Functional Morphology and Homology in the Odontocete Nasal Complex: Implications for Sound Generation

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ABSTRACT The site and physiologic mechanism(s) responsible for the generation of odontocete biosonar signals have eluded investigators for decades. To address these issues we subjected postmortem toothed whale heads to interrogation using medical imaging techniques. Most of the 40 specimens (from 19 species) were examined using x-ray computed tomography (CT) and/or magnetic resonance imaging (MR). Interpretation of scan images was aided by subsequent dissection of the specimens or, in one case, by cryosectioning. In all specimens we described a similar tissue complex and identified it as the hypothetical biosonar signal generator. This complex includes a small pair of fatty bursae embedded in a pair of connective tissue lips, a cartilaginous blade, a stout ligament, and an array of soft tissue air sacs. Comparing and contrasting the morphologic patterns of nasal structures across species representing every extant odontocete superfamily reveals probable homologous relationships, which suggests that all toothed whales may be making their biosonar signals by a similar mechanism. © 1996 Wiley-Liss, Inc.

Structure without function is a corpse; function without structure is a ghost.
(Vogel and Wainwright, '69)

The inseparable connection between structure and function was as apparent to ancient philosophers like Aristotle and to anatomists like Leonardo Da Vinci, Galen, and Vesalius as it is to our contemporaries, Vogel and Wainwright. Since the end of the last century functional morphology has been a major source of information for understanding how animals work. Recently, the newest, noninvasive, remote imaging tools have been able to provide detailed glimpses of functional components (in situ) within major topographic regions, such as the mammalian head.

We offer a new anatomic description of the odontocete (toothed whale) forehead and its potential acoustic function based upon serial images generated using medical imaging techniques (primarily x-ray computed tomography [CT]). We suggest the source of biosonar signals from dolphins and other toothed whales is contained within two previously undescribed structural complexes associated with the upper nasal passages (Fig. 1a). We term this ensemble the monkey lips/dorsal bursae (MLDB) complex. We will address three basic questions related to the generation of odontocete biosonar signals: 1) what structural components might be involved, 2) where they are located in space with respect to other structures, and, briefly, 3) how the biosonar signals might be generated. In one form or another, these questions have puzzled investigators for more than 30 years.

The primary focus of this report is to provide the first quantitative description of the size, shape, degree of asymmetry, and geometric configuration of the MLDB components (especially the fatty components) and associated structures in the odontocete forehead. These relationships are of particular interest because of their proposed function in biosonar signal generation and acoustic beam form-
mation. The fatty components have been our primary focus because they have been shown to be important acoustically. Beyond the anatomic descriptions, we will briefly discuss the probable homologous relationships between forehead structures in a variety of odontocete species representing the breadth of the suborder.

We support the Norris and Harvey ('72) hypothesis of sound generation for the sperm whale and propose a similar mechanism for biosonar signal generation that is applicable to both physeterid and delphinid whales. Furthermore, we suggest that all odontocetes use homologous structures (and a similar mechanism) to produce the pulsed sounds associated with their echolocation behavior. This hypothesis unifies the phonation mechanism for all odontocetes. Historically, more than one nasal phonation mechanism has always been required to account for the anatomic variation seen in the odontocete nose (Evans and Maderson, '73). One attempt (Cranford, '92a) was made to tie structure to function by inserting an endoscope into a phoning dolphin's (Tursiops truncatus) upper nasal passage and recording videotape images of the structures there. Those results, though preliminary, are consistent with the views we present in this report.

We have measured the shapes and sizes of the dorsal bursae, monkey lips, and melon, as well as their geometric relationships to major landmarks along the skull and air spaces, by means of serial images generated with x-ray computed tomography scanners and a heavy-duty sledge cryomicrotome. Magnetic resonance imaging was employed on a few occasions for comparative purposes. Our correlative observations employed standard dissection techniques and some histological examination. Each of these methods contributed somewhat different views of structure. In aggregate, they contributed to an overall view of the geometry involved. Our descriptions should also assist other workers in identifying and locating these structures.

In order to survey the wide variation in shape, size, and orientation of the tissues involved in sound generation and propagation within the Odontoceti, scans were made of 40 specimens representing 19 species. That sample accounts for about 30% of the suborder's species and includes representatives from all its superfamilies. This report contains measurements for a small portion of the total sample, six species (one specimen each) that together represent a range of anatomic geometry: the common dolphin (Delphinus delphis), the bottlenose dolphin (Tursiops truncatus), the Pacific white-sided dolphin (Lagenorhynchus obliquidens), the harbor porpoise (Phocoena phocoena), the franciscana (Pontoporia blainvillei), and the pygmy sperm whale (Kogia breviceps).

A comment on anatomic terminology will be useful before we introduce the components of the odontocete forehead. A good deal of the literature on the subject of odontocete forehead anatomy has not been written by anatomists. This has probably contributed to the use of inexact, inconsistent, or misleading terminology, especially concerning relative position. In the fusiform cetacean body architecture, posterior is synonymous with caudal, anterior is synonymous with rostral, dorsal is synonymous with superior, and ventral is synonymous with inferior.

ANATOMIC COMPONENTS OF THE ODONTOCETE FOREHEAD

Odontocete nasal anatomy is composed of a complex set of muscles, an intricate series of soft tissue lined nasal diverticula, a few specialized connective tissue structures, and some distinctive fatty components. Although most individual components have been previously described, the MLDB complex has not been previously recognized as a functional unit or as part of an adaptive complex. The central components of the MLDB complex are the fatty dorsal bursae (Cranford, '86, '92a), the well-known museau de singe, or "monkey lips" (Pouchet and Beauregard, 1885), the bursal cartilages, and the blowhole ligament. A description of these components from 2-D serial images and reconstructions is the foundation of our results and functional analysis.

The foreheads of odontocete cetaceans are unique among mammals (Miller, '23). They contain an adaptive complex that not only facilitates breathing in the aquatic environment but is also central for the production and propagation of most, if not all, of the impulse sounds these animals produce internally. The respiratory function has undoub-

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2The term museau de singe translates as the nose, snout, or muzzle of a monkey or ape (Dubois, '60). It is clear by the appearance of this structure in the sperm whale that Pouchet and Beauregard intended to indicate its striking resemblance to simian lips. We preferred translating their term as simian labia, but monkey lips has precedence in the literature, and so a new term seems unwarranted. Accordingly, we will retain monkey lips in our report.
edly been an important factor in shaping the configuration of the odontocete forehead, adding to its anatomic complexity.

The dolphin nasal apparatus apparently has more than one function, but in this case we will restrict our detailed examination of the nasal apparatus to consider the single function of sound generation. We will not attempt an in extenso anatomic description such as those of Lawrence and Schevill ('56) or Mead ('72). The forehead's musculature and nasal diverticula will not be described in great detail since there are adequate descriptions of the muscles and air sacs by Lawrence and Schevill ('56), Mead ('72), Schenckkan ('73), and Heyning ('89).

We will now introduce the forehead components individually and give some historical perspectives concerning them. Parts of the MLDB tissue complex, primarily the monkey lips and the dorsal bursae, have been mentioned in passing for many years without being given significant attention.

**Dorsal bursae**

Cranford ('86) described four small fat bodies (dorsal bursae) in the forehead of the spinner dolphin (*Stenella longirostris*). The dorsal bursae are normally found near the posterodorsal terminus of the melon, embedded in the walls of the spiracular cavity (Fig. 1a,b). Cranford ('88) proposed the fatty bursae as a potential site for the transduction of impulse vibrations.

The bursae are small ellipsoid fat bodies, encapsulated by a thin connective tissue sheath, or pouch, arranged in bilateral pairs. In all toothed whales (except, apparently, in sperm whales) one pair of dorsal bursae is located to the right of the midline and another to the left (Cranford, '88; see Fig. 3a). The right pair is associated with the right nasal passage, and the left pair is affiliated with the left nasal passage (each near the extreme lateral boundary of the spiracular cavity). Both of these dorsal bursae pairs have an anterior and a posterior component. Each posterior bursa is embedded in the posterior wall of the spiracular cavity immediately ventral to the ridge of the posterior monkey lip. Each anterior bursa, similarly, is embedded in the anterior wall of the spiracular cavity just ventral to the ridge of the anterior monkey lip (Fig. 1b).

In 1972, Mead discovered and briefly described the dolphin's posterior bursae and suggested (p. 103) that "the fat body maintains the shape of the posterior fold." With reference to *Tursiops truncatus*, Mead notes (p. 28),

Immediately anterior to the midportion of the blowhole ligament is an elliptical body, which seems to be composed of yellowish adipose tissue in a fine connective tissue matrix. This body lies between the blowhole ligament and the posterior wall of the nasal passage, and produces the faint ridge of the posterior fold.

The structure is clearly shown in Mead's Figure 11b (just posterior to the nasal passage and the arrow for "A"). His illustration of the deep dissection of * Globicephala melena* (his Fig. 19b) shows the "fat body" on the posterior border of the spiracular nasal passage.

The first photograph of the right pair of bursae appears to have been published by Evans and Maderson ('73). Their photograph of a horizontal section through a dolphin's head (their Fig. 1, p. 1207), clearly shows the anterior and posterior right dorsal bursae, although no mention was made of them. Heyning ('89) reports finding similar fatty regions in two of his later ziphid dissections and indicated that they could have been missed in earlier dissections.

**Monkey lips**

In the sperm whale (*Physeter catodon*) the monkey lips are solitary and resemble the region around the mouth of an ape, as noted by Pouchet and Beauregard in 1885. These dense connective tissue valves couple the anterior end of the right nasal passage with the distal sac in *P. catodon*.

Apparently there is a right and left pair of monkey lips in all odontocetes, except the sperm whales (superfamily Physetoridae). In all nonphyseterid odontocetes each pair of lips is composed of an anterior and posterior lip. The lips are formed by a slight ridge on the anterior and posterior walls of the spiracular cavity. Pressing the lips together produces a slit-like opening at the dorsal terminus of the spiracular cavity (Lawrence and Schevill, '56). This slit or commissure is easily seen by opening the vestibular sacs and viewing the specimen from above. In morbid material the lips are often found slightly

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2Our use of marine mammal nomenclature follows the standard suggested by the US Marine Mammal Commission ('76). The correct name of the sperm whale is adequately discussed by Schevill ('56) and Holthuis ('87).
Fig. 1. a: This painting of the head of the beluga, *Delphinapterus leucas*, illustrates the anatomic elements of the sound generation and beam formation apparatus within the nasal complex of the forehead. The two schematic diagrams are “road maps” to the structures depicted in the illustration. Painting by Keith Kasnot (National Geographic Image Collection). abl, anterior dorsal bursa (left); abr, anterior dorsal bursa (right); bh, blowhole; c, cranium; cs, caudal sac; iv, inferior vestibule; m, melon (main body); ma, mandible; ml, monkey lips (left); mnr, monkey lips (right); nsa, anterior nasofrontal sac; nsp, posterior nasofrontal sac; pbr, posterior dorsal bursa (right); pmb, premaxillary bones; ps, premaxillary sac; rm, rostral muscles; sc, spiracular cavity; vs, vestibular sac.
askew (as in Fig. 1b, where the posterior ridge of the monkey lip is displaced dorsally compared with the anterior lip).

Each monkey lip and corresponding dorsal bursa form an integral unit, where the bursa is contained within the lip—thus the origin of our term *monkey lips/dorsal bursae complex*. The first modern description of the dolphin's monkey lips can be credited to Lawrence and Schevill ('56). They described the dolphin's "transverse slit." Our right and left monkey lips together comprise their transverse slit. Lawrence and Schevill worked only with dolphins and did not consider homologous relationships with the sperm whale's anatomy.

Schenkkan and Purves ('73) were apparently the first to recognize the homologous relationships between these bilateral structures in the head of a dolphin (*Cephalorhynchus Hector*) and the monkey lips in the right nasal passage of a sperm whale. But Schenkkan and Purves gave the observation no further attention since they considered the larynx to be the site of sound generation. Forrest G. Wood is credited with the first suggestion that the monkey lips of the kogiid sperm whales might function as a sound generator (Norris, '64). In 1972, Norris and Harvey proposed that the monkey lips of the sperm whale (*P. catodon*) were the source of the loud impulse sounds recorded from these animals.

**Blowhole ligament**

Connective tissues, forming the supporting elements of the MLDB complex, are important components of the proposed sound generation system. These tissues maintain...
Fig 1. c: Histological preparation of a parasagittal section through the posterior wall of the spiracular cavity in *Pseudorca crassidens* (listed as D19 in Table 1). Connective tissue intervenes between the epithelium and posterior bursa and envelopes the bursa and bursal cartilage. cr, bursal cartilage; ep, epithelium; pb, posterior bursa. Anterior and posterior are indicated by A and P, respectively.
and modify MLDB shape by acting to adjust tension or pressure differentials through the actions of attached muscles.

The blowhole ligament is a stout ligament that is stretched tautly from the vertex of the skull along the posterior border of the spiracular cavity to the posterolateral edge of the premaxilla on both sides of the skull in non-

physeterid odontocetes.

The ligament traverses ventrolaterally as it passes anterior to the inferior vestibule, just dorsal to the confluence of the inferior vestibule with the spiracular cavity and ven-

tral to the posterior dorsal bursa. Figure 1b shows that the blowhole ligament is in con-

tact with the dorsal surface of the nasal plug through the wall of the spiracular cavity. Even in postmortem material the blowhole ligament remains pressed tightly against the anterodorsal surface of the nasal plug and fits into a rounded groove or sulcus formed by the curvature of the anterodorsal surface of the nasal plug. This sulcus starts laterally at the lip or node of the nasal plug and extends medially to the nasal septum. According to Lawrence and Schevill (’56, p. 114),

The blowhole ligament passes from the premaxillary bone to the lateral extremity of the slit-like opening above the plugs, where in some specimens it is stiffened by a small band of cartilage; from here a few fibers form a transverse band immediately posterior to this opening and end in the tissue beside the septum. This ligament is a very important structure that strongly anchors the commissure of the opening and makes taut the posterior wall above the plugs.

Even though this structure is not associated with the blowhole, Lawrence and Schevill appear to have named this structure the “blowhole ligament” because the primary function they considered for this stout liga-

ment was to aid in the closure of the main air passage and prevent the incursion of water further into the nasal airway.

**Bursal cartilages**

Cartilages of the nasal region have been described in detail by Klima (’87; ’95). He has identified and followed the development of the various nasal cartilages in a diverse array of odontocete taxa (including physeterids and delphinids). He described several embryonic cartilages, of which we are here concerned with just one, a small piece of cartilage that is embedded in the tissue immediately caudal to each (left and right) posterior bursa. They may be an outgrowth of the tectum nasi embryologically (possibly the cupula nasi an-

terior [Klima, ’87]). We call them the bursal cartilages because of their possible role as a stiffening agent for the posterior bursae. These cartilages are anteroposteriorly fl-


ten, widest medially, and laterally tapered in the dorsoventral plane. In the previous quote, Lawrence and Schevill (’56) reported them in “some” specimens. Heyning (’89) reported them from only large specimens, ziphids, *Delphinapterus leucas*, and *Platanista* spp., in which he associates them with the blowhole ligament. Mead (’72) did not report finding them in his dissections. Our study will suggest that all odontocetes possess these small cartilagenous blades or their homologues. Examination of sagittal histological sections through these cartilaginous blades from dolphins and porpoises shows them implanted immediately behind the posterior bursa (the right bursal cartilage can be seen in Fig. 1b, a cryosection, and in Fig. 1c, a histological section).

**Melon**

The presence of a hypertrophied fatty fore-

head in the extant Odontoceti is more consist-

ent than are teeth, a character that unites the suborder. At the same time, closer inspec-

tion reveals marked differences in lipid com-

position between major groups (Litchfield and Greenberg, ’74; Litchfield et al., ’75) and striking morphological differences in the shape of the melon at the generic level. The majority of the delphinid forehead tissue mass, commonly referred to as the melon, is composed primarily of special “acoustic fat” (Varanasi and Malins, ’71, ’72; Apfel et al., ’71; Ackman et al., ’71; Malins and Varanasi, ’75; Litchfield et al., ’76; Karol et al., ’78; Wedmid et al., ’73; Varanasi et al., ’82) inva-
ded at the ventral and lateral margins by connective tissue fibers and the embracing rostral musculature (Norris, ’64, ’68). In the sperm whale, *P. catodon*, the structure thought to be homologous to the melon is referred to as the junk (Schenkkan and Purves, ’73) or junk spermaceti, a term left over from the whaling industry. The delphinid melon rests on a dense connective tissue pad atop the bony rostrum of the skull and is anterior to the superior nasal passages and the complex of structures associated with them (MLDB complex).
Morris ('86) points out that the evolution of odontocete fatty forehead tissues has been of enormous significance to their successful radiation. Depositing these forehead fats represents a large energy investment that is not recoverable because the chemical composition of these special lipids becomes toxic to the animal’s normal metabolic pathways (Malins and Varanasi, '75). Thus, these fats cannot be used metabolically when normal energy reserves are low. A starving dolphin, for example, retains a completely robust melon even though its ribs may be obvious through the skin. Evidently a unique biosynthetic process has arisen to create these substances in situ. Studies have shown that melon lipid fractions with shorter chains, which are highly branched or increasingly saturated, transmit sounds at slower speeds than do longer chain, less branched, or less saturated molecules (Litchfield et al., '73, '79; Litchfield and Greenberg, '74; Morris, '73, '75; Varanasi et al., '75, '77, '82; Blomberg and Jensen, '76).

Odontocete forehead lipids have historically been implicated as primarily acoustic tissues (Norris, '64, '68, '80; Norris and Harvey, '72; Mead, '72; Malins and Varanasi, '75; Mackay et al., '77; Flewellen and Morris, '78; Mackay, '80b; Au, '80; Varanasi et al., '82; Hua et al., '89), and there is strong evidence for the acoustic function of these forehead fats (Schevill and Watkins, '66; Norris and Evans, '67; Evans et al., '64; Diercks et al., '71; Norris and Harvey, '74; Au et al., '75, '86, '93). Since sound is an excellent sensory modality in water, it should not be surprising that many, if not all, toothed whale species possess sophisticated acoustic faculties (see reviews in Norris, '64, '69, '75; Popper, '80; Wood and Evans, '80; Norris, '86). Because these fatty forehead tissues are roughly impedance-matched to seawater (Norris and Harvey, '74), they seem to provide an effective means of transmitting tissue-borne sound into seawater and probably also play a role in shaping the sound beam. Alternative suggestions as to the function of odontocete forehead lipid structures can be found (Clarke, '78) in reviews by Mead ('72) and Morris ('86), but the only suggestion that has gained widespread acceptance is that they are part of the means by which odontocetes shape or sharpen the emitted sound beam (Norris and Harvey, '74; Aroyan et al., '92). In the present study we have identified, described, and measured a low density pathway from the right MLDB complex to the surface of the forehead. We refer to this anatomic pathway as the PAP (potential acoustic path) because of our functional perspective, but we realize that the function is likely more complex than the term might suggest. In fact, even though intense sounds do emanate from the melon, interference is almost certainly involved in biosonar beam formation. We also realize that our PAP may be partially or entirely synonymous with the "core" of the melon referenced in the previously mentioned work of Litchfield and others.

Connective tissue theca

This connective tissue structure has not been previously described as an integral unit of odontocete forehead anatomy. A dense connective tissue theca or capsule embraces the posterior portion of the melon and merges with the nasal plug muscle ventrally. Since the theca is marked by an abrupt increase in density between fatty channels and surrounding muscle/connective tissues, it is most easily discerned from CT scans. The overall shape of the theca is reminiscent of a megaphone or horn, which may indicate an important role in biosonar beam formation and directionality.

Nasal plug nodes

The nasal plugs are fleshy masses of muscle and connective tissue that occlude the superior openings of the bony nares (Fig. 1b). In most but not all odontocetes, each nasal plug has a small node that is heavily invaded with connective tissue fibers and is often referred to as the "nasal plug lip" or node (Evans and Prescott, '62). This node is located on the dorsolateral surface of the nasal plug in delphinids and on the dorsomedial surface in porpoises. When removed from a delphinid specimen, the nasal plug node is normally concave dorsally and opens medially to form a wide concave sulcus along the dorsal surface of the nasal plug.

The presence or absence of these nodes, their location on the plugs, and their size and shape vary with the species (Schenkkan, '73). The nasal plug nodes are not found in the physterid or the platanistoid odontocetes. These nodes have been suggested to play a primary role in odontocete sound production (Evans and Prescott, '62), although the fact that they are not consistently present across the Odontoceti makes them poor candidates for signal generators during biosonar, appar-
ently a capacity of all odontocetes. The Evans and Prescott (’62) proposal (which implicates the nasal plug nodes as sound generators) was probably a major factor in raising the fervor of the debate between laryngeal vs. nasal phonation proponents.

Convincing arguments against the nasal plug nodes as sound generators have been put forth, most ably by Schenckkan and Purves (’73). Laryngeal phonation proponents gleaned their evidence primarily from anatomic studies (Schell and Lawrence, ’56; Schenckkan and Purves, ’73; Blevins and Perkins, ’73; Belkovich and Dubrovsky, ’77; Klima et al., ’86a,b; Reidenberg and Laitman, ’87, ’88; Pilleri, ’90), although some studies have measured sound fields from sound sources implanted in dead specimens (Purves, ’66; Purves and Pilleri, ’83) or from live phonating animals (Pilleri et al., ’76, ’80a,b, ’83a,b).

Nasal phonation proponents, on the other hand, have gathered evidence using a wide range of experimental designs, including behavioral observations (Norris et al., ’61), anatomic studies (Evans and Prescott, ’62; Evans and Maderson, ’73; Gao and Zhou, ’89; Rodinov and Markov, ’92), cineradiography (Norris et al., ’71; Hollien et al., ’76), triangulation calculations from contact hydrophones (Diercks et al., ’71), electromyography and pressure event measurements (Ridgway et al., ’80; Amundin and Andersen, ’83; Ridgway and Carder, ’88), ultrasound scanning (Mackay and Liaw, ’81), and sound field recordings from live animals (Au et al., ’74, ’88; Au, ’93).

Diagonal membranes

These structures have an enigmatic place in the literature about the odontocete forehead. They are thin, tough membranes that partially occlude the bony nares and often fit in a tongue and groove arrangement on the ventral surface of the nasal plugs (Fig. 1b). This arrangement could help form a tight seal between the plug and the bony nasal passage and may function to hold back air pressure within the bony nares with a minimum of muscle tension. The diagonal membranes may function as part of the air metering system during sound generation, but they also have been implicated as possible vibratory components in the process of generating some sounds (Mead, ’72). It seems clear, however, that their mass is too small to contribute, in a significant way, as a vibratory source in the transduction of high energy clicks. Their role in the production of whistles, however, as suggested by Mackay (’88), remains undemonstrated but possible.

Skull

The cetacean skull may show the most unusual arrangement of bones seen in the class Mammalia. Miller (’23) coined the term telescoping to describe the arrangement of cranial bones that occurs in both odontocete and mysticete cetaceans. This single term was an unfortunate choice because the probable forces behind the process for each suborder were so different, as were the end results. Odontocete skulls reveal the evolutionary construction of a sonar signal generation system (Norris, ’68).

Odontocete and mysticete skulls both have an elongate maxillary/premaxillary region, and both have the nares pushed back from a position at the tip of the snout (as found in most other mammals) to a position atop the head (near the vertex of the skull). Descriptions of the differences in odontocete and mysticete skulls can be found in Miller (’23), Barnes and Mitchell (’78), or Barnes (’84). In most odontocetes there is a peculiar displacement (in the region between the bony nares and the vertex of the skull) of the midline suture to the left. This condition is referred to as directional asymmetry because it is consistent both in magnitude and direction across populations and is relatively uncommon in nonodontocete animal groups. It is common in animal groups to find selection for symmetry (Thornhill, ’92; Balmford et al., ’93) or fluctuating asymmetry, which, as the term implies, varies in magnitude and direction across populations (Jolicoeur, ’63).

The curious directional asymmetry in odontocete skulls has been discussed (Miller, ’23; Howell, ’30; Mead, ’75; Heyning, ’89; Heyning and Mead, ’90) and sometimes measured (Ness, ’67; Yuirick and Gaskin, ’88), yet few studies have attempted to measure corresponding soft tissue asymmetry (Mead, ’75; Cranford, ’92a,b). Studying skulls from museum collections has the advantage of a relatively stable geometry that can, if prepared correctly, last for many years. On the other hand, soft tissue asymmetry probably preceded bony asymmetry (Mead, ’75). Until now it has been difficult to measure odontocete directional asymmetry in soft tissue without disrupting tissue geometry. Medical imaging techniques allow us to study undisturbed geometry in soft and hard tissues simultaneously.
The role of the odontocete skull in the formation of the echolocation beam has been studied by Evans et al. (64), Schenkkan (72), Romanenko ('74), Dubrovskiy and Zaslavskiy ('75), Best ('81), Alcari ('80), and Aroyan et al. ('92). Morphometric analyses of odontocete skulls, as a technique for identifying populations and establishing taxonomic relationships, have been carried out by many authors (e.g., Perrin, '75; Yurick and Gaskin, '87; Pinedo, '86). In this study we will provide quantitative descriptions of morphologic elements that may be important to sound generation and propagation.

Nasal and gular musculature

We will not consider the nasal and gular muscular anatomy in any detail. The nasal musculature is composed of a set of elements that result from the hypertrophy of the mammalian maxillonasolabialis muscle according to Howell ('30). The origins, insertions, and actions of nasal muscles have been described by Lawrence and Schevill ('56), Mead ('72), Schenckman ('73), Gao and Zhou ('88), and Heining ('89). The muscles of this region most often have broad, fan-like origins or insertions and are arranged in thin layers. Most of the individual nasal muscles have their origin on some portion of the facial fossa (Heyning, '89) and insert upon the aponeuroses of the nasal air spaces (most notably the spiracular cavity), or bones (through tendons), and the blowhole ligament. It is clear that the actions of these muscles mediate the opening, closing, and relative position of the nasal air sacs.

Nasal air sacs

Even though the nasal air spaces are complex and difficult to describe (Fig. 1a), descriptions of them abound in the literature, in part because they are so conspicuous (see review in Mead, '75). Some researchers have attempted to create casts of the air spaces in order to facilitate their description (Dormer, '74; Gurevich, '80; A. Purgue, personal communication). Modern descriptions of the nasal air spaces can be found in the work of Purves ('66), Mead ('72), Schenkkan ('71, '72, '73, '77), Dormer ('74), Green et al. ('80), Amundin et al. ('88), Gao and Zhou ('89), Heyning ('89), Amundin and Cranford ('90), and Amundin ('91a).

The complex system of nasal diverticula certainly plays a significant functional role in echolocation and beam formation as acoustic reflectors (Griffin, '80; Aroyan et al., '92). The most conspicuous characteristic of the nasal air spaces is that they are variable, both within a single species and between species (Dormer, '79; Mead, '72). Between families of odontocetes there are great differences in the shape, size, and number or configuration of air spaces; but within these groups and between individuals there is often variation in asymmetry or differences in shape and size of the air chambers (but usually not in number or relative position). Generally, each side is the mirror image of the other except that nasal air space elements of the left side are usually larger than the elements on the right side (with some exceptions). The two bony air passages between the superior and inferior bony nares are completely separate. The main soft tissue (spiracular) airway between the skull and the vestibular sac (above the bony narial passages) can be functionally divided into two separate (left and right) passageways by clamping down on the tongue and groove structure of the membranous nasal septum.

The following description of the right nasal diverticula between the nares and the blowhole is based upon Figure 1b, a right parasagittal cryosection from Tursiops truncatus. The description is offered for those readers unfamiliar with the complexity and overall configuration of delphinid nasal sac morphology.

Each side of the delphinoid nasal sac complex can be divided into premaxillary sac, spiracular cavity, inferior vestibule, anterior and posterior nasofrontal sacs, and vestibular sac (plus the caudal nasal sac in phocoenids and Delphinapterus leucas). In Figure 1b the premaxillary sac is seen as a small sliver lying atop the premaxillary bone. The right spiracular cavity begins at the superior bony nares. It rises posterosdorsally (about 4 cm) near the face of the skull before it bends abruptly anteriorly, giving off the inferior vestibule dorsally. After a short (about 0.6 cm) traverse anteriorly the spiracular cavity turns dorsally again and passes between the monkey lips (and the bursae within them) before emptying into the floor of the vestibular sac. The inferior vestibule extends dorsally from the junction with the spiracular cavity to a point just dorsal to the right posterior dorsal bursa, where it gives off two tubes. One runs medially a short distance as the posterior nasofrontal sac, and the other runs laterally and then anteromedially to
encircle the spiracular cavity as the anterior nasofrontal sac. Some workers also recognize a small outpocketing that receives the node of the nasal plug, the accessory sac (Schenkkan, '71). The components of the air sac system on the left in this specimen are the mirror image of those on the right, with some differences in size and shape of the components.

MATERIALS AND METHODS

We used a variety of images together to develop a comprehensive view of the odontocete forehead and its functional components. The shapes and interfaces of selected forehead tissue components are described from serial images collected primarily with a medical imaging technique known as x-ray computed tomography (CT). We also used magnetic resonance imaging (MR) to verify structural features and configurations seen with CT (Mackay et al., '87). Both of these methods are particularly good for imaging fatty structures (Mackay, '84).

Another set of images was produced by cryosectioning, which involves shaving very thin sections from a frozen specimen and then, after each section is removed, photographing the remaining tissue block. Some histologic sections were also made to identify tissue type and investigate structure on a fine scale.

Most of the images in this presentation are reconstructions that have been created from original serial CT scans and then processed using a Sun workstation and Vista software (Lick Observatory, '88).³

Materials

There are currently four recognized extant odontocete superfamilies: Delphinoidae (divided into three families: Delphinidae, Phocoenidae, and Monodontidae), Platanistoidea (variously divided into three or four families based on four genera), Ziphioidae (a single family Ziphiidae contains all five genera), and Physeteroidea (divided into two monogenetic families, Physeteridae and Kogiidae).

This work is based upon the cephalic anatomy from 19 species (40 specimens) of postmortem odontocetes that all died of natural or unknown causes. All extant odontocete superfamilies are represented. Specimens were dissected fresh or preserved by freezing, except the two pontoporidids, which were fixed in formalin prior to our receiving them. We chose specimens either to maximize the taxonomic breadth of our study or to compare replicates and techniques with commonly available species. This report will focus on six specimens representing a broad spectrum of morphologic configurations.

Detailed descriptions for three dolphins (the common dolphin (Delphinus delphis), the bottlenose dolphin (Tursiops truncatus), and the Pacific white-sided dolphin (Lagenorhynchus obliquidens), one porpoise (the harbor porpoise (Phocoena phocoena)), one platanistoid⁴ (the franciscana (Pontoporia blainvillei)), and one physeteroid (the pygmy sperm whale (Kogia breviceps)) are included in this report.

The sperm whales occupy one extreme of nasal anatomy. This lends prominence to sperm whales in our analysis. The pygmy sperm whale and the delphinids exemplify the range of morphology seen in the odontocete nose.

A complete list of the specimens examined in the course of this study is found in Table 1.

Methods and equipment

X-ray computed tomography

Medical imaging techniques provide an accurate means of investigating geometric relationships among soft tissue structures and are particularly useful for distinguishing fat and connective tissue boundaries. These techniques allow us to reconstruct the entire intact structure of odontocete forehead anatomy from serial sections as thin as 1.5 mm (Cranford, '88; Amundin and Cranford, '90; Amundin, '91a; Cranford, '92a). Other studies (Boice et al., '64; Hosokawa and Kamiya, '65; Green et al., '80) have produced thick serial sections of the dolphin forehead, but (as a consequence of sectioning with a bandsaw) they lacked the ability to select, resolve, or reconstruct the details of internal anatomy. We have been able to visualize and trace anatomic structures, especially fatty tissue, with somewhat more fidelity than has been possible using older techniques.

X-ray computed tomography is an excellent technique for the study of internal struc-

³Vista is an image processing package originally developed at the University of California, Santa Cruz for use in astronomical research; it has been informally distributed to sites worldwide.

⁴The taxonomic relationships within the Platanistoidea are not well understood or are at least still debated (Kasuya, '73; Zhou, '82; Barnes, '85; Heyning, '86). According to Zhou ('82), each of the four genera should be placed in its own family. We will follow this suggestion and place the franciscana in its own family, Pontoporididae.
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**Phocoenidae**

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The first column contains the ID code, composed of a single letter designation for the taxonomic family followed by a number sequence. Question marks indicate missing or unknown information. The second column indicates the origin of each specimen by institution or collection location according to these abbreviations: BRZL, coastal Brazil; CAND, Stranded Whale and Dolphin Program, British Columbia, Canada; CAS, California Academy of Sciences; DLFT, Deift University of Technology, The Netherlands; FLOR, University of Miami, Florida; GPRI, Greenland Fisheries Research Institute; HUMB, California State University, Humboldt; LACM, Natural History Museum of Los Angeles County; LML, Long Marine Lab, University of California, Santa Cruz; MLML, Moss Landing Marine Lab, California State University; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; NMFS, National Marine Fisheries Service; NOSC, Naval Ocean Systems Center; TEXS, Gulf coast stranding. The third column displays the scientific name for each specimen (neo indicates a neonate specimen). The next three columns contain collection reference number (Coll#), sex, and total length (TL). The last five columns indicate which techniques were used to examine each specimen: x-ray computed tomography (CT), magnetic resonance imaging (MR), cryomicrotomy (CR), dissection (DS), and histology (HS).

Specimen featured in this paper (represented in Figs. 3–7).

The study of cetacean species demonstrated that they are not only diverse in appearance but also in their habitat use. Each species inhabits a unique ecological niche, which is shaped by their physical characteristics and behavioral adaptations. This study highlights the importance of understanding the ecological niches of cetaceans in order to conserve these marine mammals effectively.
collected serially without intervening gaps. The pixel size in the plane of a scan is 1.5 mm. Therefore, it is theoretically possible to distinguish a structure that is 0.8 mm long in the plane of the scan.

All odontocetes were scanned with the same basic protocol, as described by Cranford (‘86). Generally, this called for serial tomograms throughout the entire head. A beam thickness of 5 or 10 mm was used for the anterior portion of the head, narrowed to 1.5 mm for the region of greatest interest (i.e., the nares, nasal plugs, air sacs, MLDB complexes, and posterior melon), and expanded for thicker sections (3, 5, or 10 mm) over the posterior portion of the cranium. Fresh or unique specimens were usually scanned from the tip of the rostrum to the occiput. In the case of replicates or partially damaged samples, scans were limited to the region of greatest interest. Specimens were normally placed in a Plexiglas registration frame built to hold odontocete heads (Cranford, ‘92a). The adjustable frame provided registration points in the scanning plane and, more importantly, a common orientation for all specimens. The original (transverse) scanning plane for all specimens (except *Kogia breviceps*) in the registration frame was perpendicular to the axis between the bony tip of the rostrum and the center of the foramen magnum. Since the hypertrophied forehead soft tissues in *Kogia breviceps* extend beyond the upper jaws, we placed their heads in the frame so that the anteriormost point on the head rested in the nose cone of the frame. Using a registration frame facilitated comparisons and provided the potential to reconstruct three-dimensional images from the two-dimensional serial images.

Reconstructions

The most powerful aspect of x-ray computed tomography is the flexibility it provides to reconstruct alternate two-dimensional image planes from the original transverse scan data. This ability is akin to "redissecting" a specimen. Although reconstructions can theoretically be made in any desired plane, this report presents axial images in three orthogonal planes (Fig. 2), the original scanning plane (i.e., transverse [Figs. 3c–8c]) and two reconstructed planes. The reconstructed planes are orthogonal to the original scanning plane (i.e., vertical (Figs. 3a–8a) and horizontal (Figs. 3b–8b) planes).

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**Fig. 2.** Schematic diagram of the analytic planes and reference axes. The three planes are referred to as vertical (sagittal), horizontal (frontal), or transverse (cross) planes.
In order to avoid any confusion associated with the inconsistent or incorrect use of terminology in the previous literature on odontocete forehead anatomy, we have established reference axes for the reader (see Fig. 2). Horizontal measurements in the original (transverse) plane are considered to be along the X axis; vertical measurements in the original plane are along the Y axis. The Z axis, in this case, is perpendicular to the original (transverse) scanning plane and parallel with the long axis of the body (see Fig. 2). This implies that horizontal and vertical measurements from a sagittal (vertical) reconstruction will be along the Z and Y axes, respectively. Finally, horizontal and vertical measurements from a (horizontal) coronal reconstruction will be along the X and Z axes, respectively.

Since our CT scans were originally collected serially and adjacent to one another (without intervening gaps), it was relatively easy to generate complete reconstructions by stripping out the same column (or row) of pixels in each original transverse tomogram and compiling them into a new file to produce an alternate plane or view. Stripping columns from serial transverse tomograms produces vertical (sagittal) reconstructions; stripping rows yields horizontal planes. In order to reduce the number of serial reconstructions for our analysis by one-half, we stripped two columns and averaged adjacent pixels (those in the same row) together to generate an average column for a sagittal reconstruction. We processed the scans similarly to produce horizontal reconstructions, except that we stripped out rows and averaged adjacent columns.

Transverse tomograms and horizontal reconstructions normally cut through only a portion of the potential acoustic path (PAP) or fatty pathway. We have chosen one tomogram from each plane (for each specimen) to illustrate various aspects of forehead structure. A horizontal reconstruction was normally chosen for its ability to illustrate the branching angle of the posterior rami of the melon (Figs. 3b–8b) leading to the proposed sound generation (MLDB) complex. A transverse tomogram was usually chosen that best exemplified the geometric relationship between one bursal complex and the other. Choosing a representative vertical (or parasagittal) reconstruction was not quite as simple or as straightforward because virtually every vertical reconstruction that passes through the right bursal complex also seems to cut through the entire PAP. Because it was difficult to choose a single sagittal tomogram as representative, we took advantage of the image processing capabilities at our disposal. Instead of choosing a single, thin (i.e., two-column average) reconstruction, we made a single thick (multiple-column average) parasagittal reconstruction.

For most sagittal (vertical) images (Figs. 3a–8a) we averaged the reconstructions over the length of the entire right bursal complex. Several columns were stripped out and all of the pixels in the same row averaged to produce a “thicker” average section. The number of columns or the “thickness” of the reconstruction was determined by the greatest width (along the X axis, more or less) of the right (anterior or posterior) dorsal bursa as seen from the (original) transverse tomograms and thus varied (between 10 and 20 mm) according to the specimen.

Cryomicrotomy

Cryosectioning allows examination of in situ soft tissue anatomy in a manner probably impossible to duplicate by hand dissection. Cryosections are excellent for following the air passages but are not as good for distinguishing fatty tissues from connective tissues—a distinction that is easy to make from CT scans. Conducting cryosectioning and CT scanning on the same specimen has proven to be a particularly powerful combination because each technique provides a set of parallel complimentary images based upon different tissue characteristics. Comparing and contrasting different images from the same specimen allows greater interpretive accuracy than for each kind of image separately. The usefulness of this combined approach for anatomic studies has been demonstrated by Raushning (‘83) and Raushning et al. (‘83).

We employed this combination of techniques using the head of a female bottlenose dolphin (Tursiops truncatus). Our specimen is listed as D3b in Table 1. The frozen head was trimmed into a block with a band saw to a size suitable for the cryomicrotome mounting plate. We placed the specimen right lateral side down on the sledge and frozen them together with carboxymethyl cellulose (CMC). Using a drill press, we then drilled registration holes into three locations in the block. Plexiglas rods placed in the holes were visible during CT scanning with a Siemens Somatom DR2 CT scanner. Later we removed the
rods and filled the holes with green-dyed water, which made them obvious during cryosectioning. Cryosectioning was conducted with a LKB heavy-duty sledge cryomicrotome. The block was shaved at 20 micron intervals and photographed every millimeter. The fresh cut surface was always wiped with alcohol to bring out tissue color prior to photographing (Fig. 1b).

Cryomicrotomy allowed us to thin-section the tissues of the MLDB complex and clarify their relationship to nearby structures (i.e., especially the air spaces but also the monkey lips, various cartilaginous structures, the diagonal membrane, and nasal plug lips). The techniques used were similar to those reported by Amundin and Cranford ('90) for the harbor porpoise (Phocoena phocoena) and Commerson's dolphin (Cephalorhynchus commersonii).

**Measurements**

The ease with which our images can be manipulated to access the geometry means that there is a virtually limitless number of measurements that may be recorded. We have chosen to make measurements within the framework of acoustic function rather than to provide a purely anatomic description. All the measurements reported here are either linear dimensions of structures that we consider to be part of the sound generation/propagation system or estimates of spatial geometry as an attempt at describing the shapes or relative positions of these structures.

In this study, accuracy depends heavily upon our ability to interpret the images. One of the main reasons for choosing these medical remote imaging methods is that the geometric information they provide remains static throughout the entire study. This means that the same specimen can be analyzed many times, nuances of anatomy uncovered, and comparisons made with other species before deciding what to measure. Comparing CT scans with cryosections or dissections provided an interpretive baseline. Beyond this, our interpretive abilities have been enhanced both by studying replicates of a few species (i.e., how much do the patterns stay the same?) and by increasing our comparative breadth (i.e., how much do the patterns differ?).

Maximum estimated linear dimensions of the bursae for each primary specimen are given in millimeters (see Tables 3–7). These estimates result from three separate measure-
as described above). All further references to disparity in this report should be understood as these disparity indexes.

Since all CT specimens were placed in a registration frame, which holds each head in the same geometric orientation (with respect to the Z axis), there is essentially only one axis around which the orientation of the specimen can vary, that being around the Z axis. This means that specimens are both parallel and in registration. This technique yields an advantage not typically enjoyed by traditional serial section studies like histology, where placement of successive specimens normally produces slightly different sectioning planes, making direct comparisons more difficult. Whenever possible our specimens were placed in the registration frame with the center of the blowhole at the highest point. Because the blowhole is located slightly off the midline, positioning the blowhole topmost results in a small rotation around the longitudinal or Z axis. The resultant rotation is listed as ROT1 in Tables 3–7 and is an attempt to quantify this rotation. A typical transverse section (taken from the region near the blowhole) shows that the lateral margins of the skull form a set of flanges or “wings,” resulting from the sliding of the maxillary bones over the frontals (Fig. 3c). The rotation (ROT1) can be seen as the deviation of these wings from exactly horizontal. A compass provided by the Vista image processing package was used to estimate the number of degrees of ROT1 (Fig. 7c shows an example).

We measured another geometric (Z axis) rotation because, if both MLDB complexes are sound sources and vibrate in near or complete simultaneity, this angle may well be important for the production of interference patterns in the emitted sound field of a living animal. Again from transverse sections, a line drawn perpendicular to the long axis of each posterior bursa will form an angle (ROT2), which represents an angular difference between the long axes of both bursal complexes (Fig. 5c).

Because bony surfaces influence the shape and position of soft tissues and acoustically reflective air spaces, and probably influence the sonar beam formation process, we chose to quantify two abrupt changes in the rise of the skull face. These approximations are defined by angular deviations from the Z axis, seen in the sagittal reconstructions. The first deviation of the dorsal aspect of the skull from horizontal is formed by the premolarial shelf just anterior to the bony naris. We will refer to this angle as the angle of the premolarial shelf. Immediately posterior to the naris, the bony face of the skull (formed by a combination of the premolarial, maxillary, ectethmoid, mesethmoid, and nasal bones) rises above the horizontal axis at an even steeper angle. We refer to this angle as the angle of the face of the skull.

Branch angle (BA) was recorded from horizontal reconstructions. It represents an estimate of the angle formed by the split between the right and left branches of the posterior melon, where the center point of the measuring compass is placed at the split (Fig. 3b shows an example). This measurement is not relevant for the sperm whales because they are so asymmetric that no branching occurs. Branching angle may also not be a meaningful term for the porpoises since the melon appears to end in a single terminus along the midline (Amundin and Cranford, '90; Amundin, '91a; Cranford, '92a), and there is no visually obvious and continuous fatty path between the melon terminus and the bursae.

In order to give the reader a better sense of the position of each MLDB complex within the head, we measured and recorded the distances from one bursa (in each set) to two major landmarks: the corresponding superior bony naris and the blowhole. The height above the naris (HAN) was measured from the most posterior transverse section containing the bursal complex. This distance was estimated by drawing a line across the opening of the superior bony naris and recording the length of a perpendicular line from there to the center of the corresponding bursa. The shortest distance to the blowhole (SDTB) was measured in the same transverse section and was measured as the distance from the center of the dorsal bursa to the nearest edge of the blowhole. Examples of HAN and SDTB measurements are shown in Figure 3c by solid black lines near the top of the specimen in the photograh.

Maximum melon dimensions (MELD) were recorded from vertical and horizontal reconstructions. The margins of the melon were selected visually as a sudden increase (i.e., steep gradient) in the pixel intensity values. The melon length (Z axis, more or less) was measured from the extreme posterior margin of the melon to a point on the anterior margin, halfway between the top and bottom borders. The height (Y axis, approximately)
was measured across the widest point of the melon perpendicular to the axis for the length measurement (see Fig. 4a). Maximum melon width (an X axis measurement) was estimated from a transverse section. Examples of MELD measurements are indicated in Figure 4a by two solid black lines crossing the melon of the specimen within the photograph.

Since the surface of the forehead is potentially important acoustically (because it may help to determine refraction patterns of the emitted sound beam into the surrounding water [see Litchfield et al., '75, '79]), we have provided an approximate measurement for forehead radius of curvature (FROC). It attempts to represent the overall curvature of the forehead as determined by eye with the aid of a compass and is meant to give a general impression of forehead curvature. Forehead curvature was measured from sagittal reconstructions (Figs. 3a–8a) using a compass to find the radius whose curvature best fits the forehead in that image. The length of the radius was measured using the scale bar for that image (i.e., measurements were standardized to eliminate the effects of differences in size).

The potential acoustic path or PAP measurements are descriptors of the lowest density anatomic path through the melon from the bursal complex to the surface of the forehead. This perceived low density channel through the forehead provides a way to visualize a simple pathway out of the head. We have measured the length of this path or channel by inspection of the density topography in vertical reconstructions and with the aid of contrast enhancement features in the Vista software. Since the acoustic beam may be produced by interference fields, the concept of a pathway introduces some conceptual difficulties. Even if the potential acoustic path is not an acoustic channel, it does, however, represent an anatomic channel that has not been measured or geometrically described by previous studies. This description may allow assessment of the importance of interference in sound beam formation (Au et al., '93). This PAP topography is probably not an artifact of postmortem changes in tissue since its existence has been noted by previous studies of recently dead specimens (Litchfield et al., '73; Norris and Harvey, '74).

Postmortem geometry may be somewhat different from the configuration used by live animals during the sound generation process (e.g., air sacs are typically collapsed in postmortem specimens, and some are known to be inflated during sound production). In fact, as pointed out previously, close inspection of Figure 1b reveals that the ridges of the monkey lips do not rest upon one another, probably indicating some deviation from a functioning geometry. On the other hand, the intact postmortem geometry reported here approximates a "functional" geometry, and computer simulations (Aroyan et al., '92) indicate that it is close enough to model acoustic function.

Computer equipment and software

General Electric CT image data were unloaded from CT formatted tapes and copied into Vista's WFPC (Wide Field Planetary Camera for Hubble space telescope) image format. The analysis and measurements from images were conducted using Vista running on a Sun Microsystems 3/110 workstation. Several user programs written in the Vista language were the main tools used for generating reconstructions and for making measurements.

Dissection and histology

Dissections were performed on all but the cryosectioned specimen. The tissues of the MLDB complex were excised and preserved for histological examination at a later date. Preliminary histological examinations were performed on MLDB tissues from four specimens: three dolphins (Delphinus delphis, Stenella coeruleoalba, Pseudorca crassidens) and one porpoise (Phocoenoides dalli). These specimens are listed in Table 1 as D9, D18, D19, and P4, respectively. Because these tissues were invariably previously frozen and thawed at least once, they presented some difficulties during histological sectioning. Several methods and materials for preparing (softening), embedding, and staining were tested. The most successful technique included preparation of tissue samples by pre-soaking in 70% cedarwood oil followed by embedding in paraffin and staining with Mallory-azan or aniline blue. This technique produced the section from Pseudorca crassidens shown in Figure 1c.

RESULTS

Descriptive morphology

In the course of this study we found primary similarities between the anatomic configurations of delphinoids, ziphids, and our only platanistoid. Members of all but one
extant odontocete family contain two MLDB complexes within a slightly to moderately asymmetric forehead. The exception is that members of the family Physaceridae have extremely asymmetric foreheads and contain a single MLDB complex.

All delphinoids examined in this study (see Table 1), regardless of sex or age, possess two bilaterally placed MLDB complexes, one located at each lateral margin or corner of the spiracular cavity. Each MLDB complex is located just below the ventral floor of the vestibular sac (Fig. 3a) and is composed of a pair of fat-filled bursae embedded in a pair of monkey lips, a resilient cartilaginous blade, and a stout ligament, all suspended within a complex array of muscles and air spaces. Most nasal muscles, from a variety of origins on the facial fossa, converge on the lateral aponuroses at the lateral corners of the spiracular cavity.

The anterior and posterior dorsal bursae on the same side are similar in size and shape. Delphinid dorsal bursae tend to be shaped approximately like elongate cones with the longest dimension oriented generally along the X axis or more or less horizontally in a transverse plane (for example, see the anterior dorsal bursa in Fig. 3c). The posterior bursae are closely associated with the caudal end of the melon (Figs. 3a–8a) but appear in scans as slightly detached from it. The melon, to a large degree, defines the shape of the forehead in nonphyseterid odontocetes and provides a pathway through which sounds are known to be propagated into the aquatic environment (Evans, '73; Au et al., '78; Au, '90, '93).

The conduit for air passing dorsally from the superior bony nares in delphinoids to the vestibular sacs is called the spiracular cavity. At the beginning of its more or less dorsoventral traverse, the spiracular cavity is divided into right and left passages by a membranous nasal septum. This septum ends dorsally a few centimeters above the bony nares, superior to which the anterior and posterior walls of the spiracular cavity can be made to interlock, functionally dividing the passage into a left and right channel. At the entry of each passage into the vestibular sac, the spiracular air space passes between a slit-like opening (the monkey lips) that conducts air into the vestibular sac. In order to reliably identify the geometry of air spaces without disrupting the specimen’s soft tissue, we cryosectioned a single specimen of *Tursiops truncatus* (D3b in Table 1), following the same protocol used by Amundin and Cranford (’90) for the harbor porpoise.

Each posterior dorsal bursa is found within a “peninsula” of tissue that is bounded on three sides by air spaces (in parasagittal section, Fig. 1b), although the spiracular air space may not actually contain air most of the time. We consider this tissue peninsula to be a functional unit. We will define it here in terms of anatomic boundaries and landmarks. The peninsula is defined rostrally by the spiracular cavity and caudally, just behind the blade of bursal cartilage and a small mass of intrinsic musculature, by the inferior vestibule. It is bounded dorsally by the border between the monkey lips and the vestibular sacs, ventrally by the blowhole ligament (along the confluence of the spiracular cavity with the inferior vestibule), and medially by the membranous nasal septum. It extends laterally to the edge of the spiracular cavity and includes the posterior dorsal bursa, the cartilaginous blade (bursal cartilage), and the midportion of the blowhole ligament. The peninsula is anchored posterodorsally through the tendons of the intrinsic muscles and to the skull by the blowhole ligament. Medially the blowhole ligament is attached to the anteroventral aspect of the vertex near the dorsal border of the membranous nasal septum. The blowhole ligament passes ventrolaterally from the vertex through the tissue peninsula and beyond the lateral extent of the spiracular cavity to insert broadly on the lateral edge of the premaxilla, or the medial maxilla, depending upon the species.

There are two pairs of monkey lips, each one associated with the functionally separate bilateral passages of the spiracular cavity at the junction with the vestibular sacs. The monkey lips are easily seen in dissection. Each lip (of both pairs) is visible as a small ridge and a pigmented stripe along the wall of the spiracular cavity. One fatty bursa is embedded within each of the monkey lips, two pairs of each. Immediately ventral to the ridges on the walls of the spiracular cavity, a slight elliptically shaped bulge or puckering is apparent. The cavity wall appears slightly more pliable in this region and is the place where the fat of the bursa abuts the wall of the spiracular cavity (Fig. 1b). The long axis of the lips is parallel and approximately equal in length to the dorsal bursae within it (this axis is also approximately perpendicular to the longitudinal body axis). Therefore, mea-
suring the length of a lip can be a close approximation for the length of the corresponding bursa.

The ridges of the lips consist of a pair of transverse keratinized tissue bands that are often demarcated by a thin pale line on the wall of the spiracular cavity where the anterior and posterior ridges rest against one another. This whitish line is normally more conspicuous on the right side, where it is seen as the absence of pigment in an area of black epithelium. During dissection, the lips are most visible as a thick darkly pigmented stripe, which runs along the ventral base of the ridge, just beneath the white line, and directly over the puckered region. It is also upon the wall of the spiracular cavity that one can observe faint grooves or striations running at right angles across the long axis of the lips. Upon closer inspection it is clear that a family of thin, regularly spaced grooves traverses the lips at right angles (i.e., across the lips).

These grooves are always seen clearly on each anterior monkey lip (and sometimes on the posterior lips) in all of the nonphysasteroid, recently postmortem material we have examined. In the physasteroids, where there is only one pair of monkey lips, these grooves can be found on both lips. When the delphinoid monkey lips are stretched mediolaterally, the grooves are almost imperceptible, but when the tension on the lips is relaxed slightly, the grooves become clearly visible. The grooves run parallel to the direction that air tends to pass in the cavity. Normally the grooves occur about once every millimeter across the entire lip in all of the smaller delphinoid material fresh enough to yield such measurements. Dorsal to the anterior lips, the grooves fade into the crenated texture of the vestibular sac epithelium. Ventrally, the grooves appear to originate from a single, larger U-shaped depression that forms on the dorsolateral surface of the nasal plug.

The caudal aspect of the posterior bursa is supported by a blade of cartilage embedded in its posterior wall. We will refer to this small blade of cartilage as the bursal cartilage (Fig. 1c). It has also been called the blowhole ligament cartilage (Heyning, '89) because the blowhole ligament runs just ventral to it. We have found these floating cartilages in every nonphysasterid specimen we examined, although they can be small and easily overlooked in smaller specimens. The elongate cartilaginous structure described by Behrmann and Klima ('85) for the sperm whale was also obvious in our dissections of Physeter and may be homologous to one or both bursal cartilages.

Each of the following descriptions will be easier to comprehend if the reader is oriented from superficial to deep and from anterior to posterior. Consequently, the description of each specimen will originate at the anterodorsal surface of the forehead and direct the reader inward and posteriorly, toward the MLDB complexes. We begin by estimating the curvature of the forehead and tracing the lowest density pathway(s) through the melon, describing any branching patterns as the posterior melon narrows. Then the relative sizes of the dorsal bursae, which are the central and most conspicuous components of each MLDB complex, are described. Maximum dimensions for each bursa along with measurements of their position in space and orientation are found in a short table accompanying each description (these standard measurements could not be made for Kogia breviceps). Following the description of the fatty structures we will describe the connective tissue theca that envelops the posterior fatty elements. Finally, each description will contain potentially important angles formed by the bones of the skull and a brief mention of the configuration of the air spaces.

The pixel intensity values in Figures 3–8, based upon electron density, are mapped onto a color spectrum, which can be generally associated with tissue types as shown in Table 2.

In each of the figure groups (Figs. 3–8) the first photo (Figs. 3a–8a) represents a parasagittal section. These parasagittal sections are always from the right of the midline because they run through the right MLDB complex and, like all other reconstructions in this report, are reconstructed from the original transverse tomograms. Figures 3b–8b represent horizontal reconstructions, and Figures 3c–8c are original transverse tomograms.

The forehead anatomy of the common dolphin (Delphinus delphis) will be used to com-

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<td>+150</td>
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<tr>
<td>Fibrous connective tissues</td>
<td>Red</td>
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<td>Muscle</td>
<td>Orange</td>
<td>+10</td>
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<tr>
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<td>Yellow-gold</td>
<td>−150</td>
<td>+10</td>
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<tr>
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<td>Green</td>
<td>−300</td>
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<td>Air</td>
<td>Blue</td>
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Fig. 3. a: Vertical tomographic reconstruction (right parasagittal section) through the right MLDB complex in *Delphinus delphis* (D4 in Table 1), the common dolphin. The reconstruction was averaged over ten pixel columns (slice thickness = 15 mm). The line through the icon for the dorsal view indicates the approximate plane of Fig. 3a. ab, anterior dorsal bursa; bc, brain; c, cranium; ct, connective tissue theca; fx, forehead apex; h, hyoid bone; m, melon (main body); n, naris; pb, posterior bursa; r, bony rostrum; s, scale (1.5 cm); vs, vestibular sac. Anterior and posterior are indicated by A and P, respectively.
Fig. 3. b: Horizontal reconstructed tomogram (frontal section) from *Delphinus delphis*. The reconstruction was averaged over two pixel rows (slice thickness = 3 mm). The compass was positioned so that the main axis of the melon (right branch) was aligned with a compass axis. This device was used to measure the branching angle (BA) by placing the center point of the compass at the intersection between the axes of each melon branch.

The dashed line on the schematic diagram approximates the branching angle. The line through the icon for the lateral view indicates the approximate plane of Fig. 3b. ab, anterior bursa; c, cranium; lm, left branch of melon; m, melon (main body); rm, right branch of melon; pb, posterior bursa; s, scale (1.5 cm). Right and left are indicated by R and L, respectively.
Fig. 3. c: Transverse tomogram (cross-section) from *Delphinus delphis*. Slice thickness is 1.5 mm. Examples of the measurements HAN and SDTB are indicated by the straight black lines near the top of the specimen in the photograph. The extreme lateral projections from the skull are referred to as the wings of the skull in the text. The lines through the icons for the lateral and dorsal views indicate the approximate plane of Fig. 3c. ab, anterior bursa; bc, brain; c, cranium; es, esophagus; h, hyoid bone; j, jugal bone; m, melon (main body); ma, mandible; mf, mandibular fat body; np, nasal plug; pb, posterior bursa; s, scale (1.5 cm); vs, vestibular sac. Left and right are indicated by L and R, respectively.
pare and contrast with the other species described in this study.

**Common dolphin (Delphinus delphis)**

This specimen of the common dolphin is identified as D4 in Table 1. In a right parasagittal section (Fig. 3a), the anterior half of the dorsal boundary of the melon follows the gently sloping curvature of the surface of the forehead. The curvature is estimated to be 0.036, relatively flattened compared to the other species in this analysis. The yellowish fatty melon is one-third as high as it is long (Fig. 3a) and almost twice as wide as it is high (Table 3). The anterior portion of the melon is increasingly invaded with connective tissue and ends anteriorly (~30 mm) before the forehead contour meets the bony rostrum at the apex.

The lowest density channel extends from the anterodorsal surface of the forehead to the right posterior terminus of the melon and is 106 mm long. The posterior third of the melon splits into two unequal lateral channels, the right being about twice the diameter of the left. The right channel is aligned with the main axis of the melon (Fig. 3b), and the left fatty ramus branches off the main body axis of the melon after a small intervening gap of muscle and fibrous connective tissue. The left channel diverges from the right (i.e., branching angle [BA]) at an angle of 45 degrees (Fig. 3b). The larger right fatty channel narrows and ends at the MLDB complex, superior to the bony nares (about 10 mm), anterior to the steeply sloping face of the cranium where two small fatty projections, the dorsal bursae, are visible in Figure 3a.

In all of the delphinoids so far examined, the MLDB complexes are located at the lateral margins of the spiracular air space between the opening of the inferior vestibule and the floor of the vestibular sac. In *D. delphis* one MLDB complex is situated at each (both) posterior terminus of the melon, approximately 30 mm apart (Fig. 3c). The right MLDB complex is oriented parallel to the X axis (Fig. 3c) and perpendicular to the Z (or longitudinal) axis of the body (looking down from above) (Fig. 3b). The left MLDB complex is not perpendicular to the Z axis but instead is perpendicular to the axis of the left branch of the posterior melon. The left MLDB complex is also rotated around the Z axis about 18 degrees with respect to the right (ROT2 in Table 3) (Fig. 3c).

Maximum dimensions of the bursae are shown in Table 3. Measuring across the long axis of the bursae (in a parasagittal plane of the head) indicates that height and width (Y and Z axes, respectively) are approximately equal for the left and right sides (left slightly smaller). The length of the bursae (approximately along the X axis) is moderately asymmetric with a disparity index (DI) of 0.57 (i.e., the right bursal complex is slightly more than two times longer than the left). A similar asymmetric pattern is evident if one measures along the axis of the monkey lips (on the walls of the spiracular cavity) during dissection. The disparity index for length of the monkey lips in this specimen is 0.49 (recall that a DI of 0.50 would mean that the left is half the size of the right). The DI of 0.30 for the premaxillary bones indicates that these widths are not as disparate (i.e., are more similar in size) as the corresponding soft tissue structures.

The sagittal (vertical) section of the connective tissue theca of *Delphinus* is reminiscent of a section through the bell of a horn (Fig. 3a). The anterior opening or aperture of this "horn" in *Delphinus* is about 45 mm high (measured vertically in Fig. 3a). The throat or funnel depth of the horn (horizontal distance from anterior opening to apex) tapers to a posterior apex in 42 mm. The thickness of the wall of the ventral surface of the theca is more or less uniform (10 mm) between the

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**Table 3. Measurements for Delphinus delphis**

- **PAP length = 106**
- **Disparity index (dorsal bursae) = 0.57**
- **Disparity index (premaxillary bones) = 0.30**

**Abbreviations used:** Height (H), width (W), and length (L) for each dorsal bursa, in millimeters. Disparity index, left/right size disparity expressed as a decimal fraction. BA, branching angle between right and left branches of the melon (in degrees); FROC, forehead radius of curvature, estimated from the anterodorsal surface of the forehead; HAN, distance above nares for right (r) and left (l) bursal complex (in millimeters); MELD, maximum linear dimensions of the melon, height (h), width (w), and length (l) (in millimeters); PAP, potential acoustic path length (in millimeters); ROT1, rotation of specimen in registration frame (in degrees); ROT2, rotational separation of right and left bursal pairs (in degrees); SDTB, linear distance to blowhole for right (r) and left (l) bursal complex (in millimeters). Definitions and detailed descriptions of how these measurements were made can be found in the Measurements section in Materials and Methods.
melon and the posterior portion of the premaxillary bone. Portions of the vestibular sac can be seen capping the dorsal aspect of the connective tissue theca (Fig. 3a). The theca is not as easily distinguished in the horizontal (Fig. 3b) and transverse (Fig. 3c) tomograms, but, if the reader looks closely, it can be seen as a deeper red hue on two sides of (Fig. 3b) or embracing (Fig. 3c) the posterior portion of the melon (which is yellow).

In this specimen the angle of the premaxillary shelf is approximately 26 degrees, and the angle of the face of the skull rises above the horizontal plane at about 60 degrees.

Bottlenose dolphin (Tursiops truncatus)

This Atlantic bottlenose dolphin is the largest specimen in our image series (Fig. 4; Table 4). We have estimated the curvature of the forehead in the parasagittal section to be 0.042. The overall forehead shape is similar to the bulbous-shaped forehead of D. delphis. In this specimen, as well as in the other delphinids investigated, the anterior boundary of the melon is not coincident with the surface of the forehead near the apex. The distance from the tip of the rostrum to the forehead apex is 100 mm. Another 40 mm can be measured between the apex and the most anterior projection of the melon. The melon is slightly more than two times longer than it is high (Fig. 4a) and is twice as wide as it is high. Where the exterior of the melon is the widest (111 mm), the melon core is 70.5 mm wide. The shortest low density path (PAP) from the surface of the forehead through the melon to the bursae is approximately 135 mm long. The Tursiops melon differs from D. delphis in that it gives off an additional dorsally projecting channel before the start of the lateral branching angle (Fig. 4a). This additional branch is about 20 mm long and 4.5 mm high and terminates on the anterior surface of the vestibular air sac (Fig. 4a). The branching angle (BA) and the Z rotation (ROT2) of the left MLDB complex with respect to the right are both smaller than in D. delphis. Again, the larger right branch of the posterior melon appears to be aligned with the central axis of the melon.

The left branch of the posterior melon diverges from the primary (right) branch. In this species, like in D. delphis, the left branch does not abut the main melon axis as a clear fatty channel of the same density but instead leaves a small (3 mm) gap of intervening muscle and connective tissue between the main melon axis and the start of the left branch. The pattern of disparity in this specimen is similar to that found in most other delphinids. Bursal asymmetry measurements indicate that the right bursa is almost two times longer than the left (DI = 0.46), not quite as asymmetric as in D. delphis. The premaxillary bone disparity is again smaller than that for soft tissue (DI = 0.27).

The narrowing of the melon in T. truncatus (defined by the boundaries of the connective tissue theca) occurs in the posterior third of the organ, as seen in D. delphis. The anterior aperture of the theca is 74 mm high, and the funnel is 62 mm deep in sagittal section (Fig. 4a). The continuity of the theca is broken dorsally by the extra branch of the posterior melon and a portion of the vestibular sac. Along the ventral margin of the melon the theca is continuous, as we have seen in the other delphinids, and is slightly less than 10 mm thick along its entire length.

The dorsal surface of the bony rostrum is slightly convex (Fig. 4a) when compared to a horizontal line along the top of the rostrum (parallel to the horizontal Z axis given by the registration frame). The angle of the premaxillary shelf is 26 degrees (with respect to the Z axis). A steeper angle of 65 degrees is formed by the face of the skull with the same (Z) axis. There are portions of the air sac system visible in this specimen. The premaxillary sac overlies the posterior extremity of the premaxillary bone. The junction between the spiracular cavity and the inferior vestibule can be seen anterior to the face of the skull and just posteroventral to the right bursal pair. The vestibular sac is found just dorsal to the bursae in Figure 4a.

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**TABLE 4. Measurements for Tursiops truncatus**

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1See Table 3 for abbreviations.
Fig. 4. a: Vertical tomographic reconstruction (right parasagittal section) from *Tursiops truncatus*, the bottlenose dolphin (D3 in Table 1). The reconstruction is an average over nine pixel columns (slice thickness = 13.5 mm). The intersecting solid black lines within the melon indicate the height and length measurements for that structure. The line through the icon for the dorsal view indicates the approximate plane of Fig. 4a. ab, anterior bursa; bc, brain; c, cranium; ct, connective tissue theca; fx, forehead apex; h, hyoid bone; m, melon (main body); n, naris; pb, posterior bursa; ps, premaxillary sac; r, bony rostrum; s, scale (1.5 cm); sc, spiracular cavity; vs, vestibular sac; x, extra branch of melon. Anterior and posterior are indicated by A and P, respectively.
Fig. 4. **Horizontal tomogram (frontal section) reconstructed for *Tursiops truncatus*. The reconstruction is an average over two pixel rows (slice thickness = 3 mm). The line through the icon for the lateral view indicates the approximate plane of Fig. 4b. ab, anterior bursa; c, cranium; lm, left branch of melon; m, melon (main body); pb, posterior bursa; pn, posterior nasofrontal sac; rm, right branch of melon; s, scale (1.5 cm); vs, vestibular sac. Right and left are indicated by R and L, respectively.
Fig. 4. c: Transverse tomogram (cross-section) from *Tursiops truncatus*. Slice thickness = 1.5 mm. The lines through the icons for the lateral and dorsal views indicate the approximate plane of Fig. 4c. bc, brain; c, cranium; h, hyoid bone; j, jugal bone; ma, mandible; mf, mandibular fat body; np, nasal plug; ns, anterior nasofrontal sac; pb, posterior bursa; s, scale (1.5 cm); vs, vestibular sac. Left and right are indicated by L and R, respectively.
Pacific white-sided dolphin
(*Lagenorhynchus obliquidens*)

In the Pacific white-sided dolphin we see a major deviation from the basic plan shown in the first two delphinid genera (*D. delphis* and *T. truncatus*). We have also been able to examine the CT scans of the white-beaked dolphin (*Lagenorhynchus albirostris*) from studies at the University of Delft (Brouwers et al., '90) and found there to be few if any obvious differences from the geometry reported here for *L. obliquidens*. The rostrum of *L. obliquidens* in our specimen is shorter (37 mm) than that of *T. truncatus*, and the forehead contour reaches almost to the rostral tip. The forehead curvature in *L. obliquidens* is estimated to be 0.034, similar to that of *D. delphis*.

Melon morphology in *L. obliquidens* is very different from the other delphinids we have examined (Fig. 5). *Delphinus, Tursiops*, and *Stenella* all have a clearly defined central melon axis aligned with the right branch of the posterior melon, leading to the right MLDB complex. *Lagenorhynchus obliquidens* has a central post or column of connective tissue that projects dorsally from the skull about midway along the rostrum, into the middle of what would otherwise be the central melon axis. In *L. obliquidens* both channels (left and right) diverge from the central forehead axis, in contrast to the previous specimens, where the main axis of the melon leads to the right MLDB complex and the left fatty channel branches off the main (right) axis. The posterior branching angle is approximately equal on either side of the central axis of the forehead, at just over 32 degrees (Fig. 5b).

Another major difference between *L. obliquidens* and the other delphinids in our comparative series is a relative lack of left/right size disparity in the MLDB complexes and premaxillary bones, although there are some differences in the shape of the channels leading to them (see fatty basins in Fig. 5a,c). Maximum linear measurements of the MLDB complexes (and the triangular fatty basins (see Fig. 5c) show a disparity index of 0.11 (i.e., slightly asymmetric) compared to about 0.50 (i.e., moderately asymmetric) in the other delphinids. Bony premaxillary asymmetry in *L. obliquidens* is less than that found in soft tissue, consistent with the condition found in the other delphinids.

Maybe the most striking difference between *L. obliquidens* and the other delphinids examined (*D. delphis, T. truncatus, and Stenella* spp.) is that there are two enlarged fatty basins (Fig. 5a), located between the main body of the melon and the MLDB complexes. We noticed similar structures in *L. albirostris, Grampus griseus*, and a neonate *Lissodelphis borealis*. These basins or expansions of the posterior melon, leading to each MLDB complex, appear more or less triangular in parasagittal section and have not been previously described. Their three-dimensional shape is roughly an inverted tetrahedron, although the actual shape is more irregular than this description suggests. The lengths of the sides of the triangle in Figure 5a are listed in Table 5, under an additional column marked triangular basin dimensions (TBD). The sides are listed in sequence as a, b, c beginning at the base of the inverted triangle (i.e., dorsal surface) and moving clockwise around the structure. The edges of these structures are clearly defined except where they merge anteriorly with the main body of the melon.

The connective tissue theca in *L. obliquidens* is shaped differently from that in *D. delphis, T. truncatus, and Stenella* spp., because the posterior melon (which partially determines the thecal boundary) is shaped differently. The anterior aperture of the theca is 50 mm high, but there is a severe constriction to 13 mm high just 21 mm into the funnel of the theca, at the anteriormost point of the triangular basin. The total (anterior-posterior) depth of the funnel of the theca is 36 mm. The theca is thin between the ventral surface of the main body of the melon and the rising shelf of the premaxillary bone in Figure 5a. It is thicker below the anterior surface of the triangular basin and narrows again as it passes over the posterior extension of the premaxillary bone. The thickness of the theca increases to approximately 10 mm and remains constant as it ascends between the posterior surface of the triangular basin and the steeply sloping face of the skull. It is thinner and difficult to detect as we trace it anteriorly and dorsally between the ventral surface of the vestibular sac and the top of the dorsal bursae. The theca then expands anteriorly, passing underneath the anterior portion of the nasofrontal sac, and ends bluntly about 15 mm below the surface of the skin (about 30 mm anterior to the blowhole).

The skull in this species shows some unusual characteristics as compared to the previous delphinids. For instance, it is clearly evident that the left/right asymmetry is much less in *L. obliquidens* than in *T. truncatus,
Fig. 5. a: Vertical tomographic reconstruction (parasagittal section) from *Lagenorhynchus obliquidens*, the Pacific white-sided dolphin (D7 in Table 1). The reconstruction is an average over 11 pixel columns (slice thickness = 16.5 mm). The line through the icon for the dorsal view indicates the approximate plane of Fig. 5a. ab, anterior bursa; bc, brain case; c, cranium; cc, connective tissue column; ct, connective tissue theca; fx, forehead apex; h, hyoid bone; m, melon (main body); n, naris; ns, anterior nasofrontal sac; pb, posterior bursa; r, bony rostrum; s, scale (1.5 cm); sc, spiracular cavity; tb, triangular basin; vs, vestibular sac. Anterior and posterior are indicated by A and P, respectively.
Fig. 5. b: Horizontal reconstructed tomogram (frontal section) through the head of *Lagenorhynchus obliquidens*. The reconstruction is an average over two pixel rows (slice thickness = 3 mm). The line through the icon for the lateral view indicates the approximate plane of section (1.5 cm). Right and left are indicated by R and L, respectively.
Fig. 5.  c: Transverse tomogram (cross-section) from *Lagenorhynchus obliquidens*. Slice thickness = 1.5 mm. The lines through the icons for the lateral and dorsal views indicate the approximate plane of Fig. 5c. A compass is placed over the head in order to facilitate measuring rotational differences (ROT1 and ROT2) (see Table 5). ac, accessory sac; bc, brain cavity; c, cranium; es, esophagus; h, hyoid bone; j, jugal bone; ma, mandible; mf, mandibular fat body; np, nasal plug; pb, posterior bursa; s, scale (1.5 cm); t, trachea; tb, triangular basin; vs, vestibular sac. Left and right are indicated by L and R, respectively.
and this is borne out in our measurements of the maximum widths of the premaxillary bones (Table 5). The angle of the premaxillary shelf (30 degrees) and the face of the skull (63 degrees), however, are comparable to the other delphinids we have measured. In dissection, we also noted that the overall configuration of the air sacs is similar to that found in other delphinids we have examined, except that the anterior/posterior expansion of the anterior portion of the nasofrontal sac is greater in *L. obliquidens* than in *T. truncatus*, a difference that has been noted by previous authors for *L. albirostris* (Schenkkan, '73; Mead, '72).

The next two descriptions are for the two smallest species in our series, *Phocoena phocoena* and *Pontoporia blainvillei*, which are both about 1.5 m as adults (Leatherwood et al., '83). The harbor porpoise (*P. phocoena*) is included in the same superfamily (Delphinoidae) as the modern dolphins but belongs to a separate family (Phocoenidae). *Pontoporia blainvillei* belongs to a separate superfamily, Platanistoidea.

Harbor porpoise (*Phocoena phocoena*)

A right parasagittal section of this specimen is shown in Figure 6a. The porpoise forehead apex and the anterior boundary of the melon extend proportionately further rostrally (only 37 mm from the rostral tip) than in the dolphin examples. The entire rostrum is short, 152 mm from the tip to the anterior margin of the bony naris. The melon of the harbor porpoise is bulbous and two-and-a-half times longer than it is high. The forehead radius of curvature is acutely rounded (Table 6). The posterior terminus of the melon occurs below the plane of Figure 6b. Unlike the configuration found in the delphinids, where the melon branches, the bulbous porpoise melon narrows posteriorly to a single terminus nestled near the midline, between and just posterior to the bony premaxillary bosses or eminences.

Both MLDB complexes are located approximately equally (18 mm) off the midline (Fig. 6c). The porpoises seem not to have the same connection of fat between the melon and the bursae as is found in the delphinids. The porpoise bursae are found about 20 mm dorso-lateral to the posterior terminus of the melon. The potential acoustic connection between the bursae and the posterior melon is, therefore, not as obvious as in other delphinoids, but a low density path does exist (indicated by the dotted line in the schematic diagram for Fig. 6a), and we include it in our PAP length estimate. This low density path begins directly ventral to the bursae and then turns anteriorly to pass under the nasofrontal sac and runs forward over the premaxillary bosses where it eventually meets the posterior tip of the melon, which then extends to the surface of the forehead. This path is approximately 105 mm long. A similar path can be drawn for *Phocoenoides dalli*. We found the same low density path (PAP) between the bursae and the surface of the melon in both species. The single, central, posterior extension of the porpoise melon is triangular in transverse section (not shown in Fig. 5c) and ends similarly in all phocoenid specimens examined by us. That is, the posterior melon narrows between the bosses of the premaxilla, ending just ventral to, and midway between, the MLDB complexes.

In sagittal section (Fig. 6a) the MLDB complexes in *P. phocoena* appear near the center of a spheroid (or slightly ellipsoidal) mass of tissue, bounded primarily by air spaces (some of which follow the contour of the skull bones). We refer to this structure as the porpoise capsule. Both (left and right) capsules are apparent if one studies a transverse section such as Figure 6c. The bursae can be seen near the center of each capsule. We measured the vertical and horizontal distances (through the bursae) across each capsule in Figure 6c. The right capsule is 36 mm high and 39 mm wide, whereas the left capsule is 33 mm high and 35 mm wide. These capsule dimensions provided us with an additional measure of soft tissue asymmetry for *P. phocoena*. Capsule dimensions as well as
Fig. 6. a: Vertical tomographic reconstruction (right parasagittal section) from *Phocoena phocoena*, the harbor porpoise (P1 in Table 1). The reconstruction is an average over eight pixel columns (slice thickness = 12 mm). The line through the icon for the dorsal view indicates the approximate plane of Fig. 6a. The compass in the image approximates the bounds of the porpoise capsule discussed in the text; this shape is unique to porpoises. The anterior and posterior right dorsal bursae can be seen just off of the center of the compass in the lower right quadrant. The dotted line in the schematic diagram indicates the lowest density pathway from the bursae to the melon and represents the potential acoustic path (PAP). ab, anterior bursa; bc, brain; c, cranium; cs, caudal sac; ct, connective tissue theca; es, pharynx and esophagus; h, hyoid bone; m, melon (main body); n, naris; ns, anterior nasofrontal sac; ph, posterior bursa; pe, premaxillary eminence; s, scale (1.5 cm); vs, vestibular sac. Anterior and posterior are indicated by A and P, respectively.
Fig. 6. b: Horizontal tomographic reconstruction (frontal section) from *Phocoena phocoena*. The reconstruction is an average over two pixel rows (slice thickness = 3 mm). The line through the icon for the lateral view indicates the approximate plane of Fig. 6b. ab, anterior bursa; bc, brain; c, cranium; cs, caudal sac; m, melon (main body); ns, anterior nasofrontal sac; pb, posterior bursa; pn, posterior nasofrontal sac; s, scale (1.5 cm); vs, vestibular sac. Right and left are indicated by R and L, respectively.
Fig 6. c: Transverse tomogram (cross-section) from Phocoena phocoena. Slice thickness = 1.5 mm. The lines through the icons for the lateral and dorsal views indicate the approximate plane of Fig. 6c. ab, anterior burse; as, air space (general); c, cranium; e, eye; h, hyoid bone; j, jugal bone; ma, mandible; mf, mandibular fat body; n, naris; s, scale (1.5 cm); vs, vestibular sac. Left and right are indicated by L and R, respectively.
### TABLE 6. Measurements for *Phocoena phocoena*

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Disparity index (dorsal bursae) = 0.10
Disparity index (premaxillary bones) = 0.6
PAP length = 103

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*See Table 3 for abbreviations.*

bursal length disparity indicated only slight asymmetry in soft tissue (DI = 0.10) and slightly less in the premaxillary bones (DI = 0.6).

The anterior portion of the porpoise theca is like that seen in dolphins (i.e., horn-shaped), but the posterior portion is not. The anterior aperture is 44 mm high, and the funnel is 50 mm deep. In contrast to other delphinoids, where the thecal funnel narrows to an apex, a sagittal section through the porpoise theca pinches down at the rear of the melon and then expands posteriorly into the spheroid porpoise capsule (Fig. 6a). Each porpoise capsule, though different in shape, could be functionally similar to the posterior portion of the dolphin theca in that it embraces the bursae and represents a dramatic difference in density from the melon. The capsule is bounded dorsally, posteriorly, and laterally by air spaces and ventrally by the skull (Fig. 6a,c). The vertical distance (Y axis) across the center of the capsule (33 mm) is greater than the vertical distance (Y axis) across its anterior opening (21 mm). The horizontal distance (Z axis) along the capsule from the anterior opening to the caudal nasal sac is 36 mm. We consider the anterior opening of the capsule to be demarcated dorsally by the most rostral tip of the vestibular sac and ventrally by the highest point on the premaxillary eminence.

All porpoise bursae that we measured were approximately the same size and shape, and their longest dimension was small (less than 15 mm) compared to that of dolphins (cf. Tables 3, 4, 5). Bursal shape (in longitudinal section) is also noticeably different. Bursae appear elliptical in porpoises and conical in dolphins. The disparity index for the porpoise bursae (0.10) shows that they are only slightly asymmetric, similar to the configuration seen in *Lagenorhynchus* spp. and sharply different from the moderately asymmetric system of the previous modern delphinids (*Delphinus, Stenella, Tursiops*). It should be noted that bursal dimensions of the porpoise reported by Amundin and Cranford ('90) were taken from the same specimen reported here. The discrepancies in dimensions are due primarily to the fact that Amundin and Cranford reported mean values over several tomograms, whereas the measurements reported here are maximum values.

The skull geometry of the porpoise is also different from that found in other delphinoids. Figure 6a displays a shorter rostrum, the profile of which is slightly convex and covers a distance of 127 mm between the anterior tip and the anterior aspect of the rounded premaxillary eminence. These rounded bony mounds (Fig. 6a), formed primarily from the premaxillary bones, are unlike the flattened shelves we have seen in other delphinoids. They are so rounded that there is no premaxillary shelf to measure. There is a distinct and smoothly concave depression in the area behind each naris just below the nasal bones (Fig. 6a), which is lined with the epithelium of the caudal (nasal) sac.

Our dissections also revealed that the porpoise air sac system is distinctive from those of other delphinoids. The anterior portion of the nasofrontal sac is located immediately in front of the anterior bursa. This is different from the placement seen in other delphinoids (Figs. 1a, 5a), where the anterior nasofrontal sac appears in front of and slightly dorsal to the anterior bursa. The vestibular sacs are not simple outpocketings or expansions of the spiracular cavity but are connected to it by a single, short medial tube in phocoenids. There is also the appearance of another sac (referred to as the caudal sac by Amundin and Cranford ('90) or as the posterior nasal sac by Heyning ('89), Curry ('92), and also possibly Moris ('69), although this is difficult to discern from the figures in Moris). The configuration of the remainder of the air sac system is generally similar to that found in delphinids. Additional information on the anatomy of *Phocoena phocoena*, especially on the geometry of the air sac system, can be found in Amundin and Cranford ('90) and Amundin ('91a).

There are other differences between the anatomic configurations of the foreheads of dolphins and porpoises. The lips or nodes of
the nasal plugs, which have been proposed as the dolphin’s sonar signal generators (Evans and Prescott, ‘62), are located on the medial edges of the plugs in porpoises instead of on the lateral margins as in delphinids.

Perhaps the most significant finding from the porpoise’s forehead is that, whereas the geometry of the posterior melon, air sacs, and bursae differs from that found in dolphins, the relationship between the dorsal bursae and the monkey lips is the same.

Franciscana (Pontoporia blainvillei)

The franciscana belongs to the superfam-
ily Platanistoidea, a group collectively known as the river dolphins. The group is composed of four endangered genera that inhabit rivers or estuaries and nearshore seas on two contin-
ents (Pontoporia and Inia from South America, Platanista and Lipotes from Asia). River dolphins have a long fossil history and retain characters that are thought to be ple-
isiomorphy (Barnes, ’78, ’85; Barnes et al., ’85).

Pontoporia blainvillei (Fig. 7; Table 7) is a small platanistoid (Brownell, ’89) with a long bony rostrum (154 mm from rostral tip to forehead apex in this specimen). By compari-
son, the rostral length (distance from the rostral tip to the right naris = 274 mm) for this diminutive species is almost as long as the rostrum for the bottlenose dolphin (the largest specimen in Figs. 3–8). The forehead of this specimen is more sharply convex, with a curvature of 0.070, than the other speci-
mens in our series. The melon is small and bulbous and traverses less than half the total rostrum length (Fig. 7a). The low density fat pathway is estimated to be 86 mm in length.

The overall configuration of the fatty struc-
tures in P. blainvillei appears to be more similar to that of the dolphins than to that of the porpoises. For instance, in P. blainvillei the fatty melon branches asymmetrically, leading to the two bursal complexes. The right branch appears to be aligned with the melon’s central axis, but the left is not, just as we have seen in delphinids. The most striking difference between P. blainvillei and the delphinids is that the two fatty paths from the pontoporiid melon to each bursal complex appear to meander like an old river. In fact, this twisting of the pathways occurs simultaneously in two different planes, as shown in Figure 7a,b. The end result seems to be a slightly longer, spiral path within the relatively smaller forehead for this species. The posterior melon narrows sharply to form a small, constricted, twisting channel that first turns dorsally and then extends posteriorly and laterally a short distance before it finally dips ventrally and medially, terminat-
ing at the posterior bursa. (Perhaps it is like the shape of the path in a trumpet or an intestine, a way of packaging a long path in a short space.) The circuitous path between the main body of the melon and the posterior bursa was measured at 30 mm. The straight line distance between the same two points is 23 mm. Whether or not this 7 mm difference in path length has any functional signifi-
cance remains to be examined.

In this species, the anterior bursa is indis-
tinguishable from the melon terminus, and the posterior bursa is actually directly poste-
rior to the melon and not dorsal to it, as seen in the delphinids. The degree of asymmetry in the fatty channels and the MLDB complex-
es (D1 = 0.08) was less than we found in L. obliquidens and P. phocoena (i.e., both slightly asymmetric)5. In fact, the soft tissue symmetry reported here is similar to that found in pontoporiid skulls (Barnes, ’84, ’85; Heyning, ’89) and is very different than what has been reported for the air spaces in this species (Schenkk, ’72, ’73).

The connective tissue theca is clearly vis-
ible in P. blainvillei. It is very much thinner ventrally (between the melon and the skull) than in the other species examined. The thick-
ness of the theca varies (Fig. 7a) as it sur-
rounds the meandering fatty channel but remains constant, at about 10 mm thick, over the entire dorsal aspect of the melon.

The skull is very different from other speci-
mens in our comparative series. The very long and narrow bony rostrum leads to a gentle upward slope posteriorly, anterior to the posterior expansion of the premaxillary bones. The reader may recall that in all of the previous specimens (except P. phocoena) there was a clear break in the slope of the bony premaxillary shelf and another increase in slope at the face of the skull. In P. blainvillei, the posterior premaxillary bones form con-
 vex mounds as in P. phocoena, except the porpoise eminences extend further pos-
terodorsally than in the franciscana.

This species is reported to have the most symmetrical skull of any extant odontocete (Ness, ’67; Barnes, ’85). Heyning’s ('89) mea-

5Since Pontoporia is small (making a pixel relatively large), the measurement must be considered more coarse than in larger specimens.
Fig. 7. a: Vertical tomographic reconstruction (parasagittal section) from the head of *Ponta poria blainvillei*, the franciscana (R2 in Table 1). The reconstruction is an average over two pixel columns (slice thickness = 3 mm). The line through the icon for the dorsal view indicates the approximate plane of Fig. 7a. The regions marked 1, 2, 3 on the schematic diagram indicate that those areas correspond to regions 1, 2, 3 in Fig. 7b. This is intended to give the reader an opportunity to understand the twisting path of the fatty channels in this species. bc, brain; c, cranium; ct, connective tissue theca; fx, forehead apex; h, hyoid bone; m, melon (main body); n, naris; pb, posterior bursa; r, bony rostrum; s, scale (1.5 cm); vs, vestibular sac. Anterior and posterior are indicated by A and P, respectively.
Fig. 7. b: Horizontal reconstructed tomogram (frontal section) from *Pontoporia blainvillei*. The reconstruction is an average over two pixel rows (slice thickness = 3 mm). The regions marked 1, 2, 3 correspond to the same numbered regions in Fig. 7a. The line through the icon for the lateral view indicates the approximate plane of section.

Fig. 7b. c, cranium; ct, connective tissue theca; lm, left branch of melon; m, melon (main body); pb, posterior bursa; rm, right branch of melon; s, scale (1.5 cm); vs, vestibular sac. Right and left are indicated by R and L, respectively.
Fig. 7. e: Transverse tomogram (cross-section) from *Pontoporia blainvillei*. Slice thickness = 1.5 mm. The lines through the icons for the lateral and dorsal views indicate the approximate plane of Fig. 7c. bc, brain; c, cranium; h, hyoid bones; ma, mandible; mf, mandibular fat body; pb, posterior bursa; s, scale (1.5 cm); vs, vestibular sac. Left and right are indicated by L and R, respectively.
TABLE 7. Measurements for Pontoporia blainvillei

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<td>Disparity index (premaxillary bones) = 0.07</td>
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<td>PAP length = 86</td>
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FROC ROT1 ROT2 BA MELD HAN SDTB
0.070 -10 30 45 h 32 1 7.5 1 17.5
w 32 r 9.0 r 18
1 73

1See Table 3 for abbreviations.

sured asymmetry in Pontoporia blainvillei skulls by providing a left/right ratio for two different width measurements of the premaxilla. His ratios were actually similarity measurements averaged for 14 skulls. Converting his premaxillary similarity ratios (90% and 91%) to our disparity index, we get values of 0.10 and 0.09, respectively. These values are similar to those we measured in the premaxillary bones (DI = 0.07) and to the values for soft tissue (0.04 and 0.18) in our two juvenile specimens of this species. In both cases, Pontoporia blainvillei shows only slight asymmetry, so the skull appears to mirror the slight disparity found in the soft tissue. Our value for disparity of the premaxillary bones in P. blainvillei is 0.07, similar to that for Lagenorhynchus and Phocoena. Ness (’67) found no demonstrable asymmetry in Pontoporia.

The air sacs, on the other hand, are extremely asymmetric (Fig. 7b). In dissection, the right vestibular sac was found to be enlarged so as to push across the midline at both the anterior and posterior margins. In this specimen the left vestibular sac was very much smaller, perhaps 60% less volume than the right (Fig. 7b). The left sac expanded only until it met with the portions of the sac crossing over from the right. The overall effect is to cap the entire nasal apparatus with air spaces, with the right sac making up much more of the covered area than the left. This extreme air sac asymmetry has been reported by Schenkkan (’72). Schenkkan referred to the “hyperdevelopment” of the right vestibular sac. We will have more comments on these profound differences (i.e., the most symmetrical skull and the most asymmetrical vestibular sacs) in Discussion. The point here is that the air the spaces are very much more asymmetric than either the soft tissue or the bony tissue.

Pygmy sperm whale (Kogia breviceps)

The sperm whales and their allies (superfamily Physeteroidea) are represented in our series by CT scans of the pygmy sperm whale, Kogia breviceps (listed as S1 in Table 1). The forehead anatomy of the sperm whales appears, upon initial inspection, so unlike all other odontocetes that it is difficult to see similarities between them. The similarities, though few, are important, while the differences are numerous.

In fact, the differences are so numerous that most previous workers have either not attempted or have been largely unsuccessful at ferreting out the homologous relationships between the noses of physeteroids and those of other odontocetes. In our study, the differences mean that most of the standard measurements we made for the other species are either not feasible or are meaningless for sperm whales.

Even so, we include the description of this specimen to extend our comparative breadth and encompass the extreme range of morphology seen in the odontocete nose. We will eventually delineate the homologous relationships between the nasal anatomy of the physeteroids and nonphyseteroid odontocetes. Several previous authors have been aware of the unique complexity within the Kogiid forehead (Danois, ’10; Kernan and Schulte, ’18; Raven and Gregory, ’33; Barnes, ’73; Schenck and Purves, ’73; Carvan, ’88; Caldwell and Caldwell, ’89).

There is only the slightest curvature to the dorsal surface of the kogiid forehead in our specimen. The forehead is approximately flat in sagittal section (Fig. 8a), projects anteriorly 100 mm beyond the upper jaw, and ends in a blunt point, similar to that seen in the basking shark. This morphological similarity may be related to the shark’s scientific name (Cetorhinus maximus). Below the rounded point the anterior surface of the head slants slightly posteriorly toward the anterior tip of the maxilla (Fig. 8a). The anterior surface of the melon grades into the slanted anterior surface of the forehead. The melon is 140 mm long, 84 mm wide, and 104 mm high. It narrows posteriorly until it abuts the anterior dome-like surface of the spermaceti organ. The interface between the melon and spermaceti organ occurs about 156 mm from the anterior most tip of the forehead. The spermaceti organ spans 47 mm between the
melon interface and the monkey lips. If we follow the course of the spermaceti organ from its interface with the melon, posterodorsally toward the skull, we find that it narrows slightly (Fig. 8b). As it approaches the skull, the spermaceti organ bends sharply (180 degrees) and anteroventrally. The spermaceti organ is surrounded along its entire length by an air space, except along the ventral border, where it is anchored to the skull by connective tissue and muscle. After the sharp bend, the fat body narrows further anteroventrally and terminates on the dorsal lip of the pair. Two tight oxbow turns are found in the narrowest portion of the lipid channel, just prior to the termination along this dorsal monkey lip.

The counterclockwise torsion (when viewed from above), as just described for the spermaceti organ, can be seen in other soft tissues and in the kogiid skull. The mesethmoid septum is skewed dramatically to the left. The right premaxillary bone forms a dish-like pedestal for the 180 degree turn in the spermaceti organ and the intervening portion of the right nasal passage. Many stalked papillae are formed in the epithelium covering the surface of the premaxillary pedestal and the lining of the right nasal passage opposite the spermaceti organ, similar to the situation first described in Physeter by Alderson (1827). The forward-pointing apex of the blowhole is opposite to that found in other odontocetes and may be further evidence for the torsion noted here.

Most or all structures associated with the left side (except the nasal passage) are either nonexistent or unidentifiable as such in dissection. Since only the right set of monkey lips and associated structures can be readily identified, the physeterids exemplify extreme asymmetry. As a consequence of this unilateral configuration, the physeterid disparity index approaches 1. The term extremely asymmetric refers to this hypertrophy of the structures on the right side and the severe or complete reduction of structures on the left. The extreme asymmetry is also evident in the bones of the physeterid skull. Unlike the other odontocete groups where the narial diameters are approximately the same (Mead, '72), there is a difference between the diameters of the physeterid nares of at least 5 to 1 (left larger than right) (Norris, '75). Interestingly, the direction of this asymmetry is opposite of that for the soft tissue (right larger than left).

The air tube that feeds the monkey lips is part of the right nasal passage. The monkey lips of Kogia rest in a connective tissue structure (erroneously termed “adipose cushion” by Schenckkan and Purves ('73)) that appears as if it were molded to hold them. This structure is shaped much like a baseball catcher’s mitt, composed of a mesh of dense connective tissue fibers, and receives the monkey lips, like a baseball, within the central concavity (Fig. 8c). Sections (Figs. 8b,c) through the approximate center of this mitt reveal three parallel paraboloid layers of air-filled crypts or pockets, separated by two thick layers of dense connective tissue. It is unclear how this configuration might be formed, but the invagination of a two-layered ball, as in gastrulation, is one way a structure like this could be produced. This mitt-like structure could be analogous or homologous to the connective tissue thaca described for the previous specimens.

Despite the apparently significant differences between the morphology of sperm whales and the other odontocetes, the intimate juxtaposition between the monkey lips and lipid tissues is consistent across the suborder. These consistent morphological relationships, we think, suggest a similar function, regardless of what the function(s) might be.

Kogia breviceps forehead morphology is near one end of a diverse spectrum of configurations seen across the suborder. We think the homologous relationships between structures within the forehead are clear enough when considered from the proper perspective, as we will soon describe. These homologous relationships, together with the considerable phylogenetic distance, between dolphins and sperm whales imply that all odontocetes probably have and use these homologous systems similarly. Even though we do not know the causes that led to the configurations we see, we are relatively certain that they are largely the result of selective pressures acting on the sound generation apparatus.

DISCUSSION

Sound generation may be an important consideration in organisms who possess keen acoustical faculties and who presumably rely heavily upon sounds for a wide variety of functions from mediating group activities to orientation, navigation, or prey location and capture. Many odontocetes hunt primarily at
Fig. 8. a: Vertical tomographic reconstruction (parasagittal section) from *Kogia breviceps*, the pygmy sperm whale (listed as S1 in Table 1). The reconstruction is an average across two pixel columns (slice thickness = 3 mm). The line through the icon for the dorsal view indicates the approximate plane of Fig. 8a. As, air space (general); bc, brain; c, cranium; m, melon (main body); ma, mandible; s, scale (1.5 cm); so, spermaceti organ. Anterior and posterior are indicated by A and P, respectively.
Fig. 8. b: Horizontal reconstructed tomogram (frontal section) from *Kogia breviceps*. The reconstruction is an average across two pixel rows (slice thickness = 3 mm). The line through the icon for the lateral view indicates the approximate plane of Fig. 8b. A compass is placed upon the image around the center of the air space/ connective tissue (mitt) system where the monkey lips and terminus of the spermaceti organ are found. The spermaceti organ ends in the postero dorsal monkey lip, in a plane just below that pictured in Fig. 8b. as, air space (general); bc, brain; c, cranium; cm, dense connective tissue catcher’s mitt; m, melon (main body); s, scale (1.5 cm); so, spermaceti organ. Right and left are indicated by R and L, respectively.
Fig. 8. e: Transverse tomogram (cross-section) through *Kogia breviceps*. Slice thickness = 1.5 mm. The lines through the icons for the lateral and dorsal views indicate the approximate plane of Fig. 8c. as, air space; b, terminus of spermaceti organ; cm, dense connective tissue catcher's mitt; ma, mandible; mf, mandibular fat body; r, bony rostrum; s, scale (1.5 cm); so, spermaceti organ. Left and right are indicated by L and R, respectively.
night or in deep water (presumably using biosonar signals).

Searching for the site(s) and mechanism(s) by which odontocetes generate biosonar signals and propagate them into the aquatic environment has intrigued investigators for decades and has led to some fascinating bioacoustic questions. We implicate a new set of structures, never before proposed in odontocete phonation, and present evidence that these structures are homologous across all odontocetes. In each group of odontocetes these structures are likely the source of at least one class of phonations: clicks or pulsed sounds. We will attempt to define homologous relationships across the Odontoceti and to propose ways in which these structures may function to produce and process sounds.

Our results show that, although there seems to be a basic similarity in component parts of the odontocete forehead, there is also considerable diversity in shape, size, and position of forehead elements, especially of the melon and associated fatty tissues, from species to species. It seems probable that this diversity of shape could influence sound quality, sound propagation pathways, and beam formation strategies.

Homology of odontocete forehead structures

Arriving at our model of the homologous relationships between structures within the odontocete forehead has, in some cases, been complicated by the developmental/evolutionary torsion that accompanies skull telescoping and the soft tissue hypertrophy in the tissues proximate to the spiracular cavity (i.e., MLDB complexes). Mead ('72, p. 29) recognized the central importance of this region when he described the spiracular cavity:

[T]his cavity appears as a transverse slit extending from the nasal plugs upwards to the blowhole. It has been generally ignored as an anatomical entity in this group, but is extremely important from a comparative standpoint, as it becomes highly modified in some other odontocetes.

In other cases, the homology issue has been obscured by the inconsistent use of terminology in the scientific literature. This has been a particular problem with respect to the adipose components.

The term spermaceti organ to refers to the elongate conical structure that is filled with lipid waxes and stretches from the deeply concave supracranial basin to the anterior tip of the forehead, along the dorsal portion of the sperm whale's head. This same structure has been referred to as the case by the seventeenth- and eighteenth-century whalers who treasured the spermaceti wax they hailed from it. Melon is another term that originated in the whaling industry and referred to the fatty mass of tissue that comprises the majority of the forehead in the smaller odontocetes.

In 1930, Howell introduced the term adipose cushion for the melon. Howell considered the relationship between the melon (adipose cushion) and the spermaceti organ and decided that they were not homologous. Raven and Gregory ('33), on the other hand, thought these two structures were homologous. Mead ('72) realized the importance of resolving this issue (p. 44) when he stated, "The question of the origin of the spermaceti organ of physeterids and its relationship to the melon of delphinids has yet to be properly examined. Regardless of this, however, the immense anatomical difference between the two structures warrants a nomenclatural distinction." He further suggested that "the term spermaceti organ should be restricted to an oil-filled cavity, separated from the other facial structures by a distinct connective tissue wall, as seen in Physeter catodon."

Norris and Harvey ('72) mentioned (p. 403) a structure in the forehead of a beaked whale (Ziphius cavirostris) that, they wrote, "may be homologous to the spermaceti organ" but did not attempt to sharpen the distinction between the melon of a dolphin and the spermaceti organ. Heyning ('89) states (p. 50) that the spermaceti organ "is found in all extant physetids and is not homologous to any structure found in other odontocetes. Therefore, it is synapomorph for the family Physetidae."

Schenkkan and Purves ('73) made the first careful comparisons between the cephalic anatomy of a dolphin (Cephalorhynchus Hectori) and a fetal sperm whale. They made observations regarding the location of these two lipid structures with respect to the main air passage. Their observations separate the origins for the spermaceti organ and melon. They concluded:

In its relationship to the other structures of the head, the spermaceti organ is in no respect homologous with the "melon" of other odontocetes as had been postulated by Raven and Gregory (1933). The sperma-
Cetacean organ is situated posterior to the nasal tract and not anterior to it as does the melon of other odontocetes. It is also contiguous with the caudal part of the nasofrontal sac, whilst the melon is separated from it by the whole nasal complex. It is clear that the spermaceti organ is an adventitious structure developed asymmetrically within the fibrocartilaginous nasal septum. We can conceive it starting as a small pisiniform body situated within the septum on right hand side of the cartilage, indeed such a body has been observed in *Cephalorhynchos hectori*.

We suggest that their reasoning strongly implicates the right posterior dorsal bursa as homologous to the spermaceti organ. On the other hand, the single "pisiniform body," mentioned by Schenkan and Purves (1973), is probably not one of the bursae reported here because the Schenkan and Purves structure is located within the septum and the bursae clearly are not.

As part of his description of *Mesoplodon densirostris* Heyning ('89; p. 20) writes:

In one specimen, a longitudinal section through the right nasal plug and blowhole ligament revealed, anterior to the cartilage of the blowhole ligament, a region of clear fat similar to the melon core tissue. It was positioned adjacent to the region of the right nasal plug where the melon extends most posteriorly. With the nasal vestibule in its normal closed position, these two regions of fat are in direct contact with each other. It is unclear, however, whether or not this pattern is typical for all specimens of this species or even the entire family because I did not find this structure until my later dissections, and may have overlooked it previously. This fatty structure is probably homologous to the similar structure found in delphinids referred to as the elliptical body (Mead, 1975).

By these statements it seems clear that Heyning did find a right posterior bursa and possibly a right posterior bursa in at least one of his ziphiid dissections (see his Fig. 16). He did not report finding similar structures on the left side in ziphiids or in other odontocetes. We have never located a posterior bursa in *Mesoplodon* spp., although the anterior bursae were typically conspicuous. Even though Heyning noted the probable homology to the fat bodies described by Mead ('75), he apparently did not consider them to be homologous with the spermaceti organ of physeterids.

In all of the odontocetes where we have found the right posterior dorsal bursa, it satisfied the positional requirement for a homologue of the spermaceti organ (i.e., posterior to the (main) spiracular air passage [Schenkan and Purves, 1973]) and the definition for a spermaceti organ as set forth by Mead ('72), namely, a fat-filled cavity separated from other facial structures by a distinct connective tissue wall. We found that it was possible to dissect the fatty posterior bursa from its connective tissue pouch in all of our delphinoid specimens.

We contend that the right posterior bursa of nonphyseterid odontocetes is homologous with the spermaceti organ of *Physeter catodon* and other physeteroids. The comparative anatomic evidence seems to suggest that the spermaceti organ is a hypertrophied form of the evolutionary precursor that led to the right posterior bursa of other odontocetes. Whether the right posterior dorsal bursa should be referred to as the spermaceti organ is a question we will address at the end of this paper.

Schematic illustrations depicting the anatomic configuration of the sperm whale forehead and a generalized dolphin are found in Figure 9. Sperm whales and dolphins may be the most distantly related living toothed whale groups (Milinkovitch et al., '93). It is our hope that the structural homologies between these two groups will logically suggest a "functional homology" that may then apply to all other odontocete groups. Let us now examine the possible forehead homologies between these two groups by use of the schematic illustrations presented in Figure 9.

One can imagine a forward rotation of the dolphin forehead configuration that would result in a configuration like that seen in the sperm whale. By this we do not suggest that one of these configurations existed first, only that it is possible to see a spatial relationship between the two arrangements, one the rotation of the other. The embryological studies of Klima ('87, '90) suggest that sperm whales and dolphins begin with similar forehead configurations but during an early stage of sperm whale development there is a dramatic expansion of the forehead anteriorly. Our schematic illustrations (Fig. 9) suggest that the (right) posterior dorsal bursa of the dolphin...
Fig. 9. Schematic diagram of homologous relationships between the structures in the foreheads of sperm whales and dolphins. The upper illustration represents the nasal configuration found in a modern dolphin and the lower illustration depicts the form within the sperm whale nose. Similarly colored structures are thought to be homologous. Orange, posterior bursa/spermaceti organ; green, anterior bursa/melon/junk; blue, air spaces; brown, skull; solid black interlocking triangles, monkey lips.
is homologous to the spermaceti organ of the sperm whale because both appear on the same side of the main air passage leading to the blowhole. Both structures also have similar relationships to other prominent structures. For example, the illustrations suggest that the junk of the sperm whale is homologous to the dolphin melon, possibly combined with the (right) anterior dorsal bursa. The melon of the dolphin is in the same anatomic position as the junk of the sperm whale and may serve the same general function (transmission and processing of emitted sound) in both toothed whales.

The location of another set of structures, the monkey lips, is also depicted in Figure 9. They are represented in the schematic drawings as a set of solid black interlocking triangles and are similarly situated immediately distal to the bursae/spermaceti organ in the nasal passage. The monkey lips are located beneath the anteriorly placed blowhole in the sperm whale and just beneath the more posteriorly placed blowhole in dolphins. The monkey lips are distinctive, similarly grooved and keratinized, and are also clearly homologous across the suborder (Schenkkan and Purves, '73). All of the specimens dissected for this study had one set (sperm whales) or two sets of monkey lips (all other odontocetes). The overall structure of these lips is similar across the Odontoceti, with the exception that the nonphyseterid monkey lips are fastened together only at the lateral corner of each passage, whereas the sperm whale's single pair of monkey lips in the right nasal passage is fastened together at both corners. The details of these lips are also similar between dolphins and sperm whales. The lips are composed of two parallel ridges that form broad interlocking arcs, and in each the ridges are traversed at right angles by a set of fine grooves that may help direct air across the lips (Norris and Harvey, '72). These lips are difficult to identify by use of CT but are easily seen with cryomicrotomy and in dissection.

The sperm whales may have forsaken the left monkey lip/dorsal bursa complex in their evolution; the right side has hypertrophied, and the left nasal passage seems to have become a simple conduit for respiratory air. Further evidence of this functional separation of the nasal passages can be seen in the delphinoids, where the blowhole is aligned over the left bony naris. A study of the dolphin skull also reveals that the left naris takes a less curved (i.e., more direct) path through the skull. Both of these features provide a more direct path for respiratory air through the left nasal passage.

At this point we would like to discuss what we regard as the homologous relationships between the connective tissue structures other than the monkey lips within the MLDB complex. These include but are not restricted to the pouch that encases the posterior dorsal bursae, the cartilaginous blade backing the pouch, and the blowhole ligament. We found that it was possible in dissection to separate the bursa from its pouch, the cartilage from the pouch, and the fibers of the blowhole ligament from these other structures. We think it is likely that the connective tissue pouch, which encases the posterior bursa fat, is homologous to the tough connective tissue case that contains the sperm whale's spermaceti organ. The blowhole ligament is conspicuous in all nonphyseterid odontocetes and is certainly homologous in these animals.

We found blades of bursal cartilage in all nonphyseterid odontocetes, with the single exception of *P. blainvillei* (where a histological examination was not conducted). These floating blades of bursal cartilage are inconspicuous. Heyning ('89), for example, reports finding the cartilage only in the larger odontocete specimens he dissected. It is reasonable that these structures are also homologous. It may be that the bursal cartilage is also homologous to the elongate cartilaginous structure seen in our dissections of the sperm whale head and reported by Behrmann and Klima ('85) and Klima ('90).

The consistent nature of the structural complexity and composition in the MLDB region across the suborder may be evidence of functional significance. Consider the complexity of the assemblage of several discrete structures of different tissue types (i.e., encapsulated fat bodies, cartilaginous blades, connective tissue lips, and ligaments) and the consistent spatial relationships between them (i.e., orientation and placement of bursae, juxtaposed to the lips and ligaments, at similar locations along the main airway). Add to that the convergence upon the MLDB region by some of the larger muscles (i.e., anteroexternus, posterointernus, and anterointernus), the connective tissue fibers of a large aponeurosis along the lateral margins of the spiracular cavity (Mead, '72), and the laterally broad attachment of the blowhole ligament. From this morphological evidence, one
A unified hypothesis for odontocete sound generation

The question of how dolphin click trains and other sounds are generated has never been firmly resolved. Three general suggestions have been made. These are laryngeal production, friction-stiction (at the nasal plugs), and production by pushing a stream of pressurized air bubbles (upward in the airway) past the sound generation surfaces (dorsal to the nasal plugs).

The first proposal, a laryngeal sound source, is advocated primarily by Purves and his colleagues (Purves and Pilleri, '83), who contend that sound generation occurs at the larynx and is piped upward and forward into the head and rostrum. Their transmission pathway begins in cartilage and then passes through muscle and finally to the rostral bones. The evidence for this view rests upon emitted sound fields that have been measured from the rostrum of phonating dolphins and from an experiment in which sounds from a whistle inserted into the tip of the larynx of a dead dolphin were emitted from the rostral tip (see reviews in Purves and Pilleri, '83; Pilleri, '90).

Their observations and experiments have several confounding features. For example, some of the sound field measurements, used as support for their hypothesis, were taken in a tank with several free-swimming animals. The accuracy of their sound field measurements is called into question not only because of the difficulty of pinpointing the position of a particular animal by observation during any brief acoustic event (i.e., a click) but also because it would be very difficult to exclude the possible acoustic contributions of other dolphins in the tank. A preponderance of evidence has accumulated in the last three decades that fails to support, and often directly contradicts, laryngeal phonation as a source for biosonar signals (Norris et al., '61; Norris and Evans, '67; Norris et al., '71; Diercks et al., '71; Norris and Harvey, '74; Dormer, '79; Ridgway et al., '80; Amundin and Andersen, '83; Mackay, '80a; Mackay and Liaw, '81; Au et al., '86; Ridgway and Carder, '88; Aroyan et al., '92).

Another proposed click production mechanism, the friction-stiction scenario, was suggested by Evans ('73) and Evans and Mader-son ('73). They implied that one elastic surface, rubbed by muscular means over another with a given amount of force, sticks, and that as the resisting force increases the elastic limit is exceeded, after which the moving surface is released (in a single relaxed oscillation event), producing a sound. Each of these release events produces a sound by impact of the sliding object against the rubbed object (stridulation). This is much like the process of rubbing your thumb pad against the inner side of the index finger, a mechanism that is difficult to control and duplicate with fidelity.

Dolphin echolocation click trains seem unlikely to be produced by the mechanism proposed by Evans and Maderson. In a friction-stiction generated train of sounds, one would expect an orderly progression of click rates related to the pressure-elasticity relations developed between the two parts of such a click generator. Such a mechanism could be expected to limit the number of clicks in a train and, therefore, the duration of click trains because the animal must reset the generator after completing one train and before beginning another. Neither of these limitations seems to typify dolphin click trains. Dolphin echolocation trains can be very long, involving seconds of time and many hundreds of clicks. In addition, individual sonar sounds may vary in frequency composition (Au et al., '85), loudness (Moore and Pawloski, '90; Romanenko, '90), and repetition rate within such trains (Norris et al., '66).

The most likely mechanism thus far proposed is that sound is produced by the passage of an airstream past or through a generator. There is a reasonable amount of experimental and observational evidence that such an airstream is involved. Norris and his colleagues ('71) reported, by use of cineradiography, that they could pinpoint the passage of air dorsally in the spiracular cavity during the production of chirps (burst-pulsed sounds) and that the passage of air was simultaneous with the acoustic event. Ridgway et al. ('80) and Amundin and Anderson ('83) recorded electromyographic and air pressure measurements from the delphinid nasal region during phonation. They found that narial air pressure builds before a phonatory event, changes during phonation, falls off as the click train or whistle ends, and repressurizes again prior to the next phonation cycle. Norris ('69) and Amundin and Anderson ('83) reported seeing sputtering and bubbles
through the open blowhole of a phonating dolphin. Cranford ('92a) reported similar observations at, or close to, the MLDB complex through an endoscope inserted into the vestibular sac of an echolocating dolphin. Amundin ('91b) required a porpoise to inhale a helium/oxygen mixture and showed that the mechanism was pneumatically driven but that tissue vibrations produced the high frequency (echolocation) component, whose spectral composition was not affected by helium.

Both nasal and gular muscle complexes are probably important for regulating air flow, adjusting tension on regulatory and/or vibratory elements, and changing the size and shape of fatty channels and acoustically reflective air spaces. The nasal muscles may also be responsible for adjustments affecting the modes of vibration or the air metering system (Ridgway et al., '80; Amundin and Andersen, '83) and may be partially mediated by the nervous terminalis (Buhl and Oelshlager, '86; Oelshlager et al., '87; Oelshlager, '92).

The gular musculature has been described for the bottlenose dolphin by Lawrence and Schevill ('56) and Green et al. ('80). These gular muscles probably generate much of the pneumatic power for the sound production process by acting upon the laryngeal cartilages (Ridgway et al., '80; Amundin and Andersen, '83). There are 19 individual muscles (most paired) comprising the powerful gular system which serve to suspend the larynx from the skull and form a sling for the flattened hyoid plate, upon which the larynx rests. Aside from their usual function in the lingual apparatus, the gular muscles most likely work to force the beak-like (arytneopiglottic) extension of the larynx into the inferior bony nares or internal choanae (Lawrence and Schevill, '65), producing the pressurization event for sound production (Norris et al., '71; Ridgway et al., '80; Marten et al., '88; Amundin and Andersen, '83).

The mechanism we propose is pneumatic, where an oscillator is driven by an airstream moving dorsally (or distally for sperm whales) in the nasal passage. This is the same mechanism proposed by Norris and Harvey ('72) for the sperm whale. The air stream apparently passes between the monkey lips, causing them to open and then slap together in a series of events whose repetition rate is regulated by factors such as air pressure and/or muscle tension on vibratory elements. We propose that a functional homology is operating in all odontocetes, since every odontocete examined has at least one set of monkey lips (usually two) and the accompanying complex of structures. In other words, we propose that the same mechanism (using homologous structures) produces the pulsed sounds emitted by all toothed whales. If true, this hypothesis unifies the mechanism for all odontocetes (Cranford et al., '87; Cranford, '90, '92a). Indeed, one appeal of this unified hypothesis is that it is the most parsimonious choice. The MLDB complex passes the first necessary test: that it be ubiquitous across the Odontoceti.

Since all odontocetes (except the sperm whales) have two functionally separate (at the nasal septum) MLDB complexes, it is possible that these two proposed sound generators could be operating simultaneously or with variable phase relationships to one another. There are a few reports of pulse doublings (Norris et al., '72; Evans et al., '88; Dawson, '88; Brill et al., '92), and reports of multiple simultaneous sounds produced by a single animal are common. Markov and Ostrovskaya ('90) have provided qualitative evidence indicating that at least two (and possibly three) sound sources could function simultaneously in T. truncatus.

In our scenario, the generators are driven pneumatically by pressurized air from the nares. Sounds are generated as an airstream is forced between the monkey lips, setting an MLDB complex (or portions of it) into vibration. The expended air is then captured by the vestibular air space, for recycling, as shown by Norris and his colleagues ('71). The periodic opening and closing or smacking of the monkey lips together should break up the airstream and determine the click repetition rate of the train. The analogy of a trumpet player comes to mind here because human lips break up the airstream in a similar fashion (Martin, '42a,b; Mackay, '80b). The difference is that the musician is concerned with the consequent vibrations set up in the air (Martin, '42a), whereas for the toothed whales the vibrations set up in tissue will be most effectively transmitted into the aqueous environment (Amundin, '91b). This is primarily because soft tissues (and especially acoustic fats) have acoustic impedance values close to water.

Nonphyseterid clicks are short transients, most less than 200 microseconds in duration (although the loud pops or bangs implicated
in prey debilitation can be 7 or more milliseconds long [Norris and Møhl, '83; Marten et al., '88; Santos et al., '90; Cranford et al., '93]. At the instant when the monkey lips slap together during click production, the bursae should quake or quiver momentarily. If the fat in the bursae is liquid at body temperature and the entire region is under some tension, vibrations in the bursae could be produced and then damped by the connective tissue matrix around the fat cells and bursae. This has implications for the duration of the sound and its efficacy for echolocation.

The nasal plugs and their nodes along with the diagonal membranes and the blowhole ligament are most likely involved in regulating air movement in the passages superior to the nares, perhaps in whistle production (Mead, '75) and in metering air across the monkey lips. It should be possible to direct the separately controllable bilateral airstreams to the corresponding set (left and right) of monkey lips and, perhaps, to break up each of those streams still further to feed multiple sites along each set of lips.

The timing of sound generation events at the two MLDB complexes (or at multiple locations along them) would produce interference patterns in the resultant beam that could form brief transients or aid in regulating the composition, spread, and/or steering of the sound beam. Such a mechanism could allow the dolphin to sharpen or broaden its cone of emitted sound at will.

In delphinids, the tapering conical shape of the posterior bursae might help prevent the buildup of standing waves because of the absence of parallel walls, although this notion may break down when a specific bursal dimension approximates the sound's wavelength. Perhaps this tapering serves in a manner similar to a basilar membrane, supporting a standing wave at a particular location(s) and thereby emphasizing a frequency or group of frequencies within a click. The taper, combined with the angular relationships (BA and ROT2) between MLDB complexes might serve another function(s), especially if the size and location of the pressurized bubble stream can be varied along the length of each pair of lips. That is, if the duration of the vibratory event and the event location (along the length of the monkey lips) are under voluntary control of the dolphin, then a rich variety of possible combinations could help explain the varied repertoire of signals recorded from delphinids.

Even as there seems to be a built-in potential for producing a variety of sounds and sound patterns in the asymmetric soft anatomy of the dolphin forehead, the relatively symmetrical morphology within the phocoenid head suggests production of less variable sounds. In fact, phocoenids do produce narrower band high-frequency sounds (relative to dolphins) with greater stereotypy (Dubrovskiy et al., '71; Møhl and Andersen, '73). In porpoises, the bursae are small, located symmetrically on either side of the melon terminus, aligned in a single transverse plane (i.e., zero branching angle and zero ROT2), and approximately equal in size and shape. It is conceivable that the "monochromatic" (very narrow bandwidth) clicks of porpoises are at least partially the result of the uniformity of these features (Goodson and Datta, '95). Conversely, variety in delphinid signals could be due to interference patterns produced by airstreams directed at particular locations along either set of monkey lips in relation to the branching angle between the branches of the melon. Certainly smaller phocoenid MLDB size reduces the ability to vary the location of the passing bubble stream. The absence of angular disparity between MLDB complexes should minimize opportunities to vary time and phase relationships. Understanding the exact mechanism(s) and sorting out the interactions between the various tissue components require further experimentation and/or model formation.

Understanding all of the factors that contribute to the signal's composition is almost certainly more complicated than it may at first appear. Consider, for example, the possible similarity between the function of the bell of a trumpet and the function of the melon's dense connective tissue theca. Certainly our description of the twists and turns in the fatty channels and their (PAP) dimensions within the theca could catalyze conjecture as to their combined function. For instance, do these structures, separately or in combination, function like the facial ornaments (noseleaf and tragi of the external ears) in the ecology of echolocating bats (Arita, '90)? Questions such as this warrant further investigation into the odontocete biosonar apparatus.

Odontocetes appear to be the only mammalian group in which the normal condition is facial asymmetry. Directional asymmetry in the MLDB complexes and its effect on sound characteristics or the sound beam also war-
rant further study. If sonar signals do indeed originate within these complexes, the size/frequency relationship inherent in MLDB complex asymmetry may allow these animals to emphasize specific frequency ranges. Phase relationships may vary between vibratory components during the sound generation process. Directional asymmetry may also be related to the avoidance of directional ambiguity in the received field as seen in barn owls (Payne, '71) and bats (Grinnell, '63). Clues to the function(s) of these specific anatomic geometries and the effects of asymmetry may be revealed by continued research using computer modeling techniques (Aroyan et al., '92).

A sound source is most efficient when it produces frequencies whose wavelengths approximate the dimensions of its radiating surface(s) (Prestwich, '94). The bursae (and the MLDB complexes generally) are approximately the right size to be biosonar signal sources; that is, the longest bursal dimensions are similar to the wavelengths for the peak frequencies emitted during echolocation. If we consider the relationship between the frequency composition of a biosonar signal from a particular species and the dimensions of our proposed sound generators (bursae), we are led toward an interesting intersection. Bear in mind that we do not have acoustic recordings from a specimen for which we have detailed geometry or morphology information (i.e., we do not have a sound record and CT scans from the same specimen).

Two types of odontocetes are consistently reported to produce sounds with a single peak in their frequency spectrum: the physeteroids, with extremely asymmetric facial anatomy, and the porpoises, with slightly asymmetrical MLDB complexes. This appears contradictory until we recognize a common denominator: both groups of animals have only one size of sound source. That is, the sperm whales have a single sound source, and the porpoises have two sound sources that, as we have seen, are similar in size and shape.

The situation is certainly more complicated in those odontocetes that have moderately asymmetric MLDB complexes (most odontocetes listed in Table 1). As a group, these animals produce a great variety of sounds (Au, '93) and possess bilateral MLDB complexes with differences in spatial orientation and variation in shape and size.

If we consider only those reports that claim to measure sounds from within the delphinid beam axis, we can cull out a few generalities (Au, '93; Au et al., '95). One or two primary peaks can often be found in the high-frequency spectrum of delphinid clicks (generally over 20 kHz). Each peak seems stable with respect to frequency, but the relative amounts of energy in each peak are apparently under voluntary control (Moore and Pawloski, '90). These generalizations are nicely illustrated with a specific example (Au et al., '95).

Au and his colleagues ('95) classify the echolocation signals from a false killer whale (Pseudorca crassidens) into four types based upon frequency structure (Fig. 10). When two primary peaks occur (type 2 or type 3), the location of the upper peak is about twice the frequency of the lower. When a single primary peak occurs (type 1 or type 4), it is found at one of the frequency locations registered in the dual peak situation (i.e., the same location as one of the two primary peaks).

These observations are consistent with the bilateral generation of odontocete biosonar signals where one MLDB complex is approximately twice the size of the other. This could account for the two spectral peaks where both complexes are in operation simultaneously. The implication is that bursal dimension is related to frequency. An alternative explanation suggests that the two peaks could represent the fundamental and one harmonic.

If bursal length is related to peak frequency, then certain intriguing predictions follow. For example, if we assume simultaneous operation of both MLDB complexes, clicks from Lagenorhynchus spp. should have two peaks close together or one peak (composed of two peaks which are difficult to distinguish on the basis of frequency). Phocoenids and Pontoporia should also produce clicks with a single peak (or two indistinguishable peaks) in the frequency spectrum because in these groups all the bursae are the same size. This logic also predicts that physeteroids should produce spectra with a single stable peak. It does not address the potential capability of a delphinid to vary the frequency within a single MLDB complex.

Click repetition rate could be regulated by adjusting one or more of a number of variables or structures, such as the posterior peninsula of tissue, the functional unit of
Fig. 10. Examples of the different signal types emitted by the false killer whale. The signal waveform is shown on the left and the normalized frequency spectrum on the right. To the right of each spectrum is the signal type and the percentage of time that signal type was observed. (Reproduced from Au et al., '96, with permission of the publisher.)
tissue. Recall that this peninsula includes the posterior portion of the MLDB complex located within the posterior wall of the spiracular cavity (Fig. 1b).

During the sound generation event, this tissue peninsula, activated by the passing stream(s) of bubbles, presumably slaps against the region of the anterior bursa. The tissue peninsula is fixed dorsally and is bounded by the inferior vestibule, the vestibular sac, and the spiracular cavity (Fig. 1b). We suggest it is this peninsula of tissue that is set into motion during the sound generation process, acting as a slapper or hammer in a system, while the anterior portion of the MLDB complex acts as the anvil. We also propose that the primary vibratory structures (within the peninsula) are the fatty dorsal bursae, although it is possible that vibrations might also, or instead, emanate from other components, such as the blade of bursal cartilage, for example. In our model the bursal cartilage is seen as a stiffener for the MLDB complex as a whole.

Our proposed mechanism is that pulses of sound are generated by moving an object, in air, and slapping it against a surface that is impedance-matched to water, through the low density fat of the melon. This should be an efficient mechanism. In fact, a similar mechanism has been used to construct a contraption that generates loud underwater sounds and was designed to repel fish from an area around power plant intake channels (McKinley et al., '87). The device is constructed from a cylindrical (50 gal) drum that is fitted with an internal mechanism to drive a hammer against one end of the drum. When the drum is placed in water, the efficiency of this device becomes apparent. The hammer is driven inside an air-filled chamber where there is minimal resistance to the hammer's motion, yet the full impact of the force generated by the momentum of the hammer against the end of the drum is imparted to the water with little loss of energy. The efficiency of this generator is in sharp contrast to a mechanism that attempts to accelerate a hammer in water, where the energy losses are much greater. K.S. Norris has postulated that cavitation might be involved in the odontocete sound generation mechanism, particularly for the most intense sounds (Au, '80; Hult, '82; Norris and Møhl, '83; Marten et al., '88; Smolker and Richards, '88; Møhl et al., '90; Santos et al., '90; Cranford et al., '93). At this point we are unaware of any evidence that addresses this notion.

The tissue peninsula (or a portion(s) of it) should impact upon the anterior wall of the spiracular cavity in a small, well-defined region just ventral to the monkey lips, where the anterior bursa is located. This peninsula is, like the hammer in the fish repulsion device, essentially suspended in an air space (formed by the spiracular cavity, the inferior vestibule, and the nasofrontal sac) immediately prior to impact. The monkey lips within the spiracular cavity could be forced open by pressurized air from the bony nares. As air rushes past the lips, the pressure drops in the cavity, closing the lips, creating an impact and leaving the lips pressed together. The hammer and anvil configuration here identified is dorsomedially positioned from the delphinid nasal plug node (the structure long regarded as the source of biosonar signals). So our choice for the location of the sound source (MLDB complex) and pneumatic sound generation mechanism is different from previous proposals which have often implicated the more ventrolaterally located nodes of the delphinid nasal plugs and a friction-based mechanism, or laryngeal production.

Our ideas about how dolphin clicks are generated are, of course, hypotheses. The hypothetical mechanism presented here is, however, consistent with recent endoscopic observations where sputtering of air was seen just above the MLDB complex as clicks were produced (Cranford, unpublished data). It is also consistent with experimental evidence (Ridgway et al., '80; Amundin, '91b) and computer modeling results that pinpoint the location of the MLDB complex as the site of sound production (Aroyan et al., '92), as described earlier.

There are at least five lines of reasoning which direct us toward acceptance of the unified hypothesis for odontocete sound generation.

1. The proposed vibratory structures (the bursae) are composed of the same or similar material (lipid) as other parts of the sound propagation pathway (i.e., the melon). The acoustic fats of the melon have, in a handful of odontocetes, been shown to be part of a primary pathway for impulse sounds transmitted out of the head. The bursae are reasonable candidates for the origin of these sounds, even though we do not yet know the specific composition of fat. It is no less significant
that the bursae are located at, or very near, the posterior terminals of the melon and juxtaposed to air spaces.

2. The bursae (and the MLDB complexes generally) are approximately the right size to be efficacious biosonar signal sources; that is, the longest bursal dimensions are similar to the wavelengths for the peak frequencies emitted during echolocation.

3. The argument from homology seems to be the most persuasive. The homologous relationships between our proposed sound generation structures are consistent across the Odontoceti (unlike the nodes of the nasal plugs, which do not occur in some odontocete species).

4. The slapping mechanism itself is elegant in its simplicity and appealing for its potential transduction efficiency (compressed air to tissue vibration).

5. Finally, anatomic complexity, as well as structural geometry, converge at our proposed sound generation sites, and computer modeling results support this structure/function hypothesis.

We would like to close this paper with a brief comment on terminology. We have some reservations about the term dorsal bursae that describes the small fat bodies we contend may be important to the generation of the brief impulse sounds in the smaller odontocetes. Certainly the fact that they are not found on the dorsal aspect of the melon in phocoenids or Pontoporia sp. casts some doubt on the universal descriptive application of the term. On the other hand, if our ideas about the homologous relationships of these structures are correct, it could be argued that we should refer to the posterior bursa as a spermaceti organ. But do we then need a new term for the anterior bursa? What if future studies find a chemical difference between spermaceti wax and bursal fat? We agree with Mead ("75) that the immense size difference between the spermaceti organ and our posterior bursa warrants a nomenclatural distinction for the sperm whale’s spermaceti organ. Perhaps, if the bursae are found to be instrumental in the generation of some or all odontocete sounds, they should be called bursae cantantes.

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