The Anatomy and Function of the Ear of the Bottle-nosed Dolphin *Tursiops truncatus*)*

by

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In two papers by DUDOK VAN HEEL (1959 and 1962) a description is given of experiments which were carried out on the audio-direction finding ability of the Common porpoise *Phocaena phocoena*. During these experiments it was found that the narrowest angle perceptible by the animal was about equivalent to that in Man, after adjustments had been made to the experimental frequencies to allow for the difference between the velocity of sound in air and sea water. This conclusion was based on the assumption that the working distance between the ears in the porpoise was about half that in Man, and it was pointed out that the relevant distance in the porpoise was that between the distal aspects of the tympanic bullae, whereas, in Man the dimensions used were those between the external ears. REYSENBACH DE HAAN (1957) and DUDOK VAN HEEL (loc cit) have stated that the well organised external auditory meatus and its associated muscles are without function in cetaceans as far as direction finding is concerned, and NORRIS (1961), although pointing out that his own experiments were inconclusive, has tacitly concurred with the view of REYSENBACH DE HAAN.

From the publications of the above authors, it would appear that none of them has examined the external auditory apparatus in detail, and since no descriptive literature has, as yet, been published relating to the external ear of *Tursiops,* the most famous of all experimental cetaceans, it was considered useful to describe this structure in *Tursiops* and to review the work of BOENNINGHAUS (1920) on the ear of the *Phocaena phocoena*. An account is also given of sound conductivity experiments which were carried out on the meatal structure of both animals.

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MATERIALS AND METHOD

The structure of the middle ear and inner parts of the meatus were examined from preserved, decalcified material in the British Museum (Natural History) and the dissection of the muscles, together with accoustic experiments were carried out on very fresh material in the Zoological Laboratory of Amsterdam. The skull and skeleton of the specimen of *Tursiops* which formed basis of the experimental work is now in the Zoological Museum, Amsterdam.

THE EXTERNAL AUDITORY MEATUS

The external auditory meatus of *Tursiops* was recognisable as a minute orifice on the side of the head 5.5 cms behind, and 1.5 cms ventral to the hinder corner of the eye, Plate I and Fig 1 (EAM). The meatus penetrated
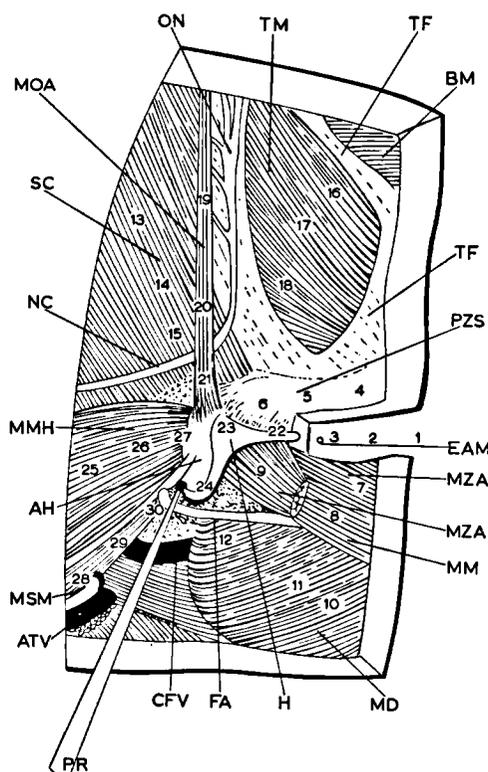

FIG. 1. Diagram to show the external auditory meatus and extrinsic muscles of the ear in *Tursiops truncatus*. The serial numbers show the points at which sound conductivity experiments were made (see Table I).

