Anatomy of the External Nasal Passages and Facial Complex in the Delphinidae (Mammalia: Cetacea)

JAMES G. MEAD

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 207

SERIAL PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

The emphasis upon publications as a means of diffusing knowledge was expressed by the first Secretary of the Smithsonian Institution. In his formal plan for the Institution, Joseph Henry articulated a program that included the following statement: "It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge." This keynote of basic research has been adhered to over the years in the issuance of thousands of titles in serial publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

Smithsonian Annals of Flight
Smithsonian Contributions to Anthropology
Smithsonian Contributions to Astrophysics
Smithsonian Contributions to Botany
Smithsonian Contributions to the Earth Sciences
Smithsonian Contributions to Paleobiology
Smithsonian Contributions to Zoology
Smithsonian Studies in History and Technology

In these series, the Institution publishes original articles and monographs dealing with the research and collections of its several museums and offices and of professional colleagues at other institutions of learning. These papers report newly acquired facts, synoptic interpretations of data, or original theory in specialized fields. These publications are distributed by mailing lists to libraries, laboratories, and other interested institutions and specialists throughout the world. Individual copies may be obtained from the Smithsonian Institution Press as long as stocks are available.

S. Dillon Ripley
Secretary
Smithsonian Institution

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 207

Anatomy of the External Nasal Passages and Facial Complex in the Delphinidae (Mammalia: Cetacea)

James G. Mead

SMITHSONIAN INSTITUTION PRESS
City of Washington
1975

ABSTRACT

Mead, James G. Anatomy of the External Nasal Passages and Facial Complex in the Delphinidae (Mammalia: Cetacea). *Smithsonian Contributions to Zoology*, number 207, 72 pages, 26 figures, 3 tables, 1975.—This study is concerned with the comparative anatomy of the external nasal passages and associated structures in delphinid odontocetes. It has been possible to assemble detailed anatomical information for nearly all of the delphinid genera. Comparative data for the other small toothed whales is considered in such detail as is available.

The function of the structures associated with the external nasal passages has been poorly understood, partly due to a lack of understanding of their anatomy. I have drawn functional conclusions from the basis of this comparative study, but these are largely unsupported by experimental data.

The nasal musculature is concerned both with opening and closing the nasal passage during respiration, and with movement of air between the nasal diverticula during sound production. The nasal diverticula are part of the acoustic system of these animals, and function both as air reservoirs and as reflective elements to focus the emitted sound field. The potential area of sound production is limited to the deep structures around the external body nares. The melon probably serves as an acoustic channel. Cranial asymmetry in odontocetes is related to specialized sound-producing mechanisms involving predominantly the right nasal passage.

The nasal structures have formed a very important functional complex in the evolution of odontocetes, and are important from a phyletic viewpoint. This study has shown that the genera *Tursiops, Stenella,* and *Delphinus* form a relatively generalized group within the Delphinidae. The bulbous-headed genera *Grampus, Globicephala,* and *Pseudorca* clearly represent independent specializations. The other families of odontocetes differ considerably from the delphinids in their facial anatomy.

The anatomical diversity in this region suggests an acoustic diversity which remains to be demonstrated experimentally.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SI PRESS NUMBER 5387. SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

Library of Congress Cataloging in Publication Data
Mead, James G.
Anatomy of the external nasal passages and facial complex in the Delphinidae (Mammalia: Cetacea)
(Smithsonian contributions to zoology, no. 207)
Supt. of Docs. no.: SI 1.27:207
1. Delphinidae. 2. Nose. 3. Face. 4. Skull. I. Title. II. Series: Smithsonian Institution. Smithsonian contributions to zoology, no. 207.
QL1.S54 no. 207 [QL737.C432] 591'.08s [599'.53] 75-619034

Contents

Anatomy of the External Nasal Passages and Facial Complex in the Delphinidae (Mammalia: Cetacea)

James G. Mead

INTRODUCTION

Historical Review

The structure of the Cetacea (whales, porpoises, and dolphins) has long fascinated anatomists and students of natural history in general. Many features of cetacean anatomy were familiar to the classical natural historians, notably Pliny the Elder and Aristotle. During the middle ages, cetacea were frequently treated in general works on natural history (Olaus Magnus, Gesner, Rondeletius, and others), but emphasis was on the fabulous aspects of the larger members of the order. The first work exclusively on the anatomy of a cetacean is John Ray's "Account of the Dissection of a Porpess" (1671). This paper is particularly interesting, in that it contains a description of the nasal passages and diverticula, as well as some speculations upon their function.

The peak of activity on cetacean anatomy occurred during the 19th century, when such workers as Turner, Flower, Murie, Rapp, Kukenthal, Stannius, and others produced thousands of pages of descriptive anatomy. During the 20th century this work was continued by Howell, Schulte, Beddard, Huber, Slijper, and others.

