A Theory for the Function of the Spermaceti Organ of the Sperm Whale

(*Physeter catodon L.*)

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WITHIN THE SPERM WHALE FOREHEAD lies the spermaceti organ, occupying as much as 40 percent of the entire length of the whale. It is a huge, somewhat flattened, cone-shaped structure. It is covered dorsally and laterally by a thick wall of intermeshing ligamentous cables, many as thick as a man's thumb. In the day of the hand whaler, this stout outer structure was called "the case." The organ is filled in life with as much as 1900 liters of a liquid, or semiliquid waxy oil, the spermaceti—the material once so prized for candles and illuminating oil. Surrounding this organ at either end and below are air sacs, which are part of a complicated series of highly asymmetrical nasal passages, valves, and associated structures. The functions of this complex have been subject to some speculation. See discussion in Appendix. Also, Raven and Gregory (ref. 1) speculated that the case and its contained spermaceti "is to make diving possible by firmly closing the outer and inner nasal passages." They go on to say:

> We infer that its main function is to act as a force pump for the bony narial passages, drawing a great quantity of air into the respiratory sacs and perhaps preventing the escape of air under the pressures of the great depths. It may also act in part as a hydrostatic organ since by severe contractions of part of its muscular sheath, the contained oil might be squeezed toward one end or the other, while the air sacs were being inflated, thus lightening the specific gravity of that end and tending to alter the direction of motion of the animal.

It is difficult to interpret exactly what Raven and Gregory mean by a "force pump," but we assume it means that movements of the spermaceti organ are capable of drawing air out of the posterior air spaces (lungs, trachea, head canals, middle ear) into the nasal sacs of the forehead. The idea,

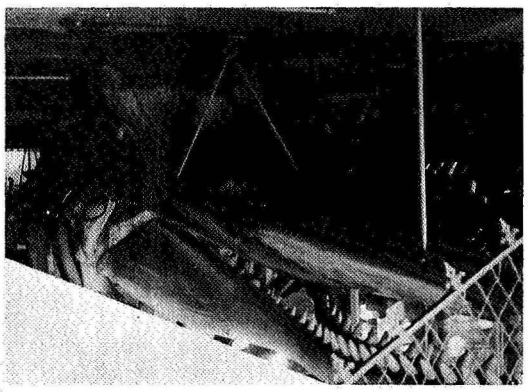

FIGURE 1a. Sperm whale skeleton at the Museum of Comparative Zoology, Harvard University. Note the low channel-shaped rostrum and the amphitheatre-like forehead. The spermaceti organ lies above the rostrum and is bounded posteriorly by the frontal sac which tightly adheres to the amphitheatre walls. Photo courtesy William Schevill, Harvard University.

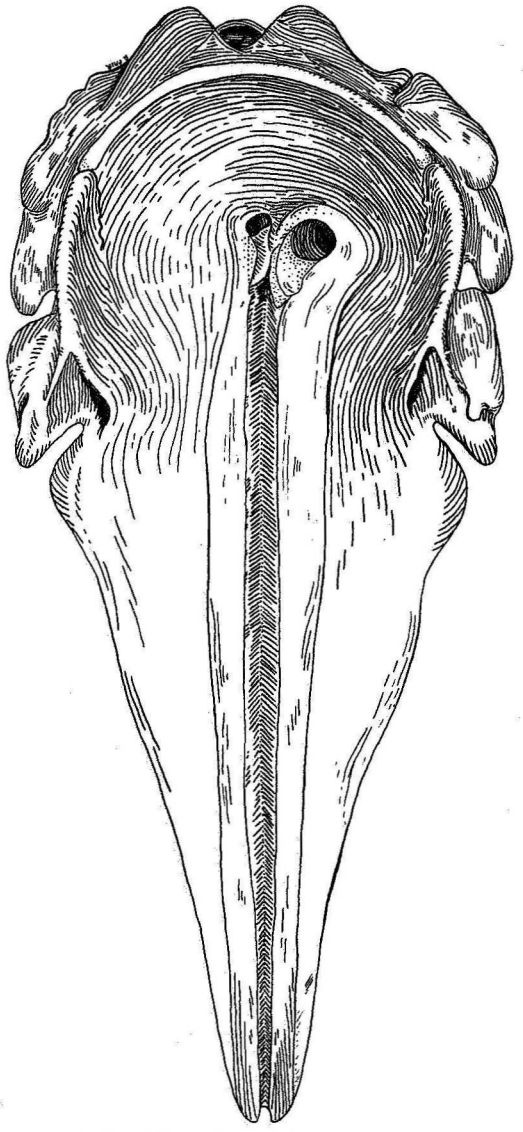

FIGURE 1b. Plan view of the sperm whale skull showing the asymmetry of the superior bony nares and their disparate sizes—from skull in Los Angeles County Museum.

we assume, is that such additional air in the nasal sacs of the head when under pressure would serve to close the nasal passages enough to prevent air loss under the pressure of diving. The ideas are certainly partly incorrect for reasons we will discuss later, and the suggested functions seem unlikely. However, we do not discount the possibility that the musculature of the forehead may be involved in a cycling of air within the sac system of the forehead.

This paper presents a new theory for the function of the complex as a whole and brings forth some supportive evidence for our views. Briefly we suggest that (1) the spermaceti organ is an acoustic resonating and sound-focussing chamber used to form and process burst-pulsed clicks; (2) the nasal passages of the forehead not only allow the repeated recycling of air for phonation during dives, but provide mirrors for sound reflection and processing; and (3) this entire system allows sound signal production especially useful for long-range echolocation in the deep sea.

To show the basis for these ideas, we will first examine the pertinent details of anat-

omy, then review what is known about the sounds of sperm whales, presenting at this time some new data, and then draw these facts together into a coherent theory. Finally we will describe a model of the sperm whale acoustic system with which we have produced simulated sperm whale signals. This simple apparatus, which was built using engineering design criteria we see in the animal, produces remarkably similar signals to those recorded from living whales.

During the course of this work, two fetal sperm whales were examined, an adult was dissected, and various samples obtained for histologic analysis. The species was observed and recorded at sea on three occasions. Various observations and measurements have been made on museum skeletal material.

These ideas were conceived nearly 4 years ago and opportunity to test them has been sought since that time. It has not come easily, so the information is presented at this time, incomplete as it is, in hope that others may be able to contribute.

The ultimate proof, rejection, or refinement of our ideas must probably await experiments on living sperm whales, but we feel that our information is sufficiently advanced and documented to make it useful at this time, especially in view of the rarity of opportunity to work on living examples of this species.

THE ANATOMY OF THE SPERM WHALE FOREHEAD

The Skull

Perhaps the most noteworthy aspect of the sperm whale skull is the amphitheatre-like, nearly parabolic forehead and the broad low rostrum extending forward from its base to the tip of the snout (fig. 1A, 1B). Because the slim elongated tooth-bearing lower jaw is wholly ventral, like that of a shark, and the rostrum lies above it, the great majority of the huge forehead of the whale is composed of soft tissue.

The bony nares pierce the rostrum near its base and are highly asymmetrical. At the surface of the rostrum in adult whales, the right naris is approximately one-seventh the cross-sectional area of the left naris and is located on the midline lying almost equidistance from all points on the curved amphitheatre (fig. 1B). This amphitheatre is formed largely by the premaxillary, maxillary and nasal bones. The larger left naris is well displaced to the left.

