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Mechanisms of Sound Reception and Conduction in the Dolphin

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Abstract—Morphology of the dolphin's lower jaw, model and behavioral experiments are discussed with the aim of exploring the mechanisms of sound reception and conduction to the lower jaw canals, taking into account the known concepts of acoustics and the theory of grouped antennas. It is shown that the left and right rows of mental foramens with the respective mandibular canal and tissues of the canals are forming the new external ear and the new external auditory duct whereby sound (in the frequency band of 0.1–160 kHz) is transmitted into the middle ear, in contrast to the dolphin's nonfunctional outer ear. This new external ear is created by nature as a receiving array of traveling-wave antennas located in the throat of an acoustic horn (the respective mandibular canal). The results give reason to assume the existence of a similar new external ear in Odontoceti.

Keywords: dolphin, sound reception and conduction, lower jaw, traveling-wave antenna, acoustic horn, sonar, hearing

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INTRODUCTION

The results of studying the mechanisms of hearing in toothed whales and dolphins are reflected in numerous works. A number of authors believe that sound passes through the external auditory meatuses and the middle ear [1–3], though there is an opinion that the auditory meatuses are not functional and can take no part at all in conducting sound to the middle ear [4–6] or serve to conduct acoustic signals of frequencies below 30 kHz [7–9]. Based on the hypothesis of sound conduction via the external auditory meatuses, Dubrovsky [10, 11] discussed the existence of functionally specific subsystems of passive (1–10 kHz) and active (~100 kHz) hearing.

Norris first supposed [12] that sound may be conducted into the fat body of the mandibular canal (MC) via the mental foramens (MFs). Somewhat later he advanced a hypothesis, generally recognized heretofore [13], that sound passes into the MC fat body directly through the mandibular posterolateral bone in the region he called an "acoustic window." Via the fat body, sound comes onto the tympanic lateral wall where the bone thickness is minimal, and the wall acts as an ear-drum, transmitting the acoustical vibrations onto the malleus of the middle ear [13–18].

Two "acoustic windows" have been shown in electrophysiological experiments [19]: one in the region of the external auditory meatus, for low frequencies (16–22.5 kHz); and the other, in the proximal part of the lower jaw, 9.3–13.1 cm away of the tip of the melon, for high frequencies (32–128 kHz).

Acoustic stimulation of the lower jaw excites significant evoked potentials in the central nervous system of the dolphin [5, 7]. However, the regions of maximal sensitivity of the jaw surface to sounds produced by a contact point emitter and also the regions of "acoustic windows" differ in every work [5, 7, 19–22], and the results thus obtained fail to explain the sound conduction mechanism.

Acoustical shielding of the dolphin's lower jaw substantially hampered target discrimination by echolocation [23–26], which supports the hypothesis of the involvement of the lower jaw in receiving echoes and conducting them to the middle and inner ear. However, the acoustic screen in this experiment covered the lower jaw from the rostral tip to the bases of pectorals; i.e., it shielded the MFs as well as the "acoustic window" and the ventral part of the head, so the sound conduction path remained uncertain.

Along with this, discussed is the possibility of simultaneous involvement of external auditory meatuses and "acoustic windows" in conducting sounds to the cochlea during formation of a spatial auditory image in dolphins [27].

There are also a number of works where authors suggest that toothed whales receive echo signals by their teeth [28–31]. Each tooth is regarded as a passive resonator excited by a reflected signal, and dental nerves, as sensors of sound pressure; each row of teeth is regarded as an equidistant array of receivers with a narrow directional response pattern, the signals of which are transmitted via dental nerves directly into the CNS (bypassing the cochlea).

On the other hand, our results [32−38] give grounds for supposing that sound is conducted to the dolphin's middle ear via the canals of the lower jaw. Since the time of these publications, new data have been obtained in support of this idea. Generalization of the original and published information concerning the mechanism of sound reception and conduction to the middle ear was the goal of this work.

The particular tasks here were to examine dolphin's lower jaw morphology and to model the sound reception and channeling in the lower jaw in terms of the known concepts of acoustics and array antenna theory.

EXPERIMENTAL

The examination material was the skulls and lower jaws of two adult bottlenose dolphins *(Tursiops truncatus)*. To study the morphology and make necessary measurements, the lower jaw was sawn in the MF region. Further in text the foramens will be denoted where necessary with numbers MFn, where n is counted from the rostral tip: $n = 1, 2, 3, 4$. The transverse dimensions of the canals were measured at maximal width and in the perpendicular direction.

Here use is made of the spatial nomenclature referring directly to the object. The plane perpendicular to the longitudinal rostro-caudal axis of the animal is called transverse. The plane dividing the body into laterally symmetric parts (left and tight) along the rostrocaudal axis is called median. The plane dividing the body into dorsal and ventral parts along the rostrocaudal axis is called frontal. It should be noted that in most works ([7, 9] etc.) use was made of the nomenclature connected with external spatial references, so that the frontal plane was called horizontal and the median plane, vertical.

The parameters of the acoustic horn of each mandible were calculated using a catenoidal horn model. From the horn theory it follows that the horn effectively radiates at frequencies above critical, f_c. At frequencies below critical, the active part of the horn radiation impedance r_r tends to zero and the impedance becomes purely reactive. Practically, for frequencies

$$f \geq 2.3 f_c \tag{1}$$

the active part of horn radiation impedance reaches 0.9 of maximal value, and reflection from the mouth can be neglected. The horn critical frequency (f_c) is determined by the circumference of its mouth (outlet opening)

$$(C_m/\lambda_c) \geq 1,$$

where C_m is the circumference of horn mouth, or a circle isometric in area to a mouth of different shape; λ_c is wavelength of horn critical frequency. In practice, chosen are

$$C_m = \lambda_c \text{ and } f_c = c_0/\lambda_c, \tag{2}$$

where c_0 is speed of sound in water (1500 m/s).

The critical frequency of a catenoidal horn can also be calculated from the rate of horn flaring

$$f_{c\beta} = (c_0\beta)/(2\pi), \tag{3}$$

where c_0 is speed of sound in the mandibular fat body, which will be taken to equal the speed of sound in water (1500 m/s); β is the index of flaring of the horn cross-section, which with distance x from the throat changes as

$$S_x = S_0(\cosh(\beta x))^2, \tag{4}$$

where S_0 is the cross-section area of the horn throat; S_x is the cross-section area of the horn at distance x from the throat.

For an acoustically "narrow" tube (channel) with a cross-section jump, the amplitudes of sound pressure of the transmitted and reflected waves can be written down as:

$$A_2 = (2\sigma_1/(\sigma_1 + \sigma_2))A_1, \tag{5}$$

$$B_1 = ((\sigma_1 - \sigma_2)/(\sigma_1 + \sigma_2))A_1, \tag{6}$$

where A_1, A_2 and B_1 are the amplitudes of incident, transmitted and reflected waves respectively; σ_1 and σ_2 are cross-sections of adjacent parts of the tube.

RESULTS AND DISCUSSION

Figures 1−4 are photographs of the dolphin lower jaw and skull used in examination. At first glance, the lower jaw looks very simple: two linear thin-walled hollow bones connected at the rostral tip by cartilage ossified with age (synostosis). The cavities of the jaw are filled with the fat body and the vascular-nervous bundle. The angle between the mandibles of this specimen in the frontal place is about 17° and smoothly increases to ~30° caudally. In the rostral part at both sides there are series of MF openings (Figs. 1−4). The lengths of the left and the right bases encompassing the MF orifices are ~81 and 87 mm respectively. The angle between the bases is larger than that between the bones, making ~24°. This is due to that the inclination of the lateral walls of the bone in the transverse place changes along the bases, and MFs are disposed at different levels dorsoventrally. The wall slope to the median place at MF1 and MF2 is ~30° and smoothly decreases to ~25° at MF3 (Fig. 2). If we assume that the longitudinal axis of the body (in the median plane) coincides with the line of the mouth (Fig. 3, LA), the base of either series of MFs in this plane is directed rostrodorsally at an angle about 8°.

The cross-section of MFs is oval. The MC is the continuation of MFs (Figs. 1, 3). MFs have distinct anterior direction, so in Fig. 2 they look almost round whereas in Figs. 3 and 4 they are strongly elongated. In the sagittal plane the MFs are directed rostrodorsally at an angle of 6°−10°. In the frontal plane the MFs are
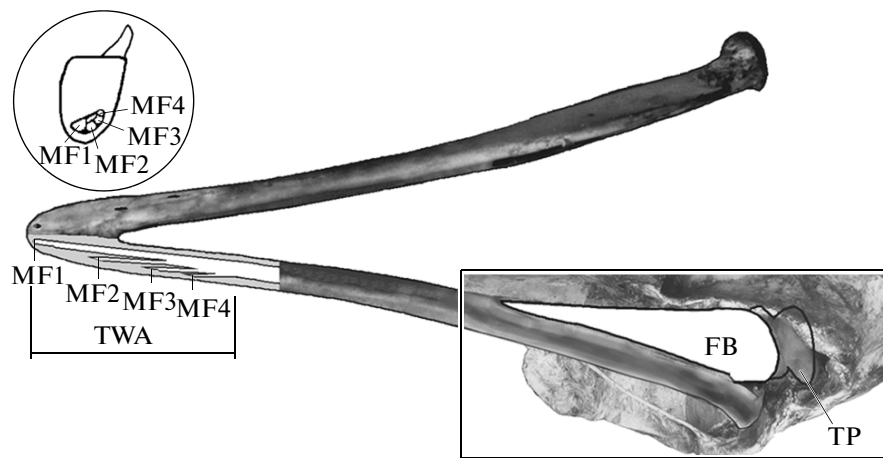
Fig. 1. Lower jaw, ventral view. Mental foramens are shown in the section along the rostral part of the right mandible. Their transverse disposition is shown in the circle (section at the inner orifice of MF4, viewed in the rostral direction and magnified). TWA denotes traveling wave antenna (MF1−MF4 series). The peribullar region is shown in the rectangle (ventral view). TP, tympanoperioticum; FB, fat body.

directed rostrolateral at an angle from $-8°$ to $0°$ (the minus sign denotes directedness toward the other half of the jaw). Because of such disposition, the end of MF at the outer side of the jaw is oblique (Fig. 4) while within the MC, straight. All MFs differ from one another in length, cross-section size and oblique end length (table). Intriguingly, the left half of the jaw has three MFs and the right half has four; this is typical not only of bottlenose dolphin but also of other Odontoceti species [13, 39].

Between the disposition and size of canals, there are certain relationships. The right-half MFs are longer than the left-half ones of the same number. The transverse size of MCs and their cross-section area in the MF region smoothly grow caudally, while the transverse size of MF decreases with MF remoteness from the rostral tip. Therefore, the ratio of cross-section areas σ_{MFn}/σ_{MC} at the entry of every MFn declines caudally. The spaces between MFs decrease with MF remoteness from the rostral tip, while the cross-section of each MF smoothly increases towards MC. Yet the most obvious and interesting fact is that the disposition of MFs in the left and the right halves of the jaw is not equidistant, showing "complementary asymmetry." In this architecture, the projection of the outer orifice of each MF (starting with MF2) onto the other half localizes between its MF orifices.

The MC width (in the frontal plane) grows with the entry of every next MF (Fig. 1) from 3.3 mm at MF1 to 7.5 mm at MF4. The MC height (dorsoventral) in this region changes less, from 3.5 mm at MF1 to 4.5 mm at MF4. The MC transversal flaring rate increases along its length (Figs. 1, 3). On the whole, the MC width grows in lateral directions from 3.3 mm at MF1 to ~15 mm at its caudal end (the mouth of the horn). The MC height (dorsoventral) changes overall to a greater extent, from 3.5 mm at MF1 to ~44 mm at

its caudal end. The shape of the cross-section of MC at its beginning (at MF1) is nearly oval, whereas at MF4 it is closer to a semicircle. At the caudal end the MC cross-section is shaped as an elongate ellipse with axes $2a = 15$ mm, $2b = 44$ mm and area ~492 mm^2. The MF1 length + MC length = 257.5 mm. The total aperture of the caudal end of the mandible, shown with dashed line in Fig. 3, has an area of ~6333.6 mm^2.

The cross-section area along each MF and MC smoothly grows caudally (Fig. 5), closely to a catenoid law ($R^2 = 0.993$). The MF and MC walls are formed by dense bone substance and are acoustically "elastic." The acoustical impedance of mandible-filling tissues is close to the impedance of sea water [40], i.e., the tissues are sound-transparent. Consequently, there are all grounds for regarding these channels as a catenoidal acoustic horn [35−38]. Interestingly, the area of

Fig. 2. Dolphin skull, with MF openings seen in the rostral area: four in the right mandible and three in the left.
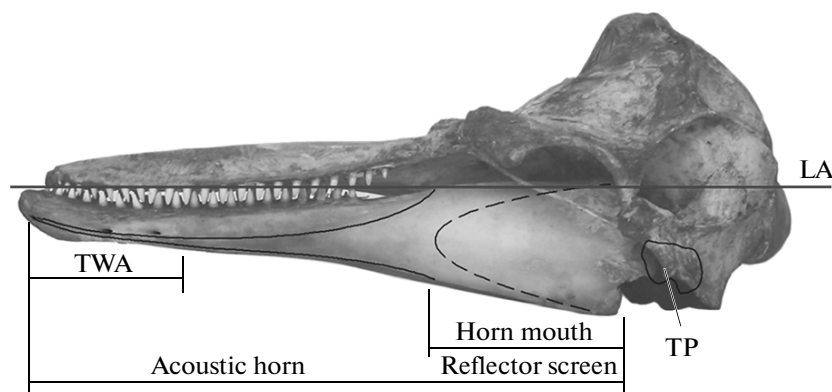
Fig. 3. Dolphin skull, left lateral view. TWA: traveling wave antenna (MF series). Acoustic horn: the MF1 and MC profile (solid line). Horn mouth: the aperture of the inner wall of the mandibular bone (dashed line). Acoustically opaque reflector screen: outer posterolateral wall. TP, tympanoperioticum. LA, longitudinal axis of the body.

the caudal opening of the lower jaw, which is regarded as the horn mouth (Fig. 5, $S2$), changes closely to the same law as does the horn cross-section, continuing its growth.

The results of previous studies [33, 35−38] indicate that the mechanisms of sound reception and conduction via the lower jaw to the middle ear are determined by the architecture, shape and size of the channels. A sound wave incident on the lower jaw excites forced vibrations in the tissues filling the MFs. Having passed the MF these vibrations radiate into the MC and propagate via the mandibular fat body to lateral wall of the tympanoperiotic complex, which comprises the middle and the inner ear. There the tympanic bone thickness is minimal (0.3−0.4 mm), and the wall acts as an ear-drum, transmitting the acoustic vibrations onto the malleus of the middle ear [13, 16−18]. Consequently, unlike the nonfunctional and partly atresic external auditory meatuses, the dolphin's lower-jaw channels perform as the left and right new external ear. At the same time, these mechanism are strictly deter-

mined by the theoretical and practical concepts of acoustics and array antenna theory [33, 35−38].

It is known that in a waveguide, only a plane sound wave conveys the signal without distortion. In practice, for these purposes use is made of waveguides at frequencies below the first radial resonance or acoustically "narrow" waveguides, in which only plane waves can propagate axially. The shape of waveguide section is of little significance. For example, the condition of a waveguide of rectangular section with side A being narrow is fulfilled at $A < 0.5\lambda$, where λ is sound wavelength; for a round-section waveguide of radius R, at $R < 0.61\lambda$. Sounds and echoes propagating via MF and MC are broadband, occupying a frequency band about 140 kHz with maximal energy about 110 kHz, which corresponds to wavelength $\lambda_{110} \sim 13.6$ mm [42−44]. Hence, both the MF, with section
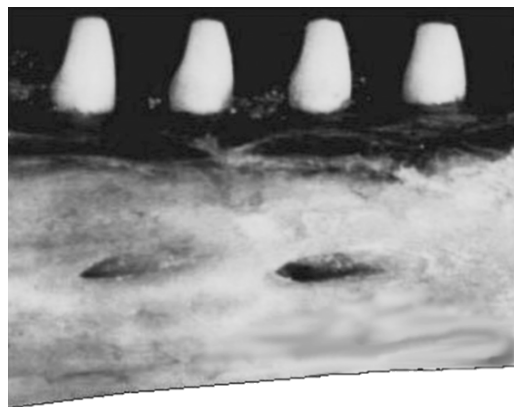
Fig. 4. Fragment of the right mandible, lateral view of MF3 and MF4. Seen is the typical shape of the oblique end of MF.
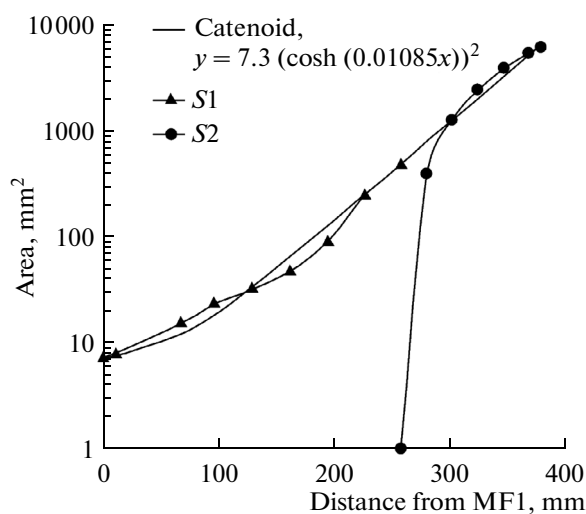
Fig. 5. Increase in the cross-section area along MF1 and MC ($S1$) and aperture area of the caudal opening of the mandible ($S2$) as dependent on the distance from rostral tip.

Main characteristics of mental foramens

MF No.	MF length, mm	MF transverse size, mm	MF cross-section area, mm²	Distance to next MF, mm	Natural MF vibration frequency, kHz	Length of MF oblique end, mm
1						
left	10	3.2 × 3.2	8.04; 8.5	50.2	75	7
right	11	3.2 × 2.9	7.28; 8	36.1	68.2	8
2						
left	27.5	2.9 × 2.2	5; 7.7	31.2	27.3	11
right	35	2.6 × 2.1	4.29; 6.04	31.5	21.5	13.5
3						
left	12	2.9 × 2.2	5; 5.7	19.15	62.7	11
right	20	2.5 × 2.1	4.12; 4.94		37.5	11.5
4						
right	10.5	1.5 × 1.3	1.53; 1.53		71.5	10

In the "MF cross-section" column, the first value is at the outside of the bone, the second one at the side of MC. MF length and natural frequency are given without taking into account the oblique end.

radius not exceeding ~1.6 mm, and the MC in the MF region (radius <3.75 mm) represent acoustically narrow waveguides throughout the dolphin's hearing range 0.1−160 kHz.

The left and right series of MFs play the role of an array of elementary receivers of a travelling-wave antenna (TWA) [33, 35−38]. This array antenna is maximally sensitive in the direction of the series of elements (i.e. MFs). Obviously, when a sound wave is incident along the lower jaw (Fig. 1), it propagates in-phase inside and outside the antenna, so that the partial pressures of the wave having passed through each MF summate in-phase inside the MC (maximal sensitivity). If the wave is incident at an angle to the antenna axis, the phase synchronism of partial pressures inside the MC is violated and the antenna sensitivity deteriorates.

Sound conduction along the MF is analyzed in the model of an acoustically narrow pipe with losses and open ending. In this case it can be supposed that losses will be caused by sound-transparent tissues filling the lower-jaw channels. It is known that during transduction of forced vibrations, the natural vibrations of the pipe may be neglected, inasmuch as they are quickly damped by losses. Forced vibrations are practically unaffected by friction, except for the resonance case. For a narrow pipe with open ends, the natural vibration frequencies f_0 are determined from equation

$$kL = l\pi,$$

where $k = (2\pi f_0)/c_0$ is wavenumber; $l = 1, 2, 3, ...$ is vibration no.; c_0 is speed of sound; L is pipe length; whence

$$f_0 = (lc_0)/(2L).$$

The magnitude of loss, or damping factor η, for the exception of resonance can be assessed from known relationships. The half-width of the resonance curve for pipe natural vibrations at −3 dB corresponds to a change in kL by $\pm\eta kL$, i.e. the relative change in frequency $\Delta f/f_0 = \pm\eta$, where "+" and "−" correspond to η values for frequencies above and below the intrinsic one. The Q factor is $1/2\eta$. Consequently, at a Q factor of MF close to 1, $\eta = 0.5$ and resonance phenomena at frequencies of natural MF vibrations (table) will not exceed 3 dB in the entire dolphin hearing range, which is also necessary for the TWA function.

The transition time for forced vibrations in MF at a maximal transmission band (~140 kHz) will be close to $1/(2\Delta f) \approx 8$ μs. In this case, transmission of sounds and echoes through MF will be provided without distortion even if their duration is minimal (~20 μs). To add, the calculated transition time for forced vibrations is consistent with the potential temporal resolution of dolphin's probing pulses, close to 12 μs [42, 44].

It is known that the set of natural frequencies of an acoustically narrow waveguide depends on the shape of its end. For a narrow pipe with an oblique end, known is the "end correction" showing how the effective "acoustic" length of the end $\Delta\ell$ changes depending on the d/λ ratio, where d is end length; λ is sound wavelength; ℓ is pipe length. In the dolphin hearing frequency range the d/λ ratio for the oblique ends of MFs varies from 0.073 to 1.1; therewith $\Delta\ell/d$ varies from 0.51 to 0.82 and fall into the region of maximal steepness of $\Delta\ell/d$ change versus d/λ. For the MF ends the calculated $\Delta\ell$ in the 10−140 kHz range are 4−9 mm. As distinct from a straight-cut pipe having a harmonic series of natural frequencies, the overtones of an obliquely ending pipe are set anharmonically, and for this reason they are less excited and decay

faster upon cessation of the forcing oscillations. Consequently, the oblique endings of MFs will improve the damping of natural vibrations and smooth the unevenness of their frequency characteristic in transmitting broadband signals.

Inside the MC, the opening of each MF represents a monopole emitter. In the best hearing range 10–140 kHz, the wave size of the monopole is $kr = 0.028$–0.99, where $k = (2\pi)/\lambda$ is the wavenumber, r is the MF radius (0.7–1.6 mm). At the frequency of peak energy of dolphin's echolocation clicks (~110 kHz) and accordingly the peak auditory sensitivity, $kr \approx 0.67$ or $2r/\lambda < 1/3$. Such a monopole can be approximated with a pulsing small sphere of equivalent area. It is known that the radiation of sound energy is proportional to the active component of the radiation impedance of the source, r_R. For a pulsing small sphere, r_R grows steeply with kr as squared frequency up to $kr = 0.5$, and further the rate decreases, with 0.8 of the maximum reached at $kr = 2$. Consequently, MFs as emitters have optimal wave size and cross-section. What is the efficiency of such emitters? A monopole radiates a power $1/(kr)^2$ times less than a flat piston of the same area and vibration speed. Substituting the numerical values given above, we get that at the click frequency, the MF-emitted power is only $1/(0.67)^2 = 2.2$ times lower than that of a flat piston. On other words, the inner orifices of MFs at the given cross-section are quite efficient emitters inside MC.

Along the MF and the MC, the cross-section area grows smoothly (Fig. 5), whereas the MF cross-section at its outlet into MC is substantially smaller than that of the MC, so each MF and the respective part of MC jointly make an acoustic horn with a cross-section jump. In the narrow pipe model applied here, the sound entering the MC will be partly reflected in accordance with expressions (5) and (6) above. Notably, the reflection coefficient is proportional to the cross-section difference ($\sigma_{MF} - \sigma_{MC}$); i.e., reflection is significantly smaller than the ratio of cross-section areas of the channels, σ_{MF}/σ_{MC}. Therefore, only a small part of the sound is reflected at the junction. Calculations show that even at MF3, where σ_{MF}/σ_{MC} is ~1 : 5, not less than 60% of sound energy passes into the MC.

Along the TWA bases, the MF aperture areas and the σ_{MF}/σ_{MC} ratio decrease caudally (table). Both these factors specify a "dropping" amplitude distribution of the volume velocity of elementary receivers in the TWA array.

On the other hand, the different distances between MFs set different time delays in sound arrival to the MC, depending on the angle of sound wave incidence onto the MF; this dependence is important in calculating the TWA directivity pattern [35, 37]. If the speed of sound in MF tissues differs from that in MC tissues, the MF length will give an additional delay in sound arrival from each MF to MC, independent of the wave incidence angle. In such a case, each series of MFs may also represent a non-equidistant array of waveguide delay lines and perhaps specify an additional phase distribution of the TWA volume velocity. It should be noted that MFs, in spite of their laconic morphology, perform several complex combined functions, and their dimensions are optimal for such performance.

Interestingly, the MFs are in the narrowest part of the lower jaw where its halves touch each other, which suggests purposeful optimization of the distance between the left and right new external ears of dolphins [32], consistent with the telescoping of the skull in the evolution of Odontoceti as shown by Miller [41]. By this virtue, the dolphin has an optimal hearing base (0.75–3.5 cm); the transverse size of MF (~3 mm) specifies the aperture of the elementary receiver, while the sum section area of MFs in the left (17.23 mm^2) and the right (18.04 mm^2) halves specifies the aperture of the new external ears and the respective TWAs [32, 33, 35–38]. Optimal aperture and base of dolphin's hearing are of key importance for best protection of the dolphin's sonar against reverberation interference [32].

The characteristics of the acoustic horn were calculated in a catenoidal horn model, $y = 7.3(\cosh(0.01085x))^2$, with parameters corresponding to MF1 and MC (Fig. 5). Within the family of exponential/hyperbolic horns, at the given lower frequency limit the catenoidal horn is the shortest one, i.e., it has the maximal flaring rate.

The throat of the horn (MF1, table) is oval-shaped, 3.2×2.9 mm with a cross-section area ~7.3 mm^2. The mouth of the horn (Fig. 3) is flat, of complex shape with a cross-section area ~6333.6 mm^2. To determine the critical frequency and the lower frequency limit, use can be made of relationships (1) and (2), whence

$$f_c = 5.3 \text{ kHz.}$$

Thus the lower frequency limit based on the horn mouth size is

$$f = 5.3 \times 2.3 = 12.2 \text{ kHz.} \tag{7}$$

From (1), (3) and (4) we find

$$\beta = 0.01085 \ (1/\text{mm}), f_c = 2.59 \text{ kHz.}$$

That is, the lower frequency limit based on the horn flaring rate is

$$f_\beta = 2.59 \times 2.3 = 5.96 \text{ kHz.} \tag{8}$$

From these calculations, the lower frequency limit of the horn and TWA, and consequently the dolphin hearing, can be estimated at about 9 kHz. This result is consistent with the lower boundary of the frequency range (8–130 kHz) where the auditory thresholds of *Tursiops truncatus* are minimal (40–50 dB re 1 µPa) [50–52]. In other words, the horn determines the frequency range of best hearing and acts as a high-pass

filter, transmitting to the middle ear the sounds above ~9 kHz.

Let us consider some properties of the horn essential in dolphin's hearing. Under the energy conservation law, a horn does not add energy to the sound. It transforms acoustic energy of high pressure and low volume velocity in the throat into energy of low pressure and high volume velocity in the mouth, with a conversion coefficient $K_h = (S_m/S_t)^{1/2}$, where S_m is mouth area, S_t is throat area. That is, the dolphin's horn increases the volume vibrational velocity of sound about $K_h = (6333/8)^{1/2} = 28$ times, compensating for the lack of amplification of vibrational velocity shown for the middle ear in Odontoceti [17]. At the same time, an acoustic horn matches the radiation impedance of the emitter (at the throat) of size much less than the wavelength with the wave impedance of the medium. Therefore, the acoustic horn of the dolphin's lower jaw matches the radiation impedance of each MF inner orifice with the wave impedance of the fat body (in the mouth). Along with that, the best hearing frequency band (8–130 kHz) is about four octaves, which agrees with the practical requirements for minimizing the distortion of horn-transmitted signals. Consequently, the horn transmits the energy of sound waves from the surrounding medium onto the auditory bone in the entire hearing range practically without distortion and reflection.

What is the most important, throughout this frequency range the horn provides a traveling wave mode in the jaw channels, which is essential to the TWA function and energy transfer. This paramount issue defines the design of the dolphin's broadband external ear as a complex of TWA an acoustic horn. In this acoustically optimal combination, TWA perform sound reception (converts the incident sound wave regardless of the incidence angle into a wave traveling along the jaw channels) and together with the rostral bones partakes in forming the directivity pattern of the new external ear, while the horn ensures optimal matching of acoustical impedances and sound transmission onto the middle ear. Thus, the left and right rows of MFs and rostral bones may be supposed to play the role of auricles, by analogy to land mammals [33, 34].

Note that the throat of the MC horn acts as a "summator" where the sounds arriving via each MF are added, with corresponding amplitudes and time delays, and emitted by the horn in the direction of the lateral wall of the tympanum disposed near the mandibular joint. Since the lower jaw can move, and the tympanum is somewhat off the horn axis, the sound energy must be channeled and focused for more efficient transmission. This function is perhaps performed by the horn mouth (emitter), the posterolateral wall of the jaw (reflector), and the fat body (sound guide).

Let us consider the role of the reflector screen (Figs. 1–3). The minimal thickness of the mandibular posterolateral wall (in *Tursiops truncatus* [45]) is 1–3 mm. The posterolateral wall in the specimen studied is ~132 mm long (rostrocaudally), and dorsoventrally it is ~55 and 88 mm at the base of the horn mouth and at the joint respectively. The wave size of this region at 110 kHz are $kL > 25$–40 dorsoventrally and $kL > 80$ rostrocaudally ($k = 2\pi/\lambda$ is wavenumber, L is characteristic size of the bone). Inasmuch as the upper and lower jaws have large wave sizes and an acoustical impedance five times greater than water, they obviously act as an acoustically opaque screen. With jaws closed, the upper rows of teeth are between the lower rows (Figs. 2, 3), which decreases sound penetration via the mouth cavity from one side of the lower jaw to the other, so the acoustic screen is expanded by addition of the upper jaw and skull. Thus, the wave size of the acoustic screen comprising both jaws will exceed the calculated values severalfold. For such a screen, the condition of geometric scattering is fulfilled, $kL \gg 1$; therefore, in assessing its efficiency we must take into account the total internal reflection angle (α). The speed of sound in dolphin skull bones is $c_b = 3400$ m/s [48], the speed of sound in water is $c_0 = 1500$ m/s, whence

$$\sin\alpha = c_0/c_b = 1500/3400 = 0.44 \text{ and } \alpha = 26.2°.$$

The width of the beam pattern of sonar clicks in the horizontal plane does not exceed 10° relative to the longitudinal axis of the body [47–49]; consequently, the sector from which the dolphin mainly received the echoes is the same. In other words, the echo signals hit the lower jaw in the angular range of total internal reflection, $\beta \leq 94°$ (Fig. 6) (including the "acoustic windows").

It should specially be noted that the acoustic screen efficiency grows multiply in the total internal reflection range. Consequently, the posterolateral wall of the lower jaw cannot be an "acoustic window," but rather it is an acoustic screen for the fat body and auditory bone against sound that might arrive laterally from the outside. This issue is also favored by the fact of the sharp rise in auditory thresholds upon acoustic shielding of the MF region [33], and also by the above results of modeling. Moreover, the posterolateral wall is concave medially and convex laterally (Figs. 1–3), so that it can reflect and focus sounds onto the tympanum. The same applies to the shape of the horn mouth. At the same time, the reflector will act as a high-pass filter, reflecting sounds above a boundary frequency f_{br}, which can be determined from condition $ka = 1$, where $k = 2\pi/\lambda$ is wavenumber, λ— wavelength at boundary frequency, $a \approx 4.5$ cm — equivalent reflector radius. Hence $\lambda = 2\pi a \approx 28.3$ cm, and $f_{br} \approx 5.3$ kHz, which is consistent with the lower boundary of the range of minimal hearing threshold [50–52]. For efficient focusing of sound it is required that the reflector size be greater than several sound wavelengths, which
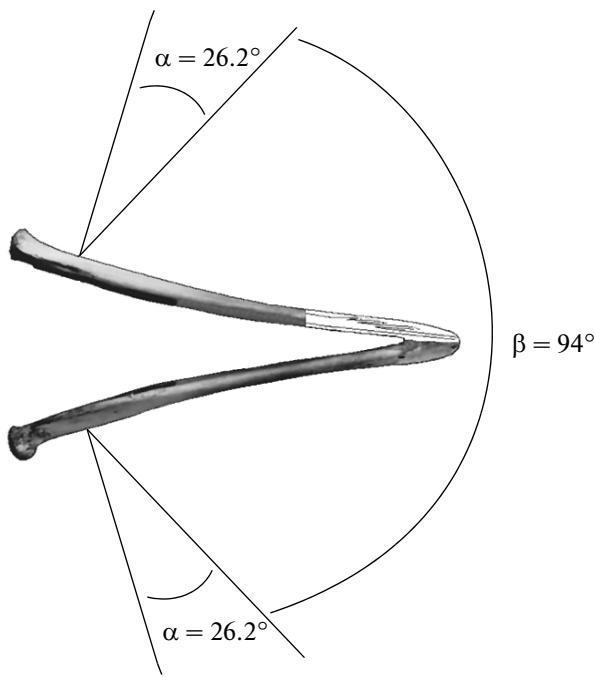
Fig. 6. Lower jaw, ventral view: α − angle of total internal reflection of the "reflector screen" region, β − sector of angles of total internal reflection of the lower jaw in the frontal plane.

is automatically fulfilled for frequencies above ~30 kHz ($\lambda \leq 5$ cm).

Thus, the results of this and previous works [33, 34] suggest that the MFs are the only way whereby the sound is passed into the MC fat body and further to the middle ear of the dolphin, ruling out sound conduction via other putative paths [1−3, 5, 7−11, 13, 19−22, 27−31].

In this connection, it is necessary to discuss the works on measuring the acoustic sensitivity of the dolphin head surface [5, 7, 20−22]. Methodically, all these works used a hydrophone or jawphone, with immediate contact of a point emitter (less than the wavelength in size) with the animal body. Thereby, in the head tissues (supposed receiver) and in the surrounding water a spherical sound wave is excited with its center determined by the position of the emitter (the «near acoustic field» of a point emitter). In contrast to that, the real sounds come to the dolphin from distances anyway not less than a meter. In this case the Fraunhofer zone ("far acoustic field"), where the phase difference between planar and spherical wave fronts is deemed small enough, begins at a distance to an undirected sound source that is defined as

$$D \geq L^2/\lambda,$$

where the receiver aperture $L \sim 8$ cm; wavelength (110 kHz) $\lambda = 1.36$ cm; thus, $D \geq 47$ cm. Consequently, the real sound reaching the dolphin from distances greater than ~47 cm is practically a plane wave.

Receivers presenting an aperture or, as in our case, an array of MFs sized larger than the wavelength serve for picking up a plane wave in the far acoustic field. Therefore, the spherical sound field of point emitters, not adequate to the receiver, could be the cause of that the mentioned works [5, 7, 20−22] reported different regions of the lower jaw to be the most sensitive, and the sensitivity maps were very complex. The authors have failed to unequivocally interpret their data, and regretfully, these results do not elucidate the sound conduction mechanism but rather complicate the model of sound perception. At the same time, the idea of the lower jaw as a system of two TWAs explains the mechanisms of sound conduction and of the formation of the hearing directivity pattern [33−38, 52]. Moreover, the results of morphological studies give grounds for supposing that the left and right peripheral divisions of dolphin's hearing comprise functional acoustical systems (Figs. 1, 3), and the elaborate pattern of architecture, shape and size of lower-jaw channels demonstrate the affinity of morphology and acoustics. It is astonishing how Nature has accommodated the entire complex of acoustical system of the new external ear in the dolphin's lower jaw!

CONCLUSIONS

It is known that in the process of adaptation to the aquatic environment, Odontoceti underwent extensive cranial modifications. The results obtained give grounds for supposing that one the most vivid modifications of their skull—telescoping [41]—is connected, among other things, with the disposition of the new peripheral auditory division in the lower jaw of Odontoceti, and the convergence of the left and right halves of the jaw in the region of MFs is caused by optimization of the aperture and base of hearing. Along with that, each series of MFs and the MC together with the rostral bones play the role of an auricle and new external auditory meatus (using the nomenclature for the ear of land mammals). But this is a qualitatively new external ear, realized by nature as a receiver antenna array and an acoustic horn of the new peripheral auditory division. It may be supposed that this division has formed as a result of adaptation of dolphin ancestors to the new conditions of habitation, both as evolutionary adaptation of the ear to water and as functional adaptation of the ear for performing new, more complicated functions in the structure of dolphin's sonars [34]. The results of the work give grounds for suggesting the existence of a similar peripheral auditory division in Odontoceti.

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