Of the smaller cetaceans, *Phocoena phocoena* (the harbor porpoise) has been the most frequently and most thoroughly described (e.g., Ray, 1671; Stannius, 1849; von Baer, 1826; Rawitz, 1900), due to its abundance along the European coast and its convenient size. The pilot whale (*Globicephala melaena*) has also been the frequent subject of anatomical investigations (Macalister, 1867; Turner, 1867; and most notably Murie, 1873), due to the frequency of its strandings along the European coasts. Aside from these, the best descriptions of the anatomy of smaller cetaceans are usually of rare and unusual animals (e.g., *Neophocaena*, Howell, 1927; *Kogia*, Danois, 1910; Kernan and Schulte, 1918; *Monodon*, Huber, 1934). Delphinine cetaceans have received less attention, and very little published information exists for *Tursiops truncatus*, the ubiquitous experimental animal of the present time.

Relatively few of the many hundreds of papers dealing with the anatomy of cetaceans contain information on the structures of the facial region. Some of the early papers (Ray, 1671; Hunter, 1787; Cuvier, 1836) on general anatomy mention the structure of the nasal passage, or comment briefly on the musculature surrounding it. Von Baer (1826) appears to have been the first to focus on the structure of the cetacean nose, based upon dissections of *Phocoena*. Sibson (1848) described the nasal apparatus in *Phocoena* and Murie (1870,

---

James G. Mead, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D. C. 20560.

1873) went into some detail in discussing the facial structures of a variety of odontocetes. Gruhl (1911) commented extensively on the diverticula in a number of species. (Purves, 1967, and Moris, 1969, have given brief descriptions of the facial anatomy of *Steno* and *Phocoena*.)

The principal recent works dealing with the anatomy and function of the nasal apparatus are those of Lawrence and Schevill (1956), who were primarily concerned with the respiratory functions of these structures, Schenkkan (1971, 1972, 1973), and Schenkkan and Purves (1973). Schenkkan (1973) presented an extensive treatment of the comparative functional anatomy of the nasal tract of odontocetes. His data filled in many of the gaps in my material and have been utilized extensively in the present paper. Many of the differences between his work and mine probably stem from the fact that *Phocoena* formed the comparative framework of his study, whereas I used *Stenella.*

Since the discovery of the possibility of echolocation in odontocetes in the early 1950s (Kellogg, et al., 1953; Schevill and Lawrence, 1956), and its experimental demonstration in 1961 (Norris et al., 1961), the anatomy of structures potentially involved in sound production and reception has received considerable attention. The question of sound reception has been treated by Reysenbach de Haan (1957) and Fraser and Purves (1960). Evans and Prescott (1962) and Norris (1964) have considered the problems of sound production, while Norris (1969) has provided the most recent general survey of the problems of echolocation in cetaceans.

The structures comprising the facial region of the odontocetes, i.e., the nasal passages and their diverticula, the fatty melon, and the muscles associated with these, have frequently been implicated in sound production (Lawrence and Schevill, 1956; Evans and Prescott, 1962; Norris, 1968). Questions relating to the mechanism of sound production, such as which structures are involved and how the acoustic energy is conducted from the sound source (s), focused, modulated, and otherwise altered, are still under debate.

General Aspects of the Facial Anatomy of Mammals

The face, as it is generally thought of in human terms, consists of the anterior portion of the head, containing the nose, mouth, and eyes. To a certain extent this area can be considered separate from the remainder of the head, or cranium. Thus conceived, the bony elements of the face are the maxillae, premaxillae, nasals, vomer, palatines, zygomatics, and frontals. This division of the head corresponds approximately with the distribution of motor elements associated with the facial nerve, and with the sensory distribution of the trigeminal nerve.

The anatomy of the mammalian face is complex (see Huber, 1930; Edgeworth, 1935; Miller et al, 1964), and presumably has been throughout much of its evolutionary history.

The soft tissues consist of a series of muscles disposed about the orifices of the face and largely concerned with manipulation of these, the skin and various specialized portions of the skin (lips, eyelids, etc.), and the vascular and nervous supplies of these elements. The structures within the facial orifices (eyes, tongue, etc.) could logically be included in this group and would greatly expand this list. However, these are extremely specialized and are better considered separately.

The nose is generally a complex structure in mammals, and even in terrestrial mammals it is capable of being opened and closed to a considerable extent. This is accomplished by various portions of the m. maxillonasolabialis acting upon the cartilages comprising the skeleton of the nasal aperture. In addition, the area of the nose is usually highly sensitive and is abundantly supplied with nerves and blood vessels. The complexity of the mammalian nose has provided the basis for a great variety of evolutionary modifications, exemplified by the noses of pigs, elephants, tapirs, bats, moles, and whales. Boas and Pauli (1908) give an excellent picture of the diversity of mammalian noses.

The cetacean face has become specialized as a result of the demands of an aquatic existence, and presents a number of differences from that of terrestrial mammals. The nose occupies a dorsal rather than a terminal position on the rostrum, and the facial musculature has become largely concerned with opening and closing the nasal aperture. Cetacea are, in fact, one of the very few groups of mammals incapable of facial expression, as the areas of the mouth and eyes are relatively immobile.

The orbit has moved laterally and ventrally and now bears a closer relationship to the base of the cranium than to the rest of the face. There has been extensive alteration of the bones of the skull (Miller, 1923), differing in detail in the two suborders of cetaceans.

