined, significantly prolonged and elastically connected with the wall of tympanum; however, both processes are of the same length. In dolphins the joint of long arm of the malleus and tympanic bone is rigid, because this arm is knitted with tympanic bone. As a result, the malleus and the incus may function only as a whole structure.

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

The basis of the stapes fixes the oval window of the inner ear tightly, but does not grow together with it, while there are data, that the basis of the stapes knits with the oval window (HYRTL 1844, BEAUREGARD

1894). The knitting of the stapes with the oval window has not been revealed by a number of researchers (YAMADA 1953, FRASER, PURVES 1954, REYSENBACH DE HAAN 1957, FLEISCHER 1973, BOGOSLOVSKAYA, SOLNTSEVA 1979). The head of the stapes is not delimited, the muscular arm is not defined. Auricular muscles are enlarged and have a fan-shaped form. The auditory ossicles are rigidly bound with each other, especially in the area of the incudomalleal joint. The tympanum is formed due to the partial growing together of tympanic and periotic bones.

The membrane tympani of both the river and sea 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 the manubrium mallei. They are connected through an elastic triangular ligament asymmetrically attached to the 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 under water. 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 oceanic species.

The tympanum has been said to be filled not only with the air, but also with an emulsion (FRASER, PURVES 1960), which we failed to reveal. The tympanum is covered with a mucous membrane, including numerous blood vessels. The most part of the cavity is filled with a cavernous plexus, consisting of a dense net of blood vessels. In the area of the tympanic membrane the venous sinuses are located.

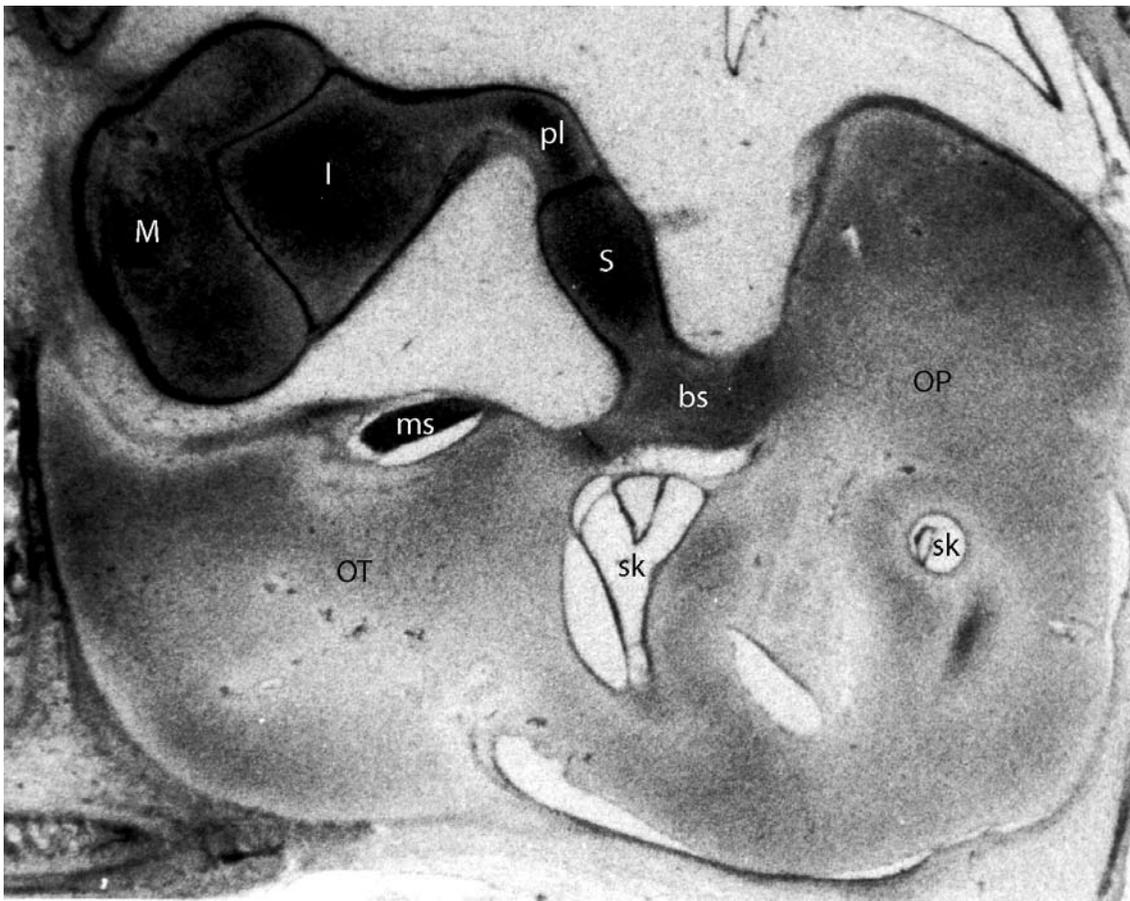
Similarities in the structure of the middle ear found in two pelagic species – dolphins and white whales (*Delphinapterus leucas*) may be seen by examining (Fig. 7).