In the living animal, the bony amphitheatre is covered over most of its area with the tightly adhering posterior wall of the frontal sac, a diverticulum of the right nasal passage. The bony rostrum, which in coronal section is shallowly dish-shaped (fig. 1A), is filled by the "junk." Junk is an old whaler's term for this fatty mass, tightly bound in connective tissue, that was less valuable than the spermaceti. It is separated from the spermaceti organ above by a broad channel-shaped anterior branch of the right nasal passage.

Spermaceti Organ and Nasal Passages

The spermaceti organ extends posteriorly from just beneath the tip of the snout to the anterior skull amphitheatre. The great relative length of the organ is accounted for in part because the snout of adult sperm whales overhangs the upper jaw by about 5 percent of the total length in adults (ref. 2). The spermaceti organ is bounded at both ends by the large vertically oriented air sacs mentioned above. The ligamentous case surrounding the spermaceti organ is extremely stout and difficult to pierce even with a sharp knife. When one does penetrate this layer

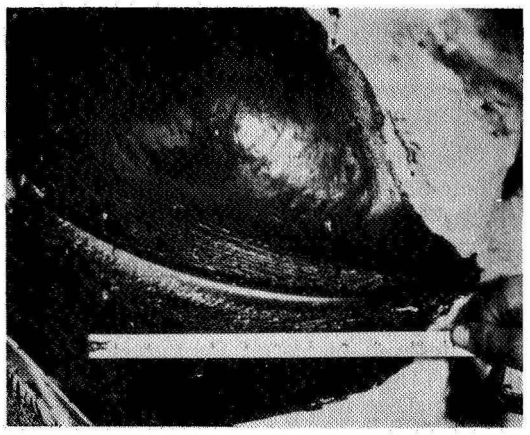

FIGURE 2a. ***Museau du Singe,*** **or monkey's muzzle, of an 11-m sperm whale dissected at Richmond Whaling Station, California. Whale has been cut through the anterior snout at the point of inflexion above the upper jaw and the distal sac reflected from the museau lips. In lower left corner note triangular band that normally rests between the lips of the museau. Bulbous upper lip of the museau is actually the anterior extension of the spermaceti organ, and the lips cross its entire width. Rule in inches.**

during dissection of a fresh specimen, liquid spermaceti exudes forth as if under considerable pressure.

To describe the organ in more detail, it seems best to start from the anterior end of the animal and work posteriorward to the amphitheatre of the skull. The anterior surface of the sperm whale snout is strongly indented both laterally and transversely across the whale's forehead a few inches above the upper jaw, and flares out above into the bulbous forehead which bears the asymmetrically placed single S-shaped blow hole on its anterolateral surface.

If one makes a horizontal cut into this indentation, very dense connective tissue is first encountered, which is much thicker above and below the indentation. After penetrating a centimeter or two through this tissue, the distal sac is encountered, which spreads across the width of the snout. By reflecting the walls of this sac, the *museau du singe*, or monkey's muzzle (fig. 2A), is exposed (see refs. 3 and 4). This structure consists of a pair of extremely stout black lips, occupying nearly the entire width of the posterior wall of the distal sac (fig. 2B). They close the anterior end of the right nasal passage.

The spermaceti organ ends anteriorly in the upper lip of the *museau du singe* as a very flattened oval of liquid-filled space that gives way anteriorly to more tightly bound lipid material and finally to dense connective tissue within the upper lip. The organ becomes much deeper as one explores posteriorly, in the form of a wedge, curving slightly over the junk until it reaches the amphitheatre of the skull. There its posterior wall consists of a smooth, nearly circular, vertically oriented wall that forms the smooth anterior face of the frontal sac. This wall looks very much like the head of a bass drum, although it is much more flaccid, and one may press it inward with a modest pressure of the thumb.

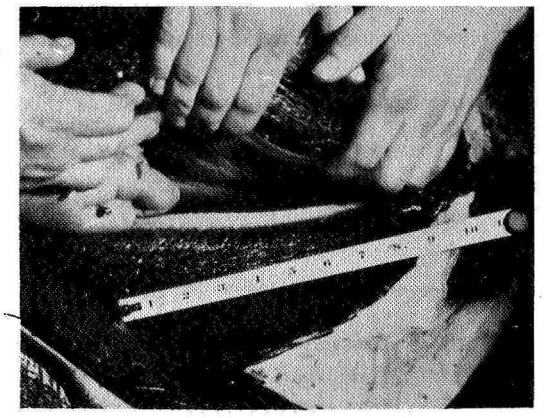

FIGURE 2b. Pulling museau lips apart requires considerable force. Notice cornified band between two hands on right and black grooves behind.

Looked at in their totality, the nasal passages form a nearly horizontal U-shaped loop, formed of sacs and canals, running from one bony naris forward to the tip of the snout and back again into the other bony naris (fig. 3). At its left anterior corner, this loop is pierced by the S-shaped blowhole. If we follow this loop around, starting at the right bony naris, first encountered is a muscular valve that is presumably capable of closing the right naris. Dorsal to this plug, the right passage bifurcates and one branch extends nearly vertically and expends into the frontal sac. This sac covers nearly the entire anterior face of the skull amphitheatre (fig. 1A).

The other branch enters between the junk

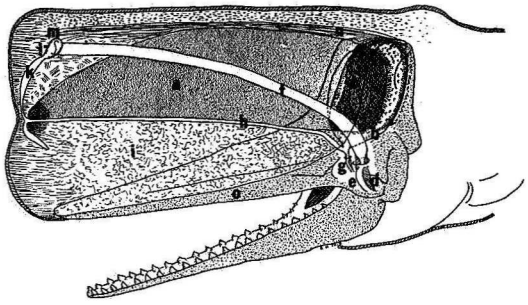

FIGURE 3. General diagram of nasal passages and spermaceti organ of sperm whale forehead. Oblique view to show relative positions of right and left nasal passages.

- **A. Spermaceti organ**
- **B. Frontal sac**
- **C. Skull amphitheatre lined with fluid-filled knobs**
- **D. Pterygopharyngeus muscle**
- **E. Left bony naris**
- **F. Left nasal passage**
- **G. Right bony naris**
- **H. Right nasal passage**
- **I. Junk**
- **J. *Museau du Singe***
- **K. Distal sac**
- **L. Connecting sac**
- **M. Blowhole**
- **N. Ligamentous case**
- **O. Rostrum**

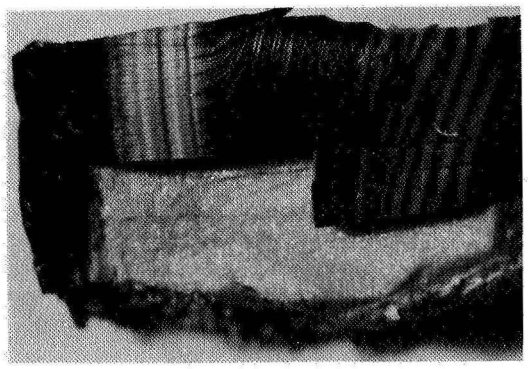

FIGURE 4a. Section cut through lower lip of *museau du singe* of an 11-m sperm whale, showing the blackened grooves behind (right) that swing perpendicular to cornified band that arcs along lip border. Note three raised ridges of the band and two grooves, and also the fine hair-like extensions of the grooves that cross the cornified band. At left is seen the stiff crenulated tissue of the distal sac found above and below the museau lips.

and the spermaceti organ and passes forward as a broad thin-walled horizontal sac. Near the tip of the snout, it narrows and passes between the lips of the *museau du singe*. Posterior to the *museau* the sac walls, both above and below, are marked by a peculiar group of numerous approximately parallel black lines that curve across the sac at roughly right angles to the body axis on both dorsal and ventral sac walls, as mirror images of one another (fig. 4A). They then turn and run along the trend of the longitudinal body axis for a short distance before reaching the posterior edge of the curving *museau*. They are so arranged that at the posterior border of the lips they are spaced with great regularity across the arc of the lips approximately 0.05 mm apart in our specimen. If one views these lines in reflected light, it is at once obvious that they are not simple pigmented stripes but actually shallow grooves that become deeper (0.03 mm) as they approach the lip

FIGURE 4b. Cross section through the museau of the same whale. To the left (a) are blackened grooves cut obliquely. At (b) note the very thick pellucid cornified tissue of the lip band. Grooves and ridges are not very evident in cross section.

border (fig. 4B). The groove profile is saw-toothed where the grooves cross the width of the sac. Thus, if one moves a dissecting needle anteriorly across the sac wall, a broad interspace between grooves is first encountered, and the needle then moves downward into a groove whose anterior wall is an abrupt face. The grooves on the upper and lower sac walls are mirror images of one another and thus, when the sac walls are pressed together, a series of tubelike curving channels probably results. Fine hairlike grooves actually can be traced across the *museau* running at right angles to the curve of the lips (see fig. 4A). We believe these grooves to be an adaptation allowing uniform disbursement of the tiny volumes of air that occupy the sacs during deep dives—a point we will return to later.

The lips of the *museau du singe* empty into the distal sac, a roughly triangular flaccid black-walled air space swinging off to the right as one explores dorsally from the *museau*. The sac effectively covers the entire anterior end of the spermaceti organ.

At the left corner of the *museau* a passage, the *connecting sac*, connects the distal sac with the vestibule, a small space lying just below the S-shaped blowhole and thence connecting into the left nasal passage. The otherwise black anterior wall of the distal sac bears a white horizontal ridge of stiff connective tissue, which fits precisely into the anterior line of the *museau* lips (fig. 5).

The left nasal passage passes posteriorly from the blowhole along the lateral surface of the spermaceti case as an elongated pipe-like tube whose thick opposite walls interlock with one another in a roughly S-shaped cross section. This shape seems to be an effective way to allow complete closure (as would be necessary under high hydrostatic pressure) and also to permit rapid and wide opening without stretching the tissues. Surrounding the entire tube are circular muscles that seem capable of exerting constrictive pressure on the narial canal. This passage then dips ventrally into the very large and asymmetrically placed left naris, which is also occluded by a muscular mass.

It seems likely that the large direct connection of the left naris is used during rapid expiration and inspiration of the "blow" and is thus the respiratory pathway capable of handling large volumes of air very rapidly, while we speculate that the much smaller and more complicated right passage, interrupted by the *museau* and broken into sacs in two places, is concerned with phonation and that both passages are linked to-

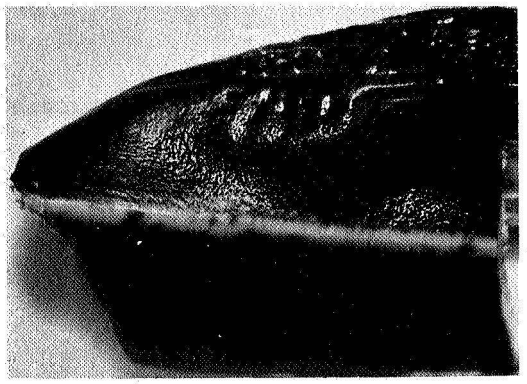

FIGURE 5. Triangular ridge of the anterior wall of the distal sac, which in life fits tightly into the indented line of the museau lips.

gether, thus allowing recycling of the air used in phonation.

Museau du Singe

At the anterior end of the right nasal passage, emptying into the distal sac, are the remarkable lips mentioned earlier. They occupy the entire width of the distal sac. The lips remain tightly pressed together even after dissecting away the stout overlying connective tissue. One can force a hand between them, but the pressure is sufficient that circulation would be cut off if the hand were left inside for long. This pressure apparently results not from muscle tension but simply from the dense connective tissue structure of the lips and surrounding snout. When the lips are pulled apart, one can see bands of very hard, almost horny whitish cornified tissue running in a perfect arc on the inner labial surfaces (fig. 2b). Closer inspection shows that each such band is composed of three concentric flattened ridges with two flat-bottomed grooves between. The upper and lower lips mortice together when closed almost as if machined.

Lying anterior to this band, both above and below, the borders of the lips fall away in a band of rather stiff crenulated folded black tissue. It is interesting that the pygmy sperm whales (*Kogia* sp.) possess similar lips and morticed borders, but they are located within the skull amphitheatre posterior to the small spermaceti organ. The same is true of a single Hyperoodontid whale that we examined in this regard, a Cuvier's Beaked Whale (*Ziphius cavirostris*) taken on Oahu, Hawaii, and examined by the senior author. In it a small subcylindrical fatty organ, that may be homologous to the spermaceti organ, occupied an excavation in the surface of the rostrum and communicated posteriorly to the right nasal plug that was lined on its surface by a mortice-bordered *museau*. We feel that the presence of this remarkable structure in these different groups of whales indicates a community of ancestry which, however, must be fairly ancient since the groups were clearly defined in Miocene time (ref. 5).

The upper lip of the *museau* gives way to a hemispherical dome whose surface forms the posterior wall of the distal sac. The connective tissue overlying the outer wall of the distal sac and the lower lip of the *museau* is extremely thick and very dense reaching a thickness of more than 15 cm in an 11-m whale.

Frontal Sac

It is our contention that the frontal sac, which lies adhered to the face of the skull amphitheatre, is the posterior member of a pair of sound mirrors bounding the ends of the spermaceti organ. We further suggest that its posterior wall serves to preserve the integrity of this mirror during the prodigious dives of sperm whales and during any body orientation (fig. 6A). To examine these ideas we must look at the detailed anatomy of both walls. The posterior wall of the sac is covered with a pavement of smooth, rounded, fluid-filled knobs and overlies the skull amphitheatre. The knobs vary in diameter from 4 to 13 mm with a mean diameter of about 9 mm. Each is formed of tough walls of collagenous fibers and is filled with serous fluid. Between the knobs lie grooves varying from 3 to 12 mm deep. Scattered throughout these channels are thin membranous transverse septa that divide the channels into many discrete parts, each part consisting of a small ramifying set of passages (fig. 6B). The anterior sac wall is dramatically different from the posterior wall, being a smooth compliant surface.

As the whale dives, external pressure must

FIGURE 6a. Frontal sac of an 11-m sperm whale. The man's hands grasp the dorsal ridge of the skull amphitheatre and touch the posterior wall of the frontal sac (a) that lies adherent to it. Note pavement of fluid-filled knobs. Reflected forward is the posterior wall of the spermaceti organ (b) which forms the anterior wall of the sac. Organ has been emptied of spermaceti and the wall, which is normally vertical and conforming to the contour of the knob-covered posterior wall, lies "deflated."

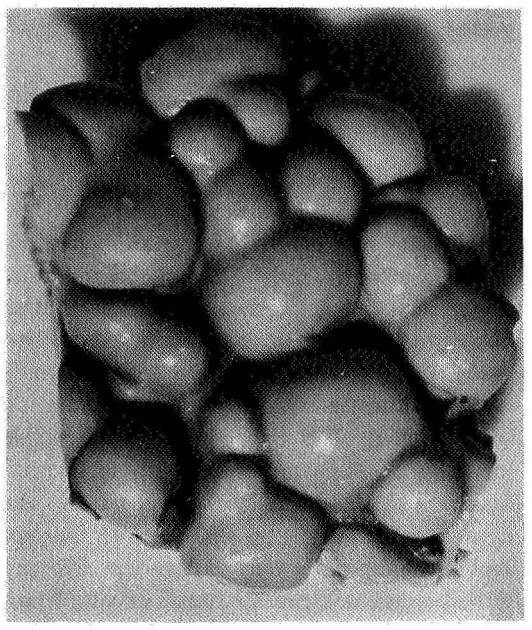

FIGURE 6b. Detailed view of knobby posterior wall of frontal sac. Note membranous separations at (a).

keep these two walls pressed against each other most of the time. Only when the animal exerts muscular pressure upon the air contained in its respiratory system can the walls be expected to part. As the animal reaches great depths, the available air volume will become so small that it would not be possible to part the walls more than millimeters at most, if at all. For instance, sperm whales have been recorded swimming at 2250-m depth (Whitney, William, *in litt.*), where air volume in the respiratory tracts will be reduced to 1/250 the surface volume. At such a depth the only air space possible would be deep between the knobs.

Because the knobs of the posterior wall are fluid filled, they are deformable but incompressible (fig. 7). As the soft anterior wall presses over them, it must conform part way into the channels between knobs, restricting air to these channels. The seal thus produced, in combination with the septa, will lock a filigree of air between the knobs within a series of small areas defined by the septa. In effect, a filigree of air films set on edge with regard to the spermaceti organ will result and will be maintained regardless of the body orientation of the animal. The fluid-filled knobs, wherever they remain uncovered by an air film, will partially transmit incident sound in a relation between knob diameter and wavelength, while the filigree will reflect. Even an air film a fraction of a millimeter thick is essentially a perfect sound reflector (ref. 6). The result should be that any sound hitting the sac wall from the spermaceti organ should be partly reflected completely by the air filigree and partly filtered and passed posteriorly through the knobs in relation to their dimensions and the frequency

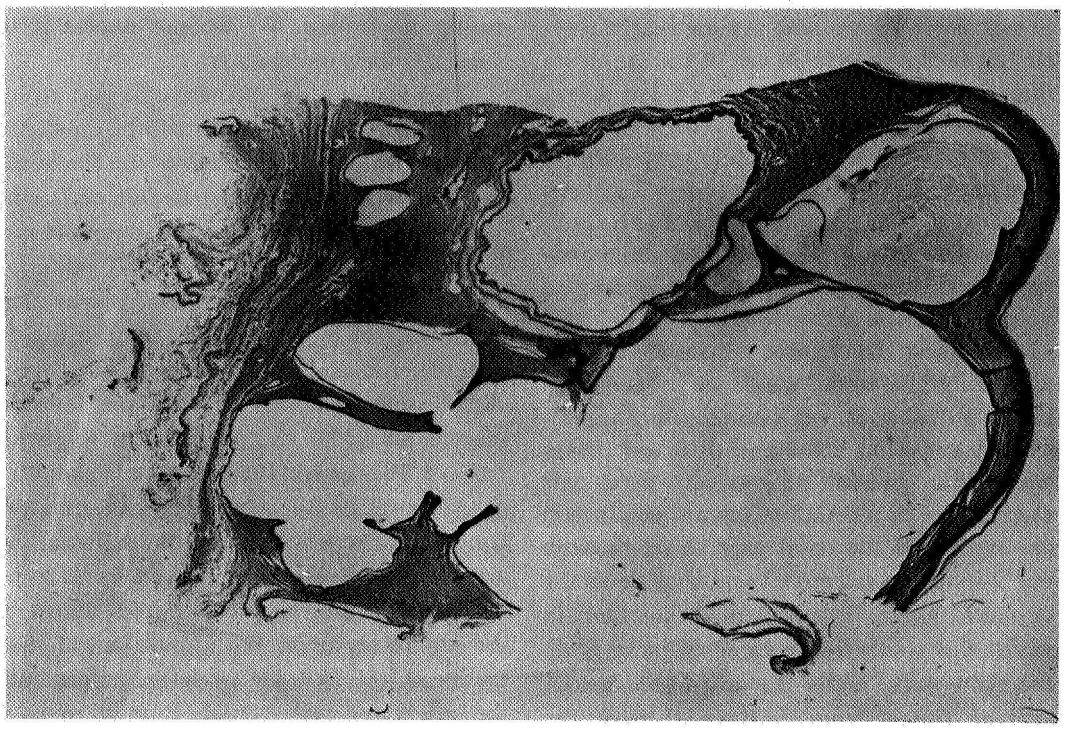

FIGURE 7. Section through the knobs of the posterior wall of the frontal sac showing their hollow nature and fibrous structure.

composition of the incident sound. This effect may be expected to vary with the depth of dive as the available air volume varies, and hence the coverage of the knobs by an air film varies in completeness.

Air Recycling

Sperm whales routinely dive for an hour, or perhaps more (ref. 7). Those who have listened to sperm whales uniformly report continuous click production from them, including records from animals deep beneath the surface (ref. 8). Our own encounters tend to confirm this view. Thus, if air is used in sperm whale click production, it must be recycled since its total volume is relatively low and completely insufficient for continued sound production (over such long periods) if used only once.

Those odontocetes that have been observed while phonating under water do so largely without release of air. Occasionally a stream of bubbles will accompany a sound emission, usually a whistle in porpoises, but much more commonly, none is released at all. Close inspection of such phonating animals shows movements of the blowhole valve and complex swellings over the superior nasal sacs at the time of phonation, suggesting the use of air in sound production. It is known that air pressure levels inside the air sac system may be considerably higher than ambient pressure (ref. 9).

Thus, if the sperm whale phonates generally in the way the delphinid porpoises men-

tioned above do, we may assume that it recycles air in the process. Much of the sac structure and other soft anatomy of the sperm whale forehead bears a phylogenetic relationship to that found in delphinid porpoises, although one rather ancient in time (Oligocene or older), so this contention is probable. Both groups possess complex sacs and nasal passages; both have paired passageways deep to a single blowhole and so forth.

Assuming that sperm whales do recycle air during phonation, which we believe to be highly probable, how is such recycling accomplished and what is the path it takes? Three possibilities present themselves. First, air might move in a complete circuit, coming up one naris past the nasal plug valve, through the U-shaped canal circuit and back down the opposite naris. The obvious direction in which this would be expected to move is up the right naris, under the spermaceti organ, through the *museau du singe*, through the distal sac, through the connecting sac, the vestibule, and back down the left narial passage to the left bony naris. It seems unlikely that it could move in the opposite direction since such movement would be against the *museau*, which, since it is not actuated by muscles, would seem to be opened only by air pressure from behind, acting in the manner of a stop-check valve.

The second possibility is that air might move back and forth in the loop of canals and sacs. This seems unlikely, once again because the *museau* appears incapable of being opened except by pressure from behind. Thus we infer that air cycles through the circuit starting at the right naris and returning into the left naris. The third possibility is that it might move up both passages simultaneously, but it seems obvious that this could only happen with the blowhole open, as is the case during respiration. We do not expect it to occur routinely underwater.

This leads to the question: "What structure pumps the air?" If air returns down the left naris from the sac system of the forehead, the first junction between the left and right naris occurs just dorsal to the arytenoid extension of the larynx where the posterior bony nares enter a common bony excavation at the base of the skull. The larynx is highly muscularized and might function as a recycling pump equipped as it is for forward movements within the nasopalatine sphincter (see ref. 10), or what seems more likely to us, pumping might be accomplished within the bony nares themselves. As in the *museau*, the arytenoid extension of the larynx seems to be a valve opened by air pressure from deeper in the respiratory tract. We suspect its spoutlike tip limits recycled air from excursions into the larynx and deeper, perhaps in all odontocetes, and that air thus simply moves down the left bony naris, enters, and is pumped within the right naris during recycling. A pumping mechanism within the bony naris seems the most likely location, since a positive pressure could probably best be developed by the action of muscles on an airway over a substrate of rigid bone, rather than against soft tissue. Within each naris is an elongate muscle mass, the pterygopharyngeus muscle, that seems capable of occluding the passage when contracted, and when relaxed, to open it again. Lawrence and Schevill (ref. 10) describe it as follows: "Its origin is from the anterior wall of the upper part of each bony naris." This arrangement could conceivably function in a manner of a peristaltic pump. We can bring no evidence to bear which tends to resolve which structure, if either, might be involved.

SPERMACETI AND OTHER ODONTOCETE OILS

Spermaceti is a complex waxy oil, liquid in the living whale. Its density is 0.782 gm/cm^3 at 60° C. K. J. Diercks of the Defense Research Laboratory, University of Texas, kindly determined the sound transmission velocity in spermaceti as a function of frequency (table 1).

Within the range of frequencies tested, spermaceti is nearly nondispersive with regard to frequency. We have been able to obtain velocity measurements on the melon oil of the hyperoodontid whale, *Ziphius cavorostris*, and a figure for melon oil of a porpoise, presumably *Tursiops truncatus*, has been cited to us by E. C. Evans (*in litt.*). Both propagate sound much more slowly than does spermaceti.

TABLE 1.—*Sound Transmission in Some Odontocete Oils*

Frequency (kHz)	Velocity (m/sec)	Temperature (°C)
Spermaceti 21	2638	36
26.77	2654	36
30	2619	36
36	2669	36
40	2684	36
Ziphius cavorostris melon pulse, broadband	1356	27.1
Porpoise (presumably *T. truncatus*)	1352.2	28.2

SPERM WHALE SOUNDS

Nearly every time one listens underwater in the vicinity of sperm whales, one hears a monotonous series of clicks (ref. 8). These clicks are sometimes very intense; measurements range from 73.9 dB re. 1 dyne/cm^2 to 75 to 100 dB re. 1 dyne/cm^2, both presumably at 1.0 meter (Whitney William, *in litt.*, ref. 11). Sperm whale clicks may carry for a matter of miles underwater. Most delphinid clicks, by contrast, cannot be heard as much as 1000 m. Although some workers have reported single clicks in sperm whales (ref. 12), all the sperm whale signals we have examined could be resolved into a burst-pulsed structure. Claims to the contrary seem to be based upon different nomenclature rather than a basic variation in signal structure since Busnel and Dziedzic figure a sound spectrogram showing a burst pulsed character within a signal they consider to be a single burst. These burst pulses consists of six to eight complex transients, each 0.5 to 1 msec in length, rapidly damped from the initial high intensity signal into background level. The entire click is usually close to 25 msec in length.

In the many hours of listening to sperm whales by several investigators, two have reported signals other than clicks (refs. 12 and 13). These signals, which were rare in the records of these two investigation teams, consisted of squeals recorded in the vicinity of a sperm whale pod. Their rarity requires that their production by sperm whales must still be considered insecure.

Typically, sperm whales emit trains of clicks given at repetition rates up to 60 to 80 per sec. Such trains may sometimes be quite prolonged, continuing for a minute or more. The highest repetition rates occur when a sperm whale is apparently examining a nearby object, as when a phonating whale swam over to and hit our hydrophone. It is interesting to correlate the click rates of delphinids such as *Tursiops truncatus* during such behavior (400 to 500 sec, see ref. 14) with these rapid rates of the sperm whale. Since the burst pulsed clicks of the sperm whale each consists of six to eight pulses, while delphinid signals consists of single transients, we can calculate that each animal is emitting between 400 and 500 brief pulses of sound/second when it is engaged in close-up inspection.

Within the cacophony of clicks coming from a pod of sperm whales, one can discriminate trains from individuals. Typically the

repetition pattern will allow one to inspect the entire train (fig. 8). What emerges is that some features of the click train are constant while others vary. Among the constant items is a "signature" that can be discerned in the structure of the individual pulses that make up each burst pulse. This appears to be typical of each individual whale. The spacing of pulses within the burst pulses of such a click train is quite constant, although some of our recordings show some pulses at irregular intervals that we cannot be sure do not represent another more distant animal or variability from some other source. One may lay a multipoint proportional divider over the burst-pulse clicks of a single animal and find uniformity throughout a long click train. The spacing of pulses (interpulse interval) varies from animal to animal, and we assume this variation is due to different lengths of spermaceti organs. Interpulse intervals range from 2 to 4.8 msec (ref. 8).

On the other hand intensities, frequency composition, presence of minor transients, and duration of individual pulses change sequentially as one inspects the clicks of a long train. We take these variations to be due largely to the changing headings relative to the recording hydrophone taken by the animal as it swims through the water. The constant features of the signals we take to be due to regularities in the geometry of the generating and transmitting structures of the whale and in its mode of sound production. We suggest that the regular spacing of pulses within a burst pulse represents reverberations of a single signal within the spermaceti organ.

We propose that a single intense click is emitted at one end of this organ and that the first pulse probably represents this initial signal transmitted directly into the water ahead of the whale, while the remaining pulses represent reverberations of the backwardly directed portion of this signal between the two air mirrors that bound the ends of the spermaceti organ. Obviously there are several unanswered questions here that need to be explained. Where are the clicks produced? How do they leave the spermaceti organ?

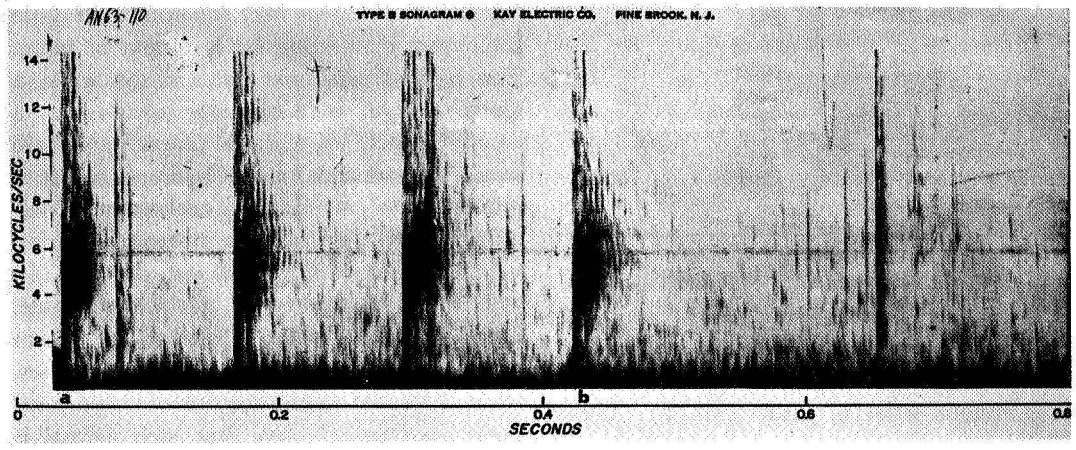

FIGURE 8. Sperm whale burst pulse clicks showing broad band character of first pulses of the click (a) and subsequent narrowing of the band as the burst pulse is damped (b). Courtesy William Schevill, the horizontal stripe near 6 kHz is an artifact. Filter bandwidth is 600 Hz.

Are the geometry and dimensions of the spermaceti organ such that this explanation could be true?

First let us look at the dimensions and geometry of the spermaceti organ in relation to emitted signals. Since we know the speed of sound in spermaceti, and we know the lengths of spermaceti organs relative to the total length of sperm whales, it is a simple matter to calculate the spacing we would expect to occur between pulses of a burst pulse, if they represent reverberations. As sperm whales grow older, relative length of the spermaceti organ appears to increase somewhat as the spermaceti organ more and more overhangs the upper jaw (ref. 2). However, for our purposes, a figure varying from about 25 to 40 percent of the total length of young adult animals appears correct.

If our theory is correct, the regular spacing between pulses represents two traverses down the length of the spermaceti organ between the bounding sound mirrors. This must be true wherever the initial sound is produced relative to the spermaceti organ. Thus we can calculate:

$$\text{Length, spermaceti organ (meters)} = \frac{0.5\ (\text{interpulse interval})\ (\text{sec})}{\text{speed of sound in spermaceti organ}\ (\text{m/sec})}$$

To test our theory we need sounds recorded from an animal of known dimensions; a difficult bit of data to obtain from a live sperm whale at sea. However, an unusual opportunity came our way while recording underwater sounds 29 km off Mejillones in northern Chilean waters on August 16, 1968. On a very calm day a single sperm whale was sighted while the recording team was cruising the coast in a 9-m felucca (a local double-ended fishing vessel). The animal approached the vessel, emitting a constant train of sounds, swam directly alongside, and actually hit the hydrophone with its head before the crew panicked and raced away. The recording crew was able to make an estimate by eye of its length relative to that of the boat as it surfaced alongside the vessel. They estimated it to be as long as the boat or about 9 m.

Regarding the length of the spermaceti organ compared to body length in this animal, we refer to Nishiwaki, Ohsumi and Maeda (ref. 2) who list the length of the severed head in a 9-m whale as about 29 percent of body length, or 2.6 m.

When the signals recorded from this single animal were analyzed, they were found to have an interpulse interval of 2 msec, and when this is converted to spermaceti organ length (2.65 m), a predicted animal length of 9.18 m is obtained; a remarkable correspondence with the observed length (fig. 9). The longest interpulse intervals which have been recorded from sperm whales (4.8 msec.) would have come from animals about 16 m long, according to our predictions.

Other questions remain unanswered: If the air sacs that bound the spermaceti organ are sound mirrors, how does sound escape after traversing the organ to produce the component parts of the burst pulse? We suggest that the distal mirror at the anterior end of the organ may be functionally incomplete and may allow sound emission over part of its area while maintaining its reflective integrity elsewhere. The exact exit site suggested is the upper lip of the *museau du singe*, where the ridge of the anterior sac wall must normally lie tightly pressed against and between the lips (see fig. 3). Further the spermaceti organ terminates anteriorly in the upper lip of the *museau* as a broad wedge invading the tissue of the lip, and thus a direct channel for sound may be present. Rigid heavily crenu-

lated tissue lines the lips both above and below the *museau* and must serve to prevent tight contact of the spermaceti organ and anterior sac walls in these areas thus maintaining a partial mirror.

An alternative exists. It is possible that sound exits through the well developed mesorostral cartilage of the upper jaw and that sound is somehow piped into this structure from the rear after being reverberated back and forth in the spermaceti organ. Because of the circuitous course sound would have to follow, we consider this possibility more unlikely. Once again, measurements from a captive emitting whale are needed.

If the sound generator was located some distance away from the spermaceti organ, the interpulse interval between the first and second pulses of a burst pulse should reflect this be being either longer or shorter than that between the remaining pulses that should be evenly spaced. In general, pulses within a burst-pulsed click appear to be equidistant, so we conclude that the sound generator is either very close to an end of the spermaceti organ or actually located there. This pinpoints two structures as possible sound generators: the *museau du singe* located at the anterior end of the organ and the right nasal valve located above the right superior bony naris. The *museau* is, of course, in proper position, while the right nasal valve is located some distance anterior to the posterior end of the spermaceti organ and directly under it. Measurements of the skull of a 13-m animal show that approximately 10 percent of the total length of the spermaceti organ lies posterior to the entry of the right bony naris on the superior surface of the skull. If sounds are produced in this location, a signal with complex spacing of pulses should result. The

FIGURE 9. Sperm whale burst-pulsed click recorded from 9-m whale swimming alongside 9-m felucca, 29 km off Mejillones, Chile, August 16, 1968. 2 msec/cm sweep, 0.2 volt/cm amplitude. Recording by Leanne Hinton.

part of the pulse that is propagated forward would arrive in a straight path to be followed by reverberations from within the spermaceti organ following in such a fashion that the first interspace between pulses would be slightly more than half the interval between subsequent pulses. At the same time, reflections from this signal, which were propagated posteriorly at the moment of emission, would be superimposed on the other parts of the signal. A complicated signal would result in which the interspaces between the pulses are far from uniform. Because the burst pulses of sperm whales show regularity, we feel, therefore, that it is unlikely that sounds are produced at the right nasal plug. Once again the *museau* seems the most likely locus.

How then could sounds be produced by the *museau*? We have no direct data to present on such sound productions but can infer the following from the anatomical arrangements we see. First the *museau* being a one-way or stop-check valve suggests that it is opened and closed by air pressure from behind. Thus we suggest that it is actuated by air pressure built up from below the superior

bony naris and that this pressure forces air along the groove system previously described against the back of the *museau*. The air pressure at some point can be expected to overcome the connective tissue tension which normally keeps the lips closed. At this point the lips might open and slap back together again producing an initial pulse.

It is quite possible that this is a gross oversimplification of this proposed sound production mechanism. We are intrigued by the extensions of the groove system over the *museau* lips. These narrow very markedly as they pass across the morticed border of the *museau*. We wonder if it is possible that as the lips are forced apart by air pressure and return to their normal closed position, if a Bernouilli effect might be produced in which the velocity of air passing forward across the lips is speeded past the speed of sound and produces a tiny "sonic" boom, somewhat in the manner of the production of sound by snapping shrimp. The high intensity of sperm whale clicks suggests that more than a simple clapping together of the lips may be involved in the sound production.

SPERM WHALE MODELS

If our theory about sound production in the sperm whale is approximately correct, it should be possible to simulate the sound production apparatus in the laboratory and to see if we could thus produce signals like those recorded from sperm whales. Our attempt was to take the structural characteristics we found in the sperm whale and to use these directly in the construction of the model. The criteria we used were these:

(1) Dimensions of spermaceti organs

(2) Position and completeness of the sound mirrors located at either end of the organ

(3) Speed of sound in cetacean head oil (since our models were constructed in air, these velocities were corrected for the velocity difference between air and spermaceti)

(4) Simple broad band impulsive nature of the initial click of a sperm whale burst pulse, which is considered to represent the initial sound emission.

Three models were constructed. The first consisted of a vinyl pipe 20.6 cm in diameter and 85.5 cm long with one end closed by a solid vinyl plug and the other partly closed by a solid vinyl plug having a 7.6-cm diameter hole in the center. This chamber was excited by a 7.6-cm loud speaker that was driven by the arrangement shown in figure 10. The loud speaker was located near the opening in the chamber. A simple 1.2-msec pulse was used to excite the chamber. This excited the longitudinal mode of the chamber

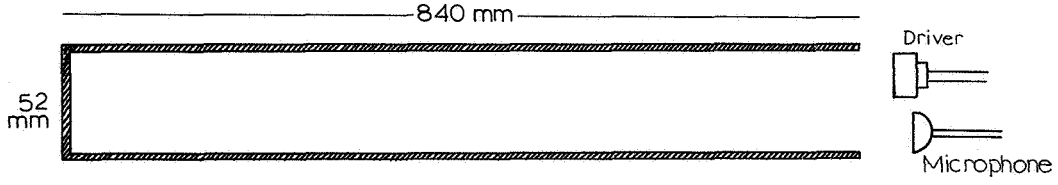

FIGURE 10. Artificial sperm whale. A single 200-μsec pulse was used to drive the chamber, which was constructed of PVC pipe and filled with air.

as well as other modes because of reflections from the walls. From this single pulse there was generated a train of gradually decaying pulses that contained 20 or more distinct pulses. The signal envelope very much resembled those of *Physeter* clicks. The successive reflections were 4.6 msec apart compared to the pulse spacings published for *Physeter* which were 2.0 to 4.8 msec apart and contained five or six distinct pulses. Obviously the natural click was much more rapidly damped than this initial artificial click. The second model consisted of a 200-cm vinyl pipe with one end closed with a solid vinyl plug and the other open. The same electrical system was used except that a miniature driver unit from a military headphone (type D3T, 50-ohm impedance) was used to excite the column. By using a simple single pulse 200 misec long, a train was generated that more closely resembled a train of *Physeter* clicks (fig. 11). There was slightly more damping within the successive pulses.

The third arrangement was identical to that in no. 2 except that the pipe length was reduced to 100 cm. The oscillator was set to 2060 Hz so that it passed approximately two cycles. These values were chosen to produce a train as nearly like that as *Physeter* as possible. Several things of interest were noted during these tests. First, by adjusting the rate at which signals were introduced into the column, we could produce very great changes in the intensity of emitted sounds presumably by reinforcements within the column. Second, the size of the speaker used to introduce sounds to the column greatly changed the stability of the emitted signal. A speaker nearly the width of the column was capable of producing very stable sounds while a smaller one was less capable. This is suggestive, once again, that the *museau* is the site of sound production since it represents a pair

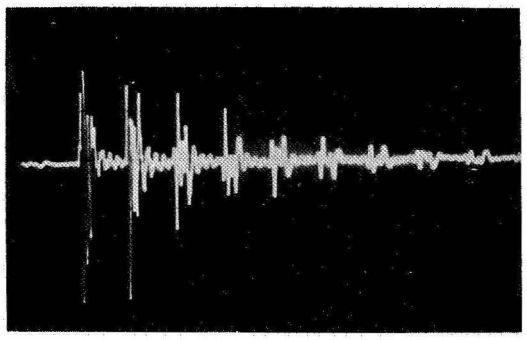

FIGURE 11. Artificial sperm whale burst-pulsed click produced by the 52 × 840 mm acoustic model. Amplitude 0.1 volt/cm. Sweep 5 msec/cm. Note rapidly damped character of the signal and 4.8-msec separation of pulses within the click.

of lips that span the entire anterior width of the spermaceti organ and presumably it is actuated by air as a unit. The 200-cm pipe length was chosen to represent the path for sound in air that would correspond to a similar path in spermaceti in terms of transit time. The interclick interval within the pulses produced matches closely those seen in sperm whale signals.

FUNCTION OF SPERM WHALE BURST PULSES

The unique burst pulses of the sperm whale (fig. 9) are remarkably different from those of delphinid whales in that the repetition rate between burst pulses is generally much lower, reaching a maximum of 60 to 80 per second as opposed to more than 1000/sec in social cries of delphinids, and because sperm whale signals are given as clusters or bursts of rapidly damped clicks separated by long silent periods, as opposed to continuous trains of more or less constantly repeated single clicks in the case of delphinids.

Four features of the sperm whale system suggest that it may function as a long dis-

tance echolocation system for use in the open sea. First, if the sperm whale uses its burst pulsed signals for echolocating, one expects that they are used at considerable distance, probably during the dives of the animal into the deep sea. If the sperm whale operates in the same manner as has been shown for delphinids (ref. 14), in which the echo of the signal is received before another signal is emitted, then we can expect that the very slow repetition rates are related to long distance echolocation. In most cases where sperm whales have been listened to in the open sea, the repetition rates have been very slow indeed, ranging between what are best considered as individual clicks to those given at rates of less than 20 per second. Nearly all trains examined by Backus and Schevill (ref. 8) had repetition rates less than 7 per second, and thus would have allowed echoes to return in the interspace between clicks from targets 100 m or more ahead of the animal. The high rates we recorded here (60 to 80 per second) were from an animal inspecting us at very close range.

The second feature of sperm whale burst pulse clicks as echolocation signals seems optimum for long distance use in another way. A moderate amount of information can be obtained from the echo of a single click, but considerably more can be obtained from the echoes of the several pulses within a burst-pulsed click, which are given at short intervals relative to one another. Such subtleties as texture and internal composition may be better demonstrated by these compound clicks than single ones. Yet, as we have seen, long distance echolocation using single clicks in a train presents problems. The ranges may simply become too long to allow the animal to receive the echo in an interspace between pulses and still obtain the refined information that comes from analysis of many pulse-echo pairs. Burst pulses alleviate this problem in that much more complete information can be carried within a burst-pulse echo, and this information can come back in the interspace between burst pulses.

A third feature of the burst pulse that seems possibly useful to the sperm whale is that these signals allow discrimination of size whereas single clicks may not. A large squid, for example, being hit by the burst pulses of a click, will return an echo that is "mushy." The individual pulses of the click will hit the squid at many points along its length, and thus the echos of the individual pulses will merge into one another and a mushy echo will result; whereas a small target will return the pulses as discrete entities in the form of a simple echo of the original signal.

The fourth and final feature of the burst-pulse system of sperm whales, which impresses us as being related to long distance echolocation, is that the pulses of a click may very well act in the sperm whale's sound processing system in the same way that such transients would act in our own—namely through summation. The very long distances at which sperm whales likely seek their prey will involve attenuation and spreading losses of such magnitude that sperm whale clicks will reach very low levels relative to background noise in a relatively modest distance even though the initial intensity is quite high. If each of the clicks as it is received by the sperm whale causes a summation effect in the brain, the animal will be able to pick the burst pulse from background noise at a considerably reduced level compared to its ability to discriminate a single click under similar environmental circumstances. This effect was brought home with great force to one of us (Norris) by listening to the discharge of a pistol in an anechoic chamber in which a modest pop was heard and then later in an

echo chamber in which the apparent intensity of the same pistol sound was so great as to cause physical pain. The effect was produced in the first case by a single traverse of the sound across the author's receiving equipment and, in the second case, by several thousand traverses of the same sound across the ear which produced a summation effect in the hearer's brain.

SUMMARY AND CONCLUSIONS

Several lines of evidence point toward the spermaceti organ of the forehead of sperm whales as a reverberation chamber used in the production of the unique burst-pulsed signals of the sperm whale. This evidence also suggests that sounds are produced at the valvular lips of the anterior end of the spermaceti organ called the *museau du singe* and that these lips are actuated by air pressure within the right nasal passage. Structural features of the passages suggest that air is recycled from the right naris through the right nasal passages and *museau* into the left nasal passage under the blowhole and back down the left nasal passage into the left bony naris, and thence back again in a complete cycle. The suggestion is made that peristaltic-type pumps may exist within the bony nares themselves.

The structure of the two vertically oriented air sacs that bound the ends of the spermaceti organ suggest that they are sound mirrors. The posterior sac (the frontal sac) possesses a knob-covered posterior wall that is probably an adaptation allowing maintenance of the sound mirror in any body orientation and during deep dives. Finally this complex anatomical system is suggested as a device for the production of long range echolocation sounds useful to the sperm whale in its deep sea habitat, in which food must be located at considerable distances in open water.

The authors feel that these ideas must be considered as hypotheses until measurements can be taken from living sperm whales.

ACKNOWLEDGMENT

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A number of people have contributed to the development of these ideas and their partial testing. Forrest Wood III of the Naval Underseas Center, Point Loma, has several times commented that he felt the right sperm whale narial apparatus was for sound production and the left for respiration. David Bottles gave us much help with dissections and photography. V. Knudson, L. del Sasso, and S. McKay have contributed to our thinking about sperm whale acoustics, although they, of course, cannot be held accountable for what came from those discussions. William Schevill and Richard Backus have helped a great deal with discussions and data concerning sperm whales. Kenneth Bloome, Berit Bloome, and Leanne Hinton were instrumental in obtaining our recording of the sperm whale off Chile. We thank Robert Brownell for making a fetal sperm whale available to us. We also thank Thomas Dohl for his assistance at many points during this work.

APPENDIX

Since this paper has been in press, another theory for the function of the spermaceti organ has appeared in the literature (ref.

15). This theory suggests that the spermaceti organ functions to maintain neutral buoyancy in the whale both at the surface and at depth. By temperature control of the sac, the whale is postulated to rise to the surface from great depth with no physical effort. Several aspects of these ideas seem improbable to us. First a buoyancy change dependent upon the capriciously changing thermal structure of sea water will cause the whale's buoyancy relations to be altered from place to place, as, say, when it swam from gyre water having a deep and stable thermocline, like that off Hawaii, to well mixed water at current divergences. The organ could function only where the whale penetrated a thermal boundary. Over much of its range such boundaries are deep or are wholly absent where vertical mixing is strong.

The energetic values involved seem to eliminate the theory as well. The huge mass of the organ relative to the size of the whale would require great and rapid heat input to change the temperature of its spermaceti. Clarke calculates 1.6×10^4 calories to heat 1450 kg of spermaceti from 7.8° C to 33.5° C, expected figures needed to produce a small but possibly useful buoyancy change of 91.5 kg. It is proposed that this heat is provided metabolically, and the author states: "Many details of the spermaceti organ suggest that it is a heat exchanger. All the spermaceti oil is contained in minute vesicles held within a dense network of capillaries so that the circulation could heat the oil rapidly. . . ." We consider this statement incorrect and misleading. Our dissections showed the spermaceti wax to be extremely loosely held in very large vesicles. The fact that hand whalers could lower one of their number into the opened case to bail out spermaceti with a bucket gives the best perspective we know on this question. It seems inconceivable to us that the gossamer webwork of connective tissue and blood vessels that invades the spermaceti could be an efficient heat exchanger capable of repeated heating and cooling of such massive amounts of lipid tissue in short periods of time. Further, to have a buoyancy organ on one end of the body seems a grotesque arrangement. The moments produced would tend to tip the animal, in a single direction (either down or up), while what is known of underwater sperm whale tracks suggests, as one would expect, erratic searching movements (W. Whitney, *in litt.*).

Further there is no evidence that sperm whales passively float to the surface after dives. Instead normally they are obviously swimming strongly throughout them. A whale undergoing a 2500-m dive must travel about 4.8 km just to dive and return from such a depth, and when one adds a searching component, additional travel distance is required. The whale has to swim 4 knots or more just to perform such a dive in the normal hour's dive time. Passive floating seems out of the question. There are a number of other objections to the theory: blood shunting during dive cycles, as it is now known, suggests supply during dives to nervous and cardiac tissues only; the commitment of energy during growth to produce such a huge but inefficient buoyancy compensation device is suspect; buoyancy is likely much more easily controlled by other means such as lung collapse or underwater emission of air. The slight negative buoyancy encountered by a diving whale is most likely to be compensated for by a slightly greater swimming effort.

DISCUSSION

MACKAY: There is perhaps one change that should be considered in your analog, and this again brings up the matter that a sound wave shape depends on the phases of the various frequency com-

ponents, that is, sounds are not fully characterized by frequency and amplitude alone.

If you take a sound wave, e.g., a sudden compression, and reflect it off a hard wall, then it comes back as a compression. However, if you reflect the compresion from a region that is "softer" than the region in which the wave is travelling, or if the reflection is from a sudden opening in an otherwise restricted region, then the reflected wave will be a rarefaction. The reflection can be equally good in either case, and it can be considered as a matter of the phases of the frequency components. In your analog there was a loudspeaker and a hard surface, whereas the reflector in the head of the whale apparently was air surrounded by tissue. The latter probably was a more-to-less dense reflecting interface from which a sound wave would be reflected with the same amplitudes of its frequency components, but they would be inverted. A more exact analog of the whale situation might thus be the blowing of a bugle.

Do you feel that there is a single oscillation at the front end and then just reverberation, or do you feel that there are several oscillations associated with the original energy source?

NORRIS: We have not been able to be sure about phase changes in the sperm whale signals we have examined, and there may well be reversals, and they may differ from our model. The complexity in the sperm-whale pulses is greater than I have shown. We thought a high-pass filter might be involved because whenever the spermacetic organ is pressed tightly over those knobs of the frontal sac wall, sound should be transmitted back into the animal's skull. For a time I thought that the emphasized frequency present in the sperm-whale signal might be due to this, but I doubt that now. It is more likely due to the geometry of the entire whole chamber.

BULLOCK: Have you compared the baleen whales with respect to the sound production in the head of odontocetes? Why do they produce only very low frequencies rather than the high or ultrasonic frequencies of odontocetes?

NORRIS: There is an entirely different structure in terms of the nasal passages. They are absent in the mysticetes. There are differences in the larynx of the two. It may well be that the mysticytes are using their larynx while odontocetes may use other sound generation loci.

QUESTION: Would you speculate that the development of this system would probably restrict the sperm whale to the deep sea?

NORRIS: Sperm whales are, indeed, typically deep sea animals. In my experience they generally stay in water several hundred feet deep, or more.

EMLEN: A behavioral question: You also noted that there are individual characteristics for individual animals that click. Is this also a social communication signal, perhaps allowing individual recognition?

NORRIS: I would be very surprised indeed if in both the porpoises and in the sperm whale, echolocation clicks didn't have a lot of social meaning. I think almost anything an animal says has social meaning.

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