In view of the modifications seen in the cetacean head, it is useful to redefine the area of the face. One of the immediately striking aspects of a cetacean skull (when viewed from above) is the flat expanse of bone formed by the dorsal surface of the rostrum and cranium. This surface is bounded by the lateral edge of the rostrum, the supraorbital process of the frontal, and the temporal and nuchal crests (Figure 1). This area can be usefully defined as the face in this group of animals, as it forms an area concerned with the operation of the highly modified cetacean nose. The orbit, while still surrounded by what is technically facial musculature, does not fit into the functional area of the face in

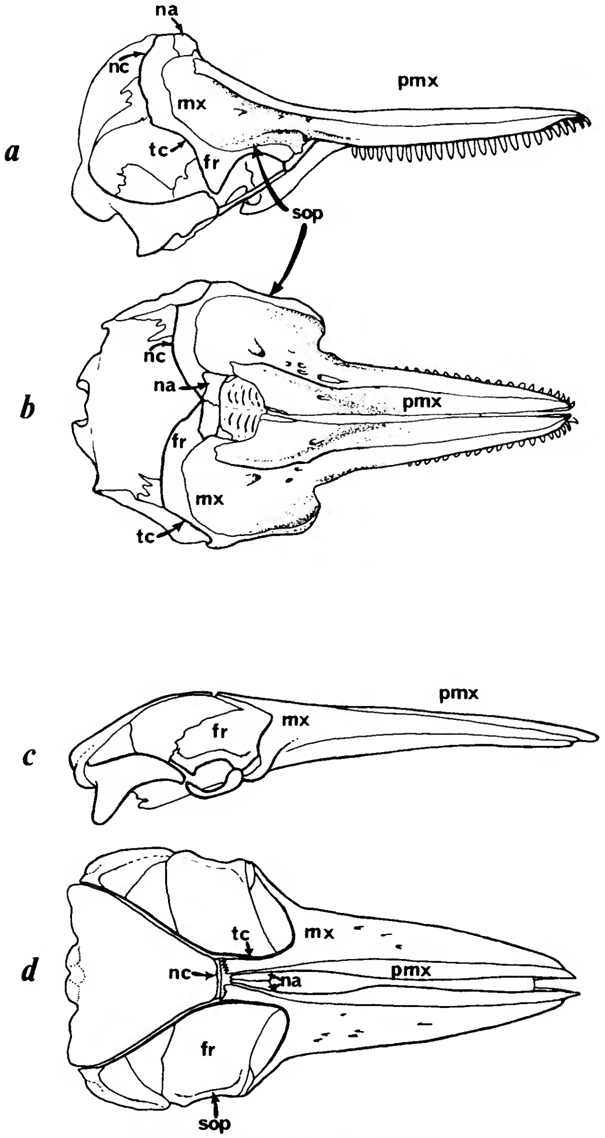

FIGURE 1.—Skulls of modern cetaceans (after Kellogg, 1928): *a, Tursiops truncatus*, an odontocete, lateral view; *b, T. truncatus*, dorsal view; *c, Balaenoptera edeni*, a mysticete, lateral view; *d, B. edeni*, dorsal view. (fr=frontal, mx=maxilla, na=nasal, nc=nuchal crest, sop=supraorbital process, tc=temporal crest, pmx=premaxilla.)

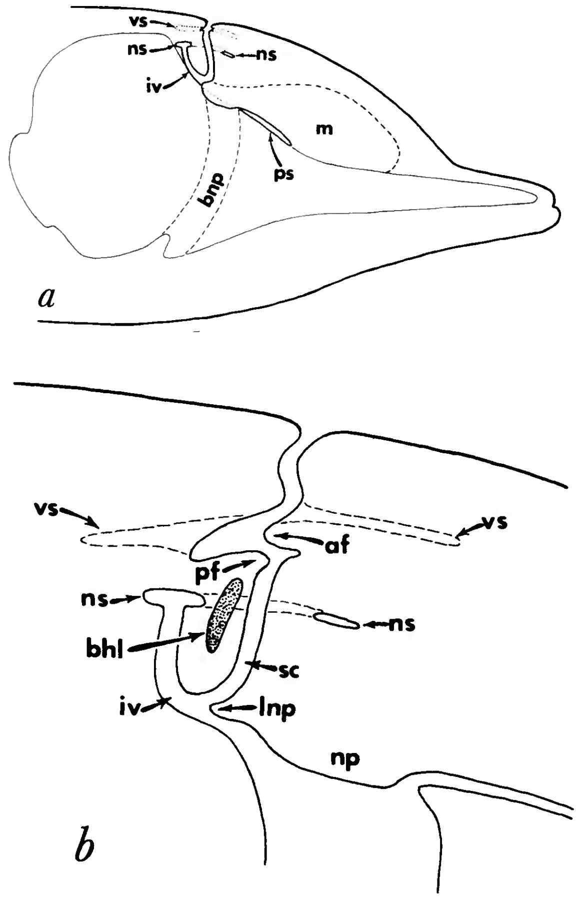

FIGURE 2.—Head of a delphinid: *a*, diagramatic sagittal section; *b*, detail of the above. (af=anterior fold, bhl=blowhole ligament, bnp=bony nasal passage, iv=inferior vestibule, lnp=lip of the nasal plug, m=melon, ns=nasofrontal sac, np=nasal plug, pf=posterior fold, ps=premaxillary sac, sc=spiracular cavity, vs=vestibular sac.)

the same manner that it does in terrestrial mammals, nor does the mouth.