the blubber in a horizontal and slightly antero-posterior plane, as a pigmented tube surrounded by fibrous tissue and was found to contain a true lumen just large enough to admit a fine bristle. After passing through 2.35

cms of blubber, the meatus became encased in a conical mass of fibrous tissue which was found to be associated with a number of auricular muscles and the distal end of the auricular cartilage. Immediately anterior to the insertion of the sternomastoid and mastohumeralis muscles, Plates I, II, III and Figs 1, 2 (MSM, MMH), a reniform fibro-elastic lobe projected from the ventral aspect of the mastoid process of the squamosal Plate I and II and Figs 1, 2, 3 (AH). This lobe had an anteriorly directed flexure and supported along its ventral margin, a band of cartilage of a characteristic shape, consisting of a sigmoid, semi-tubular strip 1—2 mm thick and 6—7 mm wide, the concavity of which contained the lumen of the external auditory meatus.
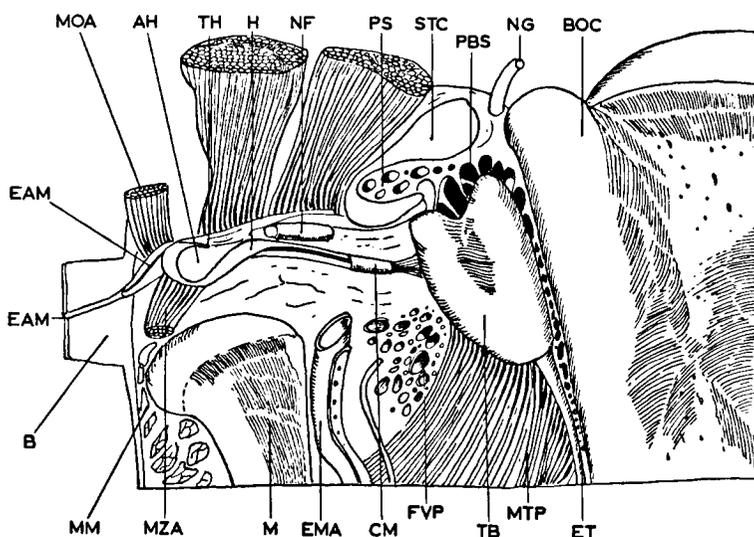
FIG. 2. Dissection of the middle and external ear of *Tursiops truncatus* (ventral aspect).

Deep to the conical mass of fibrous tissue referred to above, the lumen of the external meatus passed ventrally and anteriorly in a trough enclosed by the cartilage. The cartilage and meatus wound anteriorly and ventrally for 3.7 cms then posteriorly and dorsally and mesially towards the tympanic bulla. This proximal region of the cartilage was 8 cms in length and its convexity faced anteriorly and ventrally instead of dorsally as in the distal section.

From their inter-relationships, it seems likely that the meatal lumen, the fibro-elastic lobe and the cartilage can be regarded as a single unit, and as the homologue of the pinna of terrestrial mammals. The cartilaginous trough containing the meatal lumen can be regarded as the helix, Plate I and Figs 1, 2, 3 (H), and the fibro-elastic lobe as the antihelix (AH). The distal extremity of the helix had a small, mesially directed flange, which may be referred to the tail of the helix, Plates II, III and Figs 2, 3 (TH). At the

proximal end of the helix, 9 mms from the bulla, there was a second cartilaginous flange forming a continuous band of cartilage, completely enclosing the external meatus for 13 mms; this may be referred to as the cartilage of the meatus, Plate II and Fig. 2 (CM), JOHNSTON and WILLIS (1946). From this, a fleshy ligament covered the proximal 10 mms of the meatal tube and connected the cartilage of the meatus to the processus conicus posterior of the tympanic bulla.

The lateral extension and redisposition of the auricular cartilage from the typical mammalian form can be associated with the lengthening of the auditory canal in cetaceans and with the lateral extension of the mastoid process of the squamosal. Its subdermal position can be associated with the proliferation of the panniculus adiposus, or blubber.
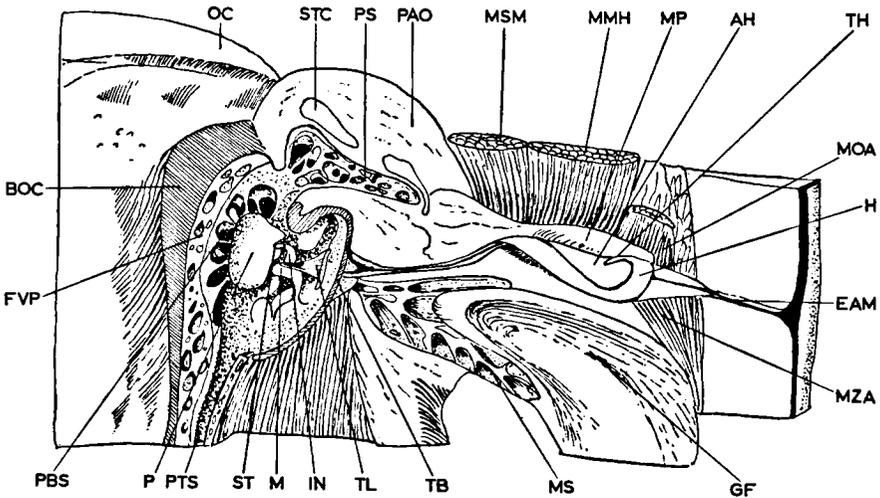

FIG. 3. Dissection of the middle and external ear of *Tursiops truncatus* after removal of half of the tympanic bulla (ventral aspect).

The helix was in relation on its anterior aspect, to the ventral margin of the glenoid fossa, Plate III and Fig 3 (GF) with which the lower jaw articulated. On its posterior aspect, it was in relation to the insertion of the sternomastoid and mastohumeralis muscles. The cartilage of the meatus passed anteriorly to the styloid cartilage, Plate II and Fig 2 (STC), and posteriorly to the posterior wing of the middle sinus, Plate III, Fig 3 (MS) and its fibro-venous plexus, Fig 2 (FVP). The mandibular branch of the facial nerve, Plate II and Fig 2 (NF) emerged from the styloid foramen posteriorly to the proximal limit of the helix. On the antero-dorsal aspect of the bulla, a thick band of muscle was inserted into the processus tubaris of the periotic and the lateral margin of the osteum tympanicum tubae and Eustachian tube. This was identified as the tensor palati muscle, Plate II, III and Fig 2 (MTP) which enclosed on its mesial aspect the pterygoid

air sac, Plate III and Fig 3 (PTS) and fibro-venous plexus. The tympano-periotic bones were, as is usual in cetaceans, separated from the cranium by the peribullary system of air spaces, Plates II, III and Figs 2, 3 (PBS).

THE AURICULAR MUSCLES

Deep to the blubber and superficial fascia, a straplike muscle originated by a strong tendon from the supraoccipital crest and passing ventrally, super-ficial to the splenius capitis, became gradually broader and more fleshy, and was inserted fleshily into the superior, distal extremity and anterior face of the antihelix. This muscle was indentified as the retrahens of MURIE (1873), the occipito-auricularis of BOENNINGHAUS (loc cit) and the auricu-laris externus of BEAUREGARD (1894), Plate I and Fig I (MOA). It was, however, perhaps because of the freshness of the material, much stouter than the muscles described by these authors and was richly innervated by small twigs from the lesser occipital branch, Plate I and Fig 1 (ON), of the second cervical nerve, Fig I (NC), In *Phocaena,* the fleshy part of this muscle was relatively much longer than that depicted by BOENNINGHAUS. Originating by an aponeurosis from the superficial fascia of the masseter muscle, Plate I and Fig 1 (MM), near the origin of that muscle on the zygomatic process squamosal, Plate I and Fig 1 (PZS), a fan-shaped group of small muscles passed postero-dorsally and were inserted fleshily into the anterior face of the antihelix. These muscles were identified as the combined attolens and attrahens of MURIE, the zygomaticoauriculus of BOENNINGHAUS, and the auriculolabialis inferior of HANKE (1914), Plate I and Fig 1 (MZA). These muscles were innervated by branches of the facial nerve.

On the left side of the animal, the general disposition of the meatus and auricular cartilages was similar to that on the right, but it was noteworthy here that in *Tursiops* the fibro-elastic lobe, or antihelix, was semi-discoid in appearance and the sigmoid cartilage of the helix had a more deeply, ventrally directed flexure. In a dissection of the meatus of the Pilot Whale, *Globicephala melaena* figured by FRASER and PURVES (1954) there appears to be no ventrally directed flexure of the cartilage of the helix, but instead, a pronounced dorsally directed flexure at the distal end. Similarly, in a specimen of *Phocaena phocoena* described and figured by BOENNINGHAUS (loc cit) the auricular cartilage has a dorsally directed flexure at its distal extremity. In the dissection of the meatus of *Phocaena* prepared by the present writers, the distal end of the meatus had a ventrally directed flexure. In BOAS (1912) figure of *Phocaena,* there is no noticeable flexure of the cartilage at all. It is conceivable that the action of the superior auricular muscle can substantially alter the shape of the helix, and that the differences in the flexure of cartilage described by various authors, can be attributed to the state of tension of this muscle at the time of dissection. The possible significance of voluntary control of the internal "pinna" will be discussed later, but it is of some interest to note at this stage that HUNTER (1787), in describing the meatus of the Porpoise, stated "It passes in a serpentive course, at first horizontally then downwards, and afterwards horizontally

PLATE I. Dissection to show the external auditory meatus and the extrinsic muscles of the ear in *Tursiops truncatus*.

again, to the membrana tympani, where it terminates. In its whole length it is composed of different cartilages, which are irregular and united together by cellular membrane, so as to admit of motion and probably of lengthening and shortening, as the animal is more or less fat".

In the first dissection of decalcified material of *Tursiops* on opening the tympanic bulla, the corpus cavernosum was found apparently to be occupying the whole of the middle ear cavity. It had to be removed piecemeal in order to expose the structure of the middle ear. On removal, it was found that the auditory ossicles were encased in a small, spherical mass of solid rock salt. As the specimen had been immersed in a decalcifying solution of brine for six months, this was taken to imply that in spite of the swollen appearance of the erectile tissue of the corpus cavernosum, an envelope of air had persisted around the ossicles, forming a cavity in which the salt had infiltrated and crystallized. The implication of this observation is that in life, whatever the state of turgidity of the corpus cavernosum, and whatever the hydrostatic pressure, a small capsule of air is maintained round the auditory ossicles, in order to facilitate their proper functioning. It was noteworthy in this respect that the epithelium of the tympanic cavity was devoid of mucous glands.

The second dissection of *Tursiops* was performed on extremely fresh material, and the structures were, therefore, considered to be suitable for sound conductivity experiments. For this purpose, a conical steel probe containing a barium titinate ceramic, was placed so that its apex touched the proximal extremity of the auditory meatus, near the tympanic annulus. This probe was then connected to a cathode follower, amplifer, oscilloscope and voltmeter. The muscles and structures in the vicinity of the meatus and the meatus itself were then touched at various points with another barium titinate probe to which was connected the output of a variable frequency oscillator. Two sets of voltmeter readings were taken at 10 Kc and 70 Kc respectively at identical points on the dissection and it soon became obvious that at both of these frequencies the cartilaginous meatal tube was by far the superior sound conductor. The decibel scale of the voltmeter used a standard of 1 MW into a 600 ohms line as zero decibels. This corresponds to 0.774 volts AC after amplification on the received signal through 80 Db and thus represents an intensity level slightly above the threshold of human hearing.

It will be seen from Table 1, that the sound intensity received from points on or near the meatus, especially those on the auricular muscles are at least 10 Db above those a few centimetres away from the tube. It is interesting in this respect that points near the insertion of the sternomastoid muscle also gave good readings. It will be recalled that the auricularis posterior muscle of terrestrial mammals originates in close proximity with the insertion of the sternomastoid. Although no sign of an auricularis posterior could be found in *Tursiops* it is more than likely that the fibrous sheath of the antihelix which connects this structure to the mastoid bone is composed of the remnant of the fascia of this muscle. It may be seen from Plate II

that none of the more distant points on the external musculature are significantly further away from the tympanic annulus than the distal end of the meatus itself. In many cases they are nearer. This difference of 10 Db intensity cannot be accounted for on the assumption that all the soft structure

TABLE I

Position	Db Above Ref at 10 Kc	Db Above Ref at 70 Kc
1	2.5	1,5
2	3	4
3	6	4
4	0	0
5	0	0
6	0	0
7	1.5	4
8	2.5	4.5
9	13	16
10	2	1.5
11	3.5	2
12	15	14.5
13	5	2.5
14	2	2.5
15	2	2.5
16	0	1
17	0	1.5
18	0	1.5
19	1	3
20	12	14
21	15	15
22	12	14.5
23	14	16
24	15	16

in the vicinity of the ear behave alike with respect to the attenuation sound waves as VAN HEEL (loc cit) asserts. During these experiments, it was found that the sound conductivity from one type of soft structure to another, and from soft structures to bone, was relatively very bad. For instance, blubber is an extremely good conductor but will not readily transmit sound to the underlying muscles. It was found that the attenuation through 60 cms of blubber alone was less than that through 2 cms of blubber plus 1 cm of subjacent muscle. Fig 1 and Table 1 show that points sumalated on the zygomatic process of the squamosal bone, all gave zero decibels transmission to the tympanic annulus. These differences in transmission had nothing to do with the presence of air bubbles in the tissues, but with the inherent variability of the molecular arrangement of the structures involved. This fact was demonstrated by passing the same frequencies through the present writers' limbs, which, presumably, contained no air bubbles. The transmission could be made to vary through about 15 Db by merely changing the tension and attitude of the muscles. Moreover, the oscilloscope display showed that

the original pure tone underwent considerable modification within the various structures, some wave trains arriving at the receiving end, several degrees out of phase with others.

If it be accepted that the external auditory meatus of cetaceans is a relatively superior sound conductor, then it may be seen that this structure is of considerable significance in audio-direction finding, not only from the point of view of time difference, but also from the point of view of sound spectrum differences produced by the various air cavities in the head. Plate II, shows that the distal extremity of the meatus lies directly lateral to the tympanic cavity and to the extensive system of peribullary air spaces which surrounds it. This system of air spaces is about 4 cms deep and 4 cms long and communicates with a maze of accessory air sinuses even more extensive in area, see FRASER and PURVES (1960), whose primary function is that of maintaining an air space in the tympanic cavity and in the peribullary sinuses at all hydrostatic pressures. Nevertheless there is evidence, FRASER and PURVES (loc cit) that in these accessory sinuses a thin film of air persists whatever the pressure conditions.
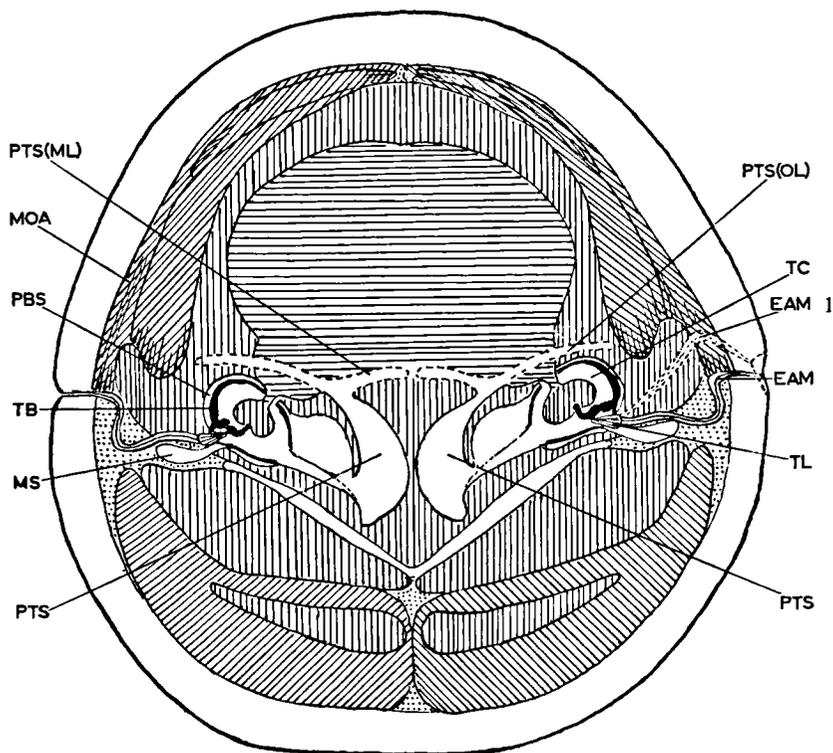

FIG. 4. Schematic representation of the air sinus system in various transverse planes of the head of a cetacean showing their relationship to the middle and external ears.

DISCUSSION

Fig 4 is a schematic drawing representing a composite illustration of the arrangement of the air spaces, excluding the nasal passages, which are to be found in various transverse planes in the head. The peribullary air spaces (PBS) alone casts a considerable sound shadow to freqencies above 40 Kc and the accessory sinuses to much lower frequencies. If the distal extremity of the meatus (EAM, EAM_1) could be made to move in and out of these shadows voluntarily, then the intensity and quality of sound received from the opposite side of the head could also be varied voluntarily. It is of very great significance that the occipito-auricularis muscle is of a strap-like form and pulls directly upwards at the distal extremity of the meatus. According to WHEELER-HAINES (1932) muscles of this type normally contract to 57% of their length when relaxed and fully stretched, the length of their fibres bearing a constant proportion to the extent to which the origin and insertion can be approximated. The fleshy part of the muscle measured 6 cms in the specimen of Tursiops figured and would thus be capable of contracting by about 2.6 cms. Now it happens that this figure is almost exactly equal to that part of the meatal length which is given by the curvature of the cartilage, so that contraction of the muscle, if powerful enough, would result in the stretching and elevation of the cartilage to its full lengh in a straight line. This action would also produce a considerable torque on the cartilage and it is significant, therefore, that the latter does not constitute a closed tube. A closed spiral tube of cartilage would, upon extension, be subject to unequal stresses at various points on its walls, which would inevitably lead to rupture of the cartilage at these points. The arrangement in Tursiops is such that the semitubular lumen of the meatus would tend to become tubular on extension without the occurrence of unequal stresses. Unequal stresses could also be avoided by the provision of a multiple cartilage system such as is found in Phocaena and some other species, e.g. Globicephala.

It is of some interest to note that there appears to be no discrete muscle acting antagonistically to the occipito-auricularis in Cetacea, nor to the auricularis superior in Man and terrestrial mammals. When it is recalled, however, that the upper, anterior extremity of the platysma myoides lies level with the base of the pinna and zygomatic bone, it may be imagined that this sheet of muscle acts as antagonistically to muscles which tend to elevate the pinna.

If the detailed mechanical structures of the external ear of cetaceans are fully functional as they appear to be, then they would operate to alter the intensity and frequency spectrum of sound received at the middle ear, exectly as they do in terrestrial mammals, but whereas, in terrestrial mammals the pinna and the head cast the "shadows", in cetaceans, these are created by internal films of air.

The observation of KELLOG (1962) and many previous workers, that Tursiops regularly scans objects at close quarters by swinging the head from side to side, is a matter for some discussion. KELLOG attributes this behaviour to the necessity for producing time and intensity differences at the two ears.

PLATE II. Dissection showing the middle and external ear of *Tursiops truncatus* (ventral aspect).
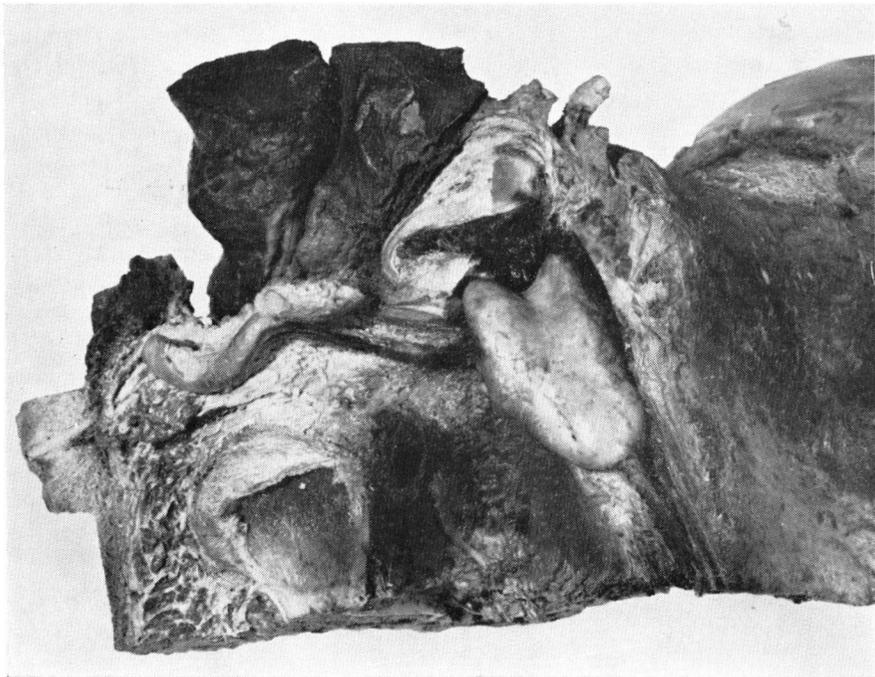

PLATE III. Dissection showing the middle and external ear of *Tursiops truncatus* after removal of half of the tympanic bulla (ventral aspect).

Whilst this may to some extent be true, it cannot be regarded as the complete explanation, for there remains for consideration the directionality of the echo-locating pulse. KELLOG states that the sounds emitted by Dolphins do not appear to be highly directional "probably no more so than the human voice", but a moment's contemplation will show that on anatomical grounds alone this cannot be true. The anatomy and mechanism of phonation in cetaceans form the subject of a paper which will be published shortly by the present writers, but a few comments may be made in advance. The non-directionality of the human voice is primarily due to the fact that the shortest wave length of sound emitted by Man is greatly in excess of the linear dimensions of the mouth. The limits for the human voice are given in Table 2.

TABLE II

Bass	F_1 to D_3	85 to 288 vibrations per second
Baritone	A_1 to F_3	106 to 340 „ „ „
Tenor	C_2 to A_3	128 to 424 „ „ „
Alto	E_2 to C_4	160 to 512 „ „ „
Soprano	B_2 to G_4	240 to 768 „ „ „

(Mc KENDRICK)

The wave length of the highest note in this table is approximately 45 cms, i.e. ten times the width of the open mouth. In these circumstances, the mouth acts as a single source, so that there is very little directionality in the sound field. If Man were able to produce sounds as high as 8 kilocycles or over, the bilateral symmetry of his mouth would ensure that the sound field would become directional along the central axis of the oral cavity. In this case the mouth would be acting as a double or multiple source. The problem is essentially one of diffraction and interference, analagous to the propagation of plane waves of light through a circular aperture, regarding the open mouth as the source of sound in accordance with HUYGHENS priciple. On the central axis of the mouth, the sound intensity would always be at a maximum, for all the disturbances from the various elementary areas constituting the plane of the open mouth and lips would arrive along the central axis in the same phase. In directions inclined to the central axis, the intensity would be less, diminishing steadily to zero when the difference between the nearest and farthest elements of the open mouth were rather more than half a wave length. In a direction still more inclined, the sound would increase again to an intensity 0.017 of that on the axis, passing through successive zero and diminishing maxima values as the inclination increased. In this case the angle at which the first silence occurs i.e. the semi-angle of the cone which delimits the primary beam is sin $^{-1}$ (0.61 λ/R) where R is the radius of the mouth. Thus the primary, or central beam, would be confined to a cone of small angle when the radius of the mouth was large compared with wave length of the sound emitted, i.e., the directionality would be sharp when the frequency of the sound was high.

Anatomical investigations and experimental work on fresh, dead specimens of *Phocaena, Lagenorhynchus* and *Tursiops* have shown that the phenomenon

of diffraction occurs to a marked degree in the propagation of laryngeal sound through the head, this being due to the bilateral symmetry of the larynx, palato-pharyngeal muscles, air cavities and skull. The general inference from these experiments was that in the odontocete cetaceans the vocal assembly acted as a triple source over a wide range of frequencies. In an earlier paper, KELLOG et al (1953) showed that the echo-locating pulses of *Tursiops* contained frequencies as high as 120 Kc and a great number of components above 25 Kc. According to these authors, SCHEVILL had recorded components up to 195 Kc.

In view of the linear dimensions of the anatomical structures involved, with respect to the wave lengths of these components, directionality due to interference, could hardly be avoided, and this fact seems to be demonstrated in the experimental results of KELLOG et al (loc cit). The authors have graphed the average relationship between intensity and frequency over a large number of porpoise clicks and there appears to be no evidence to suggest that some components of high frequency are emitted with greater amplitude than others of lower frequency or vice versa. The graph shows the typical "die away" curve of intensity with increasing frequency, a phenomenon which would be attributable both to the attenuation of high frequency sound waves in water and, as the authors suggested, to the reduced performance of the apparatus at the higher frequencies.

The oscilloscope display of the frequency analyses of a single click however, does not show this result. The display shows that there were components at 100 Kc and over, which were received at the hydrophone with greater amplitude than those at 50 Kc and under. This disparity between the average, and instantaneous intensity values, can hardly be explained, except on the assumption of interference and diffraction phenomena.

Thus the oscillating movement of the head of the porpoise at close quarters may also be correlated with an attempt to appreciate frequency spectrum differences in the echoes from directional beams of sound.

SUMMARY

1. Attention is drawn to the divergence of opinion about the functionality of the external auditory meatus in cetaceans.
2. The external auditory meatus and auricular muscles of *Tursiops truncatus* are described and figured.
3. An account is given of sound conductivity experiments which were carried out on the auditory structures in a very fresh, dead specimen of *Tursiops*.
4. The probable function of the external auditory meatus is discussed in

relationship to the arrangement of the accessory air sinuses of the middle ear.

5. The so-called "auditory scanning" behaviour in odontocete cetaceans is commented upon in the light of preliminary experimental evidence of a vocal sound diffraction pattern.

LIST OF ABBREVIATIONS

AH	Antihelix
B	Blubber
BOC	Basioccipital crest
BM	Blowhole musculature
CFV	Common facial vein
CM	Cartilage of meatus
ET	Eustachian tube
EAM	External auditory meatus
EMA	External maxillary artery
FA	Facial artery
FVP	Fibro venous plexus
GF	Glenoid fossa
H	Helix
IN	Incus
MP	Mastoid process
MA	Mandible
M	Malleus
MD	Digastic muscle
MM	Masseter muscle
MMH	Mastohumeralis muscle
MOA	Occipitoauricularis muscle
MS	Middle sinus
MSM	Sterno mastoid muscle
MZA	Zygomatico auricularis muscle
NC	Cervical nerve
NF	Facial nerve
NG	Glossopharyngeal nerve
ON	Occipital nerve
OC	Occipital condyle
P	Periotic
PR	Probe
PS	Posterior sinus
PAO	Paroccipital
PBS	Peribullary sinus
PTS	Pterygoid sinus
PTS(OL)	Pterygoid sinus, optic lobe
PTS(ML)	Pterygoid sinus, mesial lobe
ST	Stapes
STC	Styloid cartilage

TB   Tympanic bulla
TF   Temporal fascia
TH   Tail of helix
TL   Tympanic ligament

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