Thus, the biomechanical peculiarities of the mammals' middle ear whose way of life is connected with the inhabiting of aqueous medium are mainly directed to the increase of the coefficient of transmission of acoustic pressure by the middle ear. Most likely, that determines the effectiveness of the peripheral auditory system's functioning during the mammals' orientation in an aqueous medium and greatly enlarges their perceptible frequency band.

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 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 tympanum membrane's elasticity (SOLNTSEVA 1990).

Besides the sound conduction, the middle ear of mammals carries out a precautionary function by decreasing the energy of the incoming to the inner ear signal. This function is enabled by a middle ear muscle's contraction: m. tensor tympani and m. stapedius which are well developed in echolocating species (dolphins, bats) (SOLNTSEVA 1990, 1995). 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).

It is well known that sounds can travel longer distances in water than in air. Ultrasound has a higher frequency than the sound perceived by humans (up to 20 kHz) and, therefore, should spread and fade at markedly shorter distances from a sound source. Representatives of the suborder *Odontoceti*, which use ultrasound location for orientation, show adaptations for strengthening, as well as focusing, an acoustic wave. This is based on the morphological features of the animal's head (the presence of a fatty jut on the forehead, or melon), and also on the ability of the animal to produce ultrasound or short-wave signals. During the process of echolocation, the dolphin probes its ambient space with ultrasound signals, projecting pencil – thin ultrasound waves from its melon. The width of the ultrasound waves is



**Fig. 7.** Histotopography of the middle ear in dorsoventral head sections in *Delphinapterus leucas*'s embryo (embryo length is 250 mm).

a – auditory ossicles arrangement in the cavity of the middle ear is shown; malleus and 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; OP – os perioticum; OT – os tympanicum; sk – semicircular canal.

characterized by an orientation diagram of acoustic radiation, which represents a graphic relation of the pressure value of sending the acoustic signal from the angle between the acoustic axis and the direction to the point. The reflected signal comes back to the dolphin and is received by its auditory system.

In the inner ear the principle of the cochlea's structure reveals similarities in almost all mammals. A large cochlea is characteristic of all dolphin species studied. The cochlea of Amazon river dolphin is half covered with the medial lobe of the os tympanicum, whereas the cochlea of the Black Sea species is located openly, separately from other bones. The cochlear canal of Amazon river dolphin is narrower than that of Black Sea dolphins, and the crista transversalis is almost two times smaller than that of Black Sea species, in which the crista transversalis is wider and more open. This indicates that the acoustic nerve of the river dolphin is two times thinner than

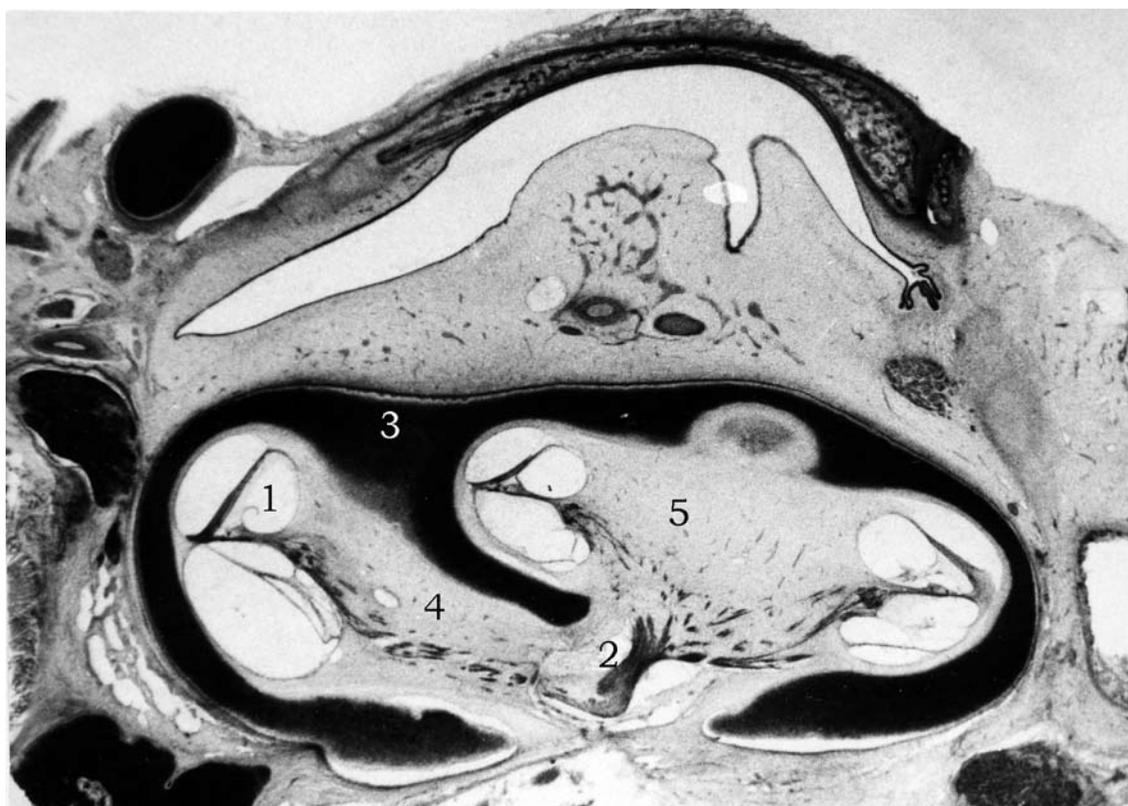
that of Black Sea dolphins. The cochlea of the river dolphin has two turns, whereas that of Black Sea dolphins has 1.5-1.75 turns.

The cochlea of the white whale as a river dolphin has two turns (Fig. 8)

The basal turn of the cochlea, which is tuned to the perception of high-frequency signals, is the best developed in all three species of dolphins studied.

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

In most mammals the structure of the organ of Corti reveals patterns of similarity. The number of



**Fig. 8.** The cochlea of *Delphinapterus leucas* has two turns.

1 – cochlear canal; 2 – cochlear branch of n. acousticus; 3 – auditory capsule; 4 – basal turn of the cochlea; 5 – apical turn of the cochlea.

receptor cells in echolocating and non-echolocating forms does not change. However, some researchers observe certain peculiarities in the structure of the organ of Corti in dolphins, in which these cells are enlarged in size and compactly located (WEVER *et al.* 1971, 1972). 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).

As is apparent from the description, all parts of the peripheral auditory system are multicomponent formations. As opposed to the outer and middle ear, 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. Usually, both in the cochlear and vestibular analyzers the topography, form and size of separate components vary. In echolocating mam-

mals, the substantial growth of the cochlea's sizes in comparison with the sizes of the vestibular apparatus, as well as other features in the structure of the cochlear canal and the cells of the organ of Corti serve as the cochlea's adaptations to the perception of frequencies of a wide range, including ultrasound (dolphins, bats). At the same time, the huge cochlea and the extraordinary small size of the vestibular apparatus in absolute hydrobionts, which possess varied orientation of hearing, can be considered to be the adaptation of inner ear to aquatic life, as the hearing of aquatic mammals dominates among distant analyzers, thus providing the survival rate of these animals in conditions of constant dwelling in an aquatic environment.

However, according to the analysis of other researcher's basic statements concerning the ways of acoustic sound conduction into the dolphin's inner ear, and also from our own morphological data obtained later, it could be considered that the sound waves can pass from the front direction of the head not through the hypodermis and the muscular tissue to the proximal part of the external auditory meatus but by classical pathway: directly through the au-

ditory inlet, the distant part of the auditory meatus and further through the area of its obliteration which represents the 'acoustically transparent' membrane formed by the epithelial cells with thickness up to 50-60  $\mu\text{m}$  through the proximal part of the auditory meatus to the tympanic membrane and the line of the auditory ossicles (SOLNTSEVA 1997).

Thus, the comparative morphological analysis of the auditory organ of the river dolphin and Black Sea dolphins has demonstrated that this organ has a common general structure characteristic of all representatives of 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 Amazon river dolphin is considerably lower than in Black Sea species; therefore, the structure of the bulla tympanica 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. I mean that the water is mixed with air bubbles and silt and sand particles, which considerably deterio-

rates echolocation in the river by interfering with the perception of reflected echo-signals. Therefore, the echolocation signals may decay over long distances, not returning to the dolphin acoustic receiver. This is one of the cases why the location-hearing apparatus of the river dolphin operates at relatively short distances, with a highest-sensitivity frequency of about 20-60 kHz.

The specific structural characteristics of the bulla tympanica of Black Sea 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.

To the blessed memory of an unforgettable colleague, author of this article Vyacheslav Alekseevich Rodionov. For many years he studied of marine mammals.

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## References

- AGARKOV G. B., B. G. KHOMENKO, A. P. MANGER 1979. Functional morphology of cetaceans. Kiev, Naukova Dumka, 223 p
- BELKOVITCH V. M., N. A. DUBROVSKY 1976. Sensory basics for orientation of cetaceans. L., Nauka, 204 p.
- BLAIR S. F. 1964. Perceptual theories of middle ear muscle function. – *Ann. Otol. Rhinolaryngol.*, **73** (3): 724.
- BOGOSLOVSKAYA L. S., G. N. SOLNTSEVA 1979. The Auditory System of Mammals. M., Nauka, 238 p.
- BUSNEL R. G., B. ESCUDIE, A. DZIEDZIC, AND A. C. HELLION 1971. Structure des clics doubles d'écholocation du Globicephale (Cetace odontocete). – *C.r. Acad. Sci. D.*, **272**: 151-163.
- DARGOLTS V. G., E. V. ROMANENKO, E. A. YUMATOV and V. G. YANOV 1981. Method of telemetric registration of blood pressure and respiration in free-swimming dolphins. – *Physiologicheskii zhurnal SSSR*, **67** (11): 1744-1748.
- DORMER K. J. 1979. Mechanism of sound production and air recycling in delphinids: Cineradiographic evidence – *J. Acoust. Soc. Amer.*, **65** (1): 229-239.
- CRANFORD T. W. 1988. The anatomy of acoustic structures in the spinner dolphin forehead as shown X-ray computer tomography and computer graphics. – In: NACHTIGALL P. E. & P. W. B. MOORE (Eds.): *Animal sonar: Processes and Performance*. N.Y.; L., Plenum Press, 67-77.
- EVANS W. E., F. T AWBREY 1988. Natural history aspects of marine mammal echolocation: Feeding strategies and habitat. – In: NACHTIGALL P. E. & P. W. B. MOORE (Eds.): *Animal Sonar: Processes and Performance*. N.Y., Plenum Press, p. 521-534.
- FIRBAS W., B. A. WALESCHIK 1973. A quantitative study on the spiral ganglion of the Chiroptera. – *J. Period. Biologorum*, **75** (1): 67-70.
- FLEISCHER G. 1973. Studien am Skelett des Gehororgans der Säugetiere, einschliesslich des Menschen. – *J. Säugetierk. Mitt.*, **21** (H. 2-3): 131-239.
- HUBER E. 1934. Anatomical notes on Pinnipedia and Cetacea. – *Carnegie Inst. Wash. Publ.*, **447**: 105-136.
- KASUYA T. 1973. Systematic consideration of recent toothed whales based on the morphology of tympano-periotic bone. – *Sci. Rep. Whales Res. Inst. Tokyo.*, **25**: 1-103.
- KUNZE W., H. KIETZ 1949. Über Hörempfindungen in Ultraschallgebiet bei Knochenleitung. Arch. Ohren-, Nasen- und Kehlkopfheilk. – *J. Arch. Ohren-Nasen-und Kehlkopfheilk.*, **135**: 683-692.
- LAWRENCE B., W. E. SCHEVILL 1956. The functional anatomy of the delphinid nose. – *Bull. Mus. Comp. Zool. Harvard College.*, **114** (4): 103-151.
- LILLY J. C., A. M. MILLER 1961. Sound emitted by the bottlenose porpoise – *Science.*, **133** (3465): 1689-1693.
- MARKOV V. I., V. M. OSTROVSKAYA 1990. Organization of communication systems in *Tursiops truncatus* Montagu – In: THOMAS J. A. & R. A. KASTELEIN (Eds.): *Sensory abilities of cetaceans*. N.Y.; L.: Plenum Press, 599-622.
- MEAD J. G. 1975. Anatomy of the external nasal passages and facial complex in the Delphinidae (Mammalia, Cetacea). – *Smithsonian Contrib. Zool.*, **207**: 1-72.
- MURIE J. 1870. Notes on the white-headed bottlenose dolphin,

- Lagenorhynchus albirostris*, Gray. – *J. Linn. Soc. London. Zool.*, **11**: 141-152.
- MURIE J. 1874. On the organization of the caaing whale, *Globicephalus melas*. – *Trans. Zool. Soc. London*, **8**: 236-302.
- NACHTIGALL P. E. 1986. Vision, audition and chemoreception in dolphins and other marine mammals. – In: SCHUSTERMAN R. J., J. A. THOMAS & F. G. WOOD (Eds.): *Dolphin Cognition and Behavior: A comparative approach*. Lawrence Erlbaum Assoc. London, 79-113.
- NORRIS K. S., K. J. DORMER, J. PEGG and G. J. LIESE 1971. The mechanism of sound production and air recycling in porpoises: A preliminary report Proc. VIII Annu. Conf. on biol. sonar and diving mammals. Fremont (Calif.), p. 113-129.
- OELSCHLAGER H. A. 1990. Evolutionary Morphology and Acoustics in the Dolphin Skull – In: THOMAS J. A. & R. A. KASTELEIN (Eds.): *Sensory abilities of cetaceans*. N.Y.: Plenum Press, p. 137-162.
- PURVES P. E., G. PILLERI 1978. The functional anatomy and general biology of *Pseudorca crassidens* (Owen) with a review of the hydrodynamics and acoustics in Cetacea – *Ibid.*, **9**: 67-227.
- RAPP W. 1837. *Die Cetaceen*. Stuttgart; Tubingen: Gotta, 182 p.
- RIDGWAY S. H., D. A. Carder 1988. Nasal pressure and sound production in an echolocating white whale, *Delphinapterus leucas* – *Animal sonar: Processes and performance*. N.Y.: Plenum Press, 53-60.
- RODIONOV V. A., V. I. MARKOV 1992. Functional anatomy of the nasal system in the bottlenose dolphin. – In: THOMAS J. A., R. A., KASTELEIN & A.YA. SUPIN (Eds.): *Marine mammal sensory systems*. N.Y.: Plenum Press, 147-177.
- RODIONOV V. A. 1996. Comparative anatomy of musculature of epicranial pathways in the Amazon and bottlenose dolphins. – In: SOKOLOV V. E. (Ed.): *The Amazon Dolphin*, M.: Nauka, 1996, p. 135-152.
- RODIONOV V. A. 1997. Some anatomic peculiarities of the Black Sea bottlenose dolphin musculature. – In: SOKOLOV V. E. & E. V. ROMANENKO (Eds.): *The Black Sea bottlenose dolphin *Tursiops truncatus* ponticus*, M.: Nauka, p. 368-419.
- RODIONOV B. A. 2001. Anatomy of the epicranial air cavities in the bottlenose dolphin (*Tursiops truncatus*) in connection with the problems of modeling. – *Papers of the USSR Acad. Sci.*, **381** (4): 566-570.
- REYSENBACH DE HAAN F. W. 1957. Hearing in whales. – *Acta otolaryngol.*, **134**: 1-114.
- SCHEWILL W. E., B. J. LAWRENCE 1953. Auditory response of the bottlenose porpoise *Tursiops truncatus* to frequencies above 100 kc. – *J. Exp. Zool.*, **124** (1): 147-165.
- SIMKIN G. N. 1977. Acoustic orientation and contact of mammals, – *Abstr. of doctoral thesis*. M., p. 1-37
- SOLNTSEVA G. N. 1990. Formation of an adaptive structure of the peripheral part of the auditory analyzer in aquatic echolocating mammals during ontogenesis. – In: THOMAS J. A. & R. A. KASTELEIN (Eds.): *Sensory abilities of cetaceans*. N. Y.: Plenum Press, 363-383.
- SOLNTSEVA G. N. 1992. Prenatal development of the peripheral part of the auditory system in mammals of different ecologies. – In: THOMAS J.A., R. A. KASTELEIN and A.YA. SUPIN (Eds.): *Marine Mammal Sensory Systems*. N.Y.: Plenum Press, 179-195.
- SOLNTSEVA G. N. 1995. The auditory organ of mammals in relation to the acoustic properties of the habitat and frequency tuning. In: THOMAS J. A., R. A. KASTELEIN & P. E. NACHTIGALL (Eds.): *Sensory Systems of Aquatic Mammals*. Woerden Netherlands: De Spil Publishers, 455-475.
- SOLNTSEVA G. N. 1999. Development of the auditory organ in terrestrial, semi-aquatic, and aquatic mammals. – *J. Aquatic Mammals*, **25** (3): 135-148.
- TOMILIN A. G. 1957. Mammals of the USSR and adjacent countries. Cetaceans. M., Izd. AN SSSR. **9**: 756 p.
- WEVER E. G., J. G. McCORMICK, J. PALIN AND S. H. RIDGWAY 1971. The cochlea of the dolphin, *Tursiops truncatus*: hair cells and ganglion cells. – *J. Proc. Nat. Acad. Sci. USA*, **68**: 2908-2912.
- WEVER E. G., J. G. McCORMICK J. G., J. PALIN and S. H. RIDGWAY 1972. Cochlear structure in the dolphin, *Lagenorhynchus obliquidens*. – *J. Proc. Nat. Acad. Sci. USA.*, **69**: 657-661.
- YAMADA M. 1953. Contribution to the anatomy of the organ of hearing of Whales. – *J. Scient. Repts. Whales Res. Inst.*, **8**: 1-79.

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