The skull of mysticetes has been modified along different lines than that of the odontocetes, the primary modification apparently being the development of a large rostrum as part of the feeding mechanism. If the braincase is taken as the point of reference, the nasal passages have not been displaced posterodorsally, as they have in odontocetes. Carte and Macalister (1868) provide the best description of the facial structures of a mysticete. The musculature associated with the nares is extensive, but there are no diverticula, nor is there anything comparable to the large melon of odontocetes. Viewed from the side, the facial region of mysticetes appears very low and flat compared to that of odontocetes.

In the odontocetes, the nasal aperture has migrated posterodorsally, and now opens on the dorsal surface of the head. The musculature associated with the nasal passage has increased in size and complexity, as have the passages themselves. Instead of a relatively simple passage, as in the mysticetes, there is a complicated series of diverticula and valves within the nose of the toothed whales (Figure 2). An accessory structure, the melon, has developed anterior to the nasal passage, greatly increasing the bulk of the facial apparatus. The acme of these is seen in the nose of the sperm whale, which constitutes on the order of one-third of the weight of the entire animal.

The development of a complex nasal apparatus, particularly the elaboration of a fatty melon, is one of the principal distinctions between odontocetes and mysticetes. The differences in the structure of the bony elements of the face can be followed well back into the fossil record (Kellogg, 1928), suggesting that the adaptive aspects of these formed one of the bases for differentiation of the two suborders. Mysticete differentiation appears to have depended upon the development of a novel feeding apparatus, while odontocetes remained relatively conservative in that aspect, and have elaborated the nasal apparatus and associated structures.

Numerous anatomists have attempted to homologize the structures of the cetacean nose with those of the other mammals (von Baer, 1826; Murie, 1870, 1873; Anthony, 1926). The diverticula have been compared with the turbinals of other mammals and with the nasal sacs of the tapir, the saiga antelope, and the horse. Murie (1870) attempted to homologize the nasal musculature with the various facial muscles of man. It is my belief, however, that the melon, nasal diverticula, and differentiation of the nasal musculature have been derived independently in cetaceans. Huber's (1934) brief homology of the nasal musculature with the m. maxillonasolabialis appears to be the most rational approach to the question of muscle homologies. The archaeocetes do not appear to have possessed a specialized nasal apparatus, making it unlikely that anything but the most generalized of mammalian homologies is applicable to the modern Cetacea.

Questions of Odontocete Facial Anatomy

A thorough understanding of the anatomy of this region is essential before we can hope to understand the functions in which it is involved. This is particularly true of a system like the odontocete nose, which does not appear to have an analogue in any other mammalian structure. I have described the components of the facial complex and their relationships to one another in order to see if they form discernible functional systems. To an extent this has been possible, particularly with simpler mechanical functions, such as opening and closing of the blowhole and nasal passages.

Many of the potential functions of this region are more subtle or complex and cannot be approached in this manner. In order to elucidate these, I have undertaken a comparative study, hoping to find structural differences which could be correlated with observed behavioral or ecologic differences.

This type of comparative approach is useful not only in terms of the answers which it provides, but also the questions which it poses. The range of external morphology in the head of small odontocetes indicates the possibility of a wide range of internal structure. If such structural diversity is demonstrated, it will suggest a functional diversity which must then be looked for in the living animals.

Specialization of the facial region of odontocetes has probably been an important factor in their evolution and is thus important phyletically as well as functionally. Relationships among the living odontocetes are poorly understood at present. An examination of one of their more important functional complexes will provide a new basis for interpreting phyletic relationships in this group. This is particularly true where questions of possible convergence are involved, as in the bulbous-headed delphinids.

The significance of the asymmetry of the skull in odontocetes has never been satisfactorily explained. This is because the relationship of the bony asymmetry to the soft tissues of the head has never been examined. Such an approach is essential to an understanding of the functional significance of this character.

A detailed anatomical study will also provide a basis for experimental work on these animals, which has previously been hampered by a lack of information on the structures involved.

The literature pertaining to these problems is voluminous and somewhat confusing. I have attempted to review much of this and to clarify some of the points of confusion.

Acknowledgments

This work was begun and substantially completed during my tenure as a graduate student at the University of Chicago, and, as any dissertation, owes a great deal to many people. Leonard Radinsky, Charles Oxnard, George Rabb, Leigh Van Valen, and Edward D. Mitchell served on the dissertation committee, read the manuscript at various stages, and provided much valuable criticism. I would like to express particular appreciation to James Hopson, my major professor, without whose patience and assistance this work would never have succeeded. I am also grateful to my fellow graduate students, particularly Timothy L. Strickler, who participated in many phases of this study, and to my wife, Rebecca.

One of the greatest obstacles faced by a comparative study of this sort is the availability of specimens. The material used in the study was provided by the following: William A. Walker, Marineland of the Pacific; Edward D. Mitchell, Fisheries Research Board of Canada; David K. Caldwell, University of Florida; the Shedd Aquarium, Chicago; William F. Perrin, Southwest Fisheries Center; Robert Jones, University of California at Berkeley; Robert L. Brownell; Allen Wolman and Dale Rice, Marine Mammal Biology Laboratory, Seattle. I would also like to thank the people, too numerous to mention, who spent time unsuccessfully trying to obtain material for this study. I am particularly indebted to Edward D. Mitchell, not only for providing material, but also for the use of his laboratory facilities and library, remunerative employment, the drawing used in Figure 10, and a continuing flow of advice.

While I was at the University of Chicago, this work was supported by grants from the Hinds Fund and a fellowship from the Center for Graduate Studies in Systematic Zoology and Paleontology at the Field Museum of Natural History.

DESCRIPTIVE ANATOMY

Introduction

I have dissected the facial region in a series of delphinids, consisting of members of the following genera: *Tursiops, Stenella, Grampus, Lagenorhynchus, Lagenodelphis, Orcinus, Pseudorca, Globicephala, Steno,* and *Cephalorhynchus.* In addition, I have dissected specimens of *Phocoena, Phocoenoides, Inia,* and *Pontoporia,* and have compiled such comparative data as is available for other genera. The families Physeteridae and Ziphiidae have been deliberately omitted, as they appear to be strikingly different and constitute a separate problem.

The techniques employed consisted of gross dissection, along with gross coronal and sagittal sections of the soft structures of the facial region. The dissections were limited to the area dorsal and medial to the supraorbital process of the frontal and the temporal crest, and anterior to the nuchal crest. Extensive photographs were taken as a record of the dissections. A large series of specimens of *Stenella,* covering a wide size range, was dissected and the nasal muscles fixed and weighed in order to determine whether there was any asymmetry in the muscular system.

I have chosen the common bottle-nosed dolphin, *Tursiops truncatus,* as the standard of comparison, and will describe it first. There are two outstanding reasons for this choice. First, *Tursiops* appears to be a relatively generalized delphinid, from which the conditions seen in the other genera could be readily derived. Second, it has become the standard experimental animal and, as such, there are data available for it that are lacking for the less common animals. Unfortunately, I found material difficult to obtain for *Tursiops,* and I have not been able to dissect enough animals to establish the range of individual variation in this species.

The descriptions that follow have not taken into account the asymmetry seen in some of the facial structures, as this will be treated in detail in a later section. In general, the descriptions of the nasal passages and diverticula begin with the deep structures and proceed to the superficial ones, while the muscular descriptions follow the opposite order.

DELPHINIDAE

DELPHININAE

Tursiops

MATERIALS.—The specimens of *Tursiops truncatus* consisted of the heads of two adult females and a 53.5 cm male fetus. One adult head and that of the fetus were dissected, while the other adult head was frozen and sectioned coronally at 2 cm intervals.

NASAL PASSAGE AND DIVERTICULA.—The central structure in the facial region of odontocetes is the nasal passage. As in all mammals, the nasal passage is a paired structure within the confines of the skull. As the paired passages exit from the skull, they are separated for a short distance by a cartilaginous nasal septum. Beyond this septum, they fuse into a single passage and proceed dorsally through the soft tissue. The nasal passages and diverticula are lined throughout with a thin, darkly pigmented, squamous epithelium.

Within the mass of soft tissue on the dorsal surface of the skull, the nasal passages send off a series of paired diverticula. In *T. truncatus,* as in most small odontocetes, there are four pairs of these situated in the soft tissues surrounding the nasal passage. These diverticula are distensible to varying degrees, but are not generally moveable within the surrounding tissues.

Immediately dorsal to their exit from the skull, while they are still separated by the septum, the nasal passages send two diverticula, the *premaxillary sacs* (Murie, 1870), anteriorly along the dorsal surface of the rostrum (Figures 2, 4). The ventral surface of these diverticula lies directly upon the periosteum of the premaxillae, while the dorsal surface is in contact with the nasal plug muscle. These are the largest of the pairs of diverticula in *T. truncatus.*

The lateral margins of the nasal passages, as they exit from the skull, are bounded (and slightly occluded) by the *diagonal membranes* (Lawrence and Schevill, 1956) (Figure 3). These membranes run at an angle from the anterolateral wall of the nasal passage, just internal to its exit from the skull, posterodorsally to attach to the posterior end of the nasal septum. They are thin membranes, consisting only of the reflected nasal epithelium with a slight amount of connective tissue and sometimes a few muscle fibers. In *T. truncatus,* as in most of the delphinids, they are 1 to 1.5 cm wide.

Along the posterior edge of the nasal passages,

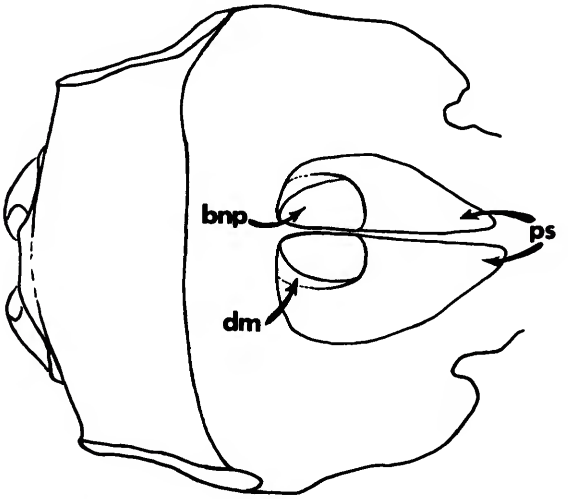

FIGURE 3.—Diagramatic dorsal view of the structures adjacent to the external bony nares in *Tursiops truncatus.* (bnp=bony nasal passage, dm=diagonal membrane, ps=premaxillary sac.)

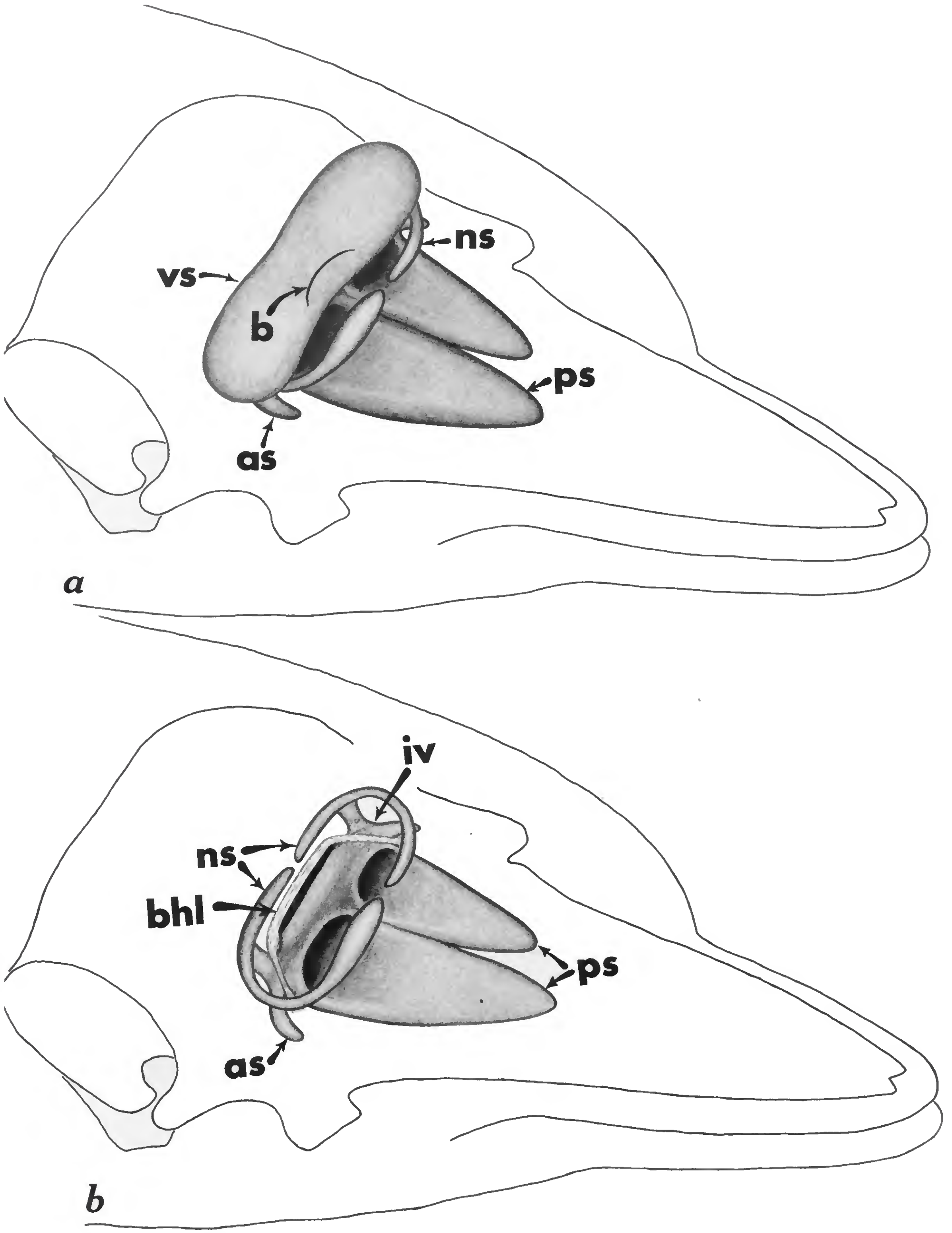

Figure 4.—Diagramatic views of the nasal diverticula of *Tursiops truncatus*: *a*, oblique view of the intact diverticula; *b*, same view, vestibular sacs and part of the spiracular cavity removed. (as=accessory sac, b=blowhole, bhl=blowhole ligament, iv=inferior vestibule, np=nasal plug, ns=nasofrontal sac, ps=premaxillary sac, sc=spiracular cavity, vs=vestibular sac.)

just external to the diagonal membranes, lies a pair of small chambers, the *inferior vestibules* (Gallardo, 1913) (Figures 2, 4). These extend dorsally and posteriorly toward the vertex of the skull. A small muscle (which will be discussed later) lies beneath the posterior wall of these chambers. The anterior wall is formed by the blowhole ligament, which runs from the anterior tip of the vertex anterolaterally to the lateral edge of the premaxilla. Dorsally the inferior vestibule opens into the nasofrontal sac, laterally into the accessory sac (described later). Schenkkan (1973) mentioned a "small ventral extension" near the entrance of the nasofrontal sacs to the nasal passage (inferior vestibule) in *Tursiops*. I did not find this in my limited material, and am unable to interpret its significance.

The *nasal plugs* (Lawrence and Schevill, 1956) are two fleshy bodies which protrude posteriorly from the anterior wall of the nasal passage, just dorsal to the premaxillary sacs (Figures 2, 4). They are oval ventrally, where they fit into the bony nares. Their free margins are produced into lips, which fit into the paired inferior vestibules (Figure 2). The body of the nasal plugs consists of the *nasal plug muscle* (Lawrence and Schevill, 1956), which lies in a dense connective tissue matrix. This muscle originates from the premaxilla anterior to the premaxillary sac. Dorsally it grades into the fat of the melon. In *T. truncatus*, as in most of the other delphinids examined, the fat of the melon extends only onto the right nasal plug, as noted by Norris (1969) in *Delphinus*.

Opening laterally from the inferior vestibule is the *accessory sac* (Schenkkan, 1971 = connecting sac of Lawrence and Scheville, 1956). This diverticulum extends laterally for a short distance, then turns anteriorly around the attachment of the blowhole ligament to the premaxilla (Figure 4). It is smaller than the other diverticula, 1 cm or less in diameter and 1 to 2 cm long. It ends blindly in the posterolateral tissues of the nasal plug muscle. As with the other diverticula, the accessory sacs are paired, the right being the larger. The mouth of this diverticulum appears to be occluded by a lateral extension of the lip of the nasal plug when the nasal plug is in place over the bony nares. Schenkkan (1971) pointed out that this diverticulum doesn't connect anything, and applied the term "accessory sac," as the term "connecting sac" was misleading. The structure termed "connecting sac" by Evans and Prescott (1962), which connects the nasofrontal sac with the nasal passage, is probably the inferior vestibule.

The *nasofrontal sac* (Murie, 1870 = tubular sac of Lawrence and Schevill, 1956) lies in the tissues surrounding the nasal passage, dorsal to the nasal plugs (Figures 2, 4). It is convenient to speak of an anterior and a posterior part of the nasofrontal sac, with respect to the nasal passage. The posterior part ends as a blind sac medially, just posterior to the nasal septum. It extends, laterally, around the edge of the nasal passage, where it becomes continuous with the anterior part. The blind termini of both parts abut against the corresponding terminus of the contralateral sac. The collapsed diameter of this sac is about 1 cm, the length of the right sac about 10 cm, the left about 7 cm. The reflection of the sac around the lateral edge of the nasal passage is referred to as the angle of the nasofrontal sac. In *T. truncatus* the angle is slightly lobulated, particularly on the right side (Gruhl, 1911). The nasofrontal sac in *T. truncatus* is darkly pigmented throughout its length. The posterior part of the nasofrontal sac opens ventrally, by means of a transverse slit, into the inferior vestibule.

The *blowhole ligament* (Lawrence and Schevill, 1956) is a strong connective tissue band, running laterally from the anterior tip of the vertex to the lateral edge of the premaxilla, just anterior to the accessory sac. It lies anterior and ventral to the nasofrontal sac, crossing anterodorsal to the communication of the latter with the inferior vestibule (Figure 4). It is widest medially, where it forms a substrate for the attachment of some of the musculature associated with the nasofrontal sacs. Laterally it becomes narrower and thicker. It sometimes gives off a branch which passes posteriorly, dorsal to the mouth of the accessory sac, and attaches to the premaxilla just posterior to the accessory sac. Purves and Pilleri (1973), in their description of *Platanista*, found the homoloque of the blowhole ligament to be cartilaginous, and considered it equivalent to the *crus lateralis* of the lower nasal cartilages of terrestrial mammals.

Immediately anterior to the midportion of the blowhole ligament is an elliptical body (Figures 10, 16), 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 (description follows).

The central portion of the nasal passage, dorsal to the nasal plugs, has generally been referred to in the literature as the *spiracular cavity* (Figures 2, 4). It is into this cavity that the inferior vestibule opens ventrally and the vestibular sacs (description follows) open dorsally. In morbid material of delphinids, this cavity appears as a transverse slit extending from the nasal plugs upward to the blowhole. It has been generally ignored as an anatomical entity in this group, but is important from a comparative standpoint, as it becomes highly modified in some other odontocetes.

Dorsal to the nasal plugs, the spiracular cavity opens into a pair of lateral diverticula, the *vestibular* sacs (Lawrence and Schevill, 1956) (Figures 2, 4, 6). These are wide flat diverticula, extending laterally from the nasal passage in a horizontal plane. They are about 6 cm wide and 4 cm long. In the morbid state the walls of these diverticula are wrinkled, indicating a certain amount of distensibility. In *T. truncatus*, as in a few other species, there is an indication of a small anterior lobe on the left vestibular sac (Figure 24). This may be variable and possibly accounts for the reverse asymmetry noted by Schenkkan (1973) in one of his specimens.

On the anterior wall of the spiracular cavity, just ventral to the vestibular sacs, is a small recess. This extends horizontally across the wall of the spiracular cavity and forms a lip (the *anterior fold* of Lawrence and Schevill, 1956) between it and the vestibular sac (Figure 2). The posterior wall of the spiracular cavity is produced into a slight ridge at this point (the *posterior fold* of Lawrence and Schevill, 1956), which fits against the recess in the anterior wall, and is overlain by the anterior fold when the nasal passage is closed.

The nasal passage opens onto the surface of the head through the *blowhole.* The blowhole is crescentic, with the concavity facing anteriorly. Seen in cross section, the anterior lip of the blowhole is convex, fitting into a concavity in the posterior wall just ventral to the posterior lip. The anterior lip of the blowhole is relatively soft and mobile, while the posterior lip is more rigid.

MUSCULATURE.—The musculature associated with the nasal passage is extremely complex and, until the work of Lawrence and Schevill (1956), had not received detailed anatomical coverage. Huber (1934) stated that this muscular complex represents an elaboration of the primitive m. maxillonasolabialis of mammals. Lawrence and Schevill (1956) recognized six layers within this complex. I have modified their plan slightly, as I was not able to separate the muscles consistently according to their definitions (particularly across the wide range of morphologic types with which I was dealing). I have, however, used their terminology with some modifications where necessary.

The most superficial of the muscles associated with the nasal passage is the *pars posteroexternus* (*pe*). This muscle originates along the posterior half of the supraorbital process, the temporal crest, and a variable portion of the nuchal crest (Figure 5). It runs medially, posterior to the nasal passage, to insert upon the vertex and into the contralateral muscle. As is the case with all of the nasal muscles, *pe* grades into the adjacent musculature. Anterolaterally it is gradational with the pars intermedius; posteriorly it is gradational with the pars anteroexternus. I have found that I could make consistent separations at its insertion, as its fibers have a much more medial orientation that those of the underlying muscle. This differs from the definition of Lawrence and Schevill (1956:119) in that it includes none of the musculature which is in direct contact with the vestibular sac.

The *pars intermedius* (*i*) consists of deep fibers from the same muscle mass as *pe*, which diverge from *pe* in an anterior direction (Figure 5). It originates deep to *pe*, along the posterior half of the supraorbital process, and inserts into the mass of heavy connective tissue dorsal to the nasal plugs. This follows the definition of Lawrence and Schevill (1956:121).

The *pars anteroexternus* (*ae*) is a much larger muscle than either *pe* or *i* (Figure 6). It originates from the anterior end of the supraorbital process to the temporal and nuchal crests and the adjacent bony surface (usually frontal, but occasionally including the maxilla). Posteromedially it occupies the fossa between the vertex and the nuchal crest. The anteriormost fibers insert across the midline into the contralateral muscle. Posteriorly the fibers come to insert first upon the anterior wall of the nasal passage, then the lateral edge, and finally the posterior wall and the dorsal edge of the blowhole ligament (Figure 6). The vestibular sac is contained within this muscle, which is loosely attached to it both dorsally and ventrally. Thus *ae* presents a series of fibers converging upon the nasal passage. Lawrence and Schevill (1956:122) defined *ae* as only the anterior portion of the muscle described above. Since I could find no consistent separation into an anterior and a posterior portion, and, as the modified definition seems to result in a functional entity, I have redefined this muscle.

Ae is most easily defined in dissection at its posterior insertion, where its anteriorly directed fibers present a marked contrast to the underlying fibers of the pars posterointernus. Although the directions of these two sets of fibers are quite different, they are thoroughly intermeshed, forming an aponeurosis just dorsal to the nasofrontal sacs. *Ae* can be separated from the pars posterointernus at its insertion, but merges with it along its origin. Anteriorly *ae* becomes continuous with the underlying fibers of the pars anterointernus at both origin and insertion, and also with the posterior fibers of the rostral muscle.

The *pars posterointernus* (*pi*) lies just deep to *ae*, taking its origin from the frontal (and/or maxilla) at the level of the eye (middle of the supraorbital process) (Figure 7). Its origin extends posteriorly, then medially into the fossa between the nuchal crest and the vertex. It inserts via a flat tendon, which runs in an arc posterior to the nasal passage, into the contralateral muscle and the aponeurosis formed with the fibers of insertion of *ae*. Lawrence and Schevill's definition of *pi* (1956: 123) includes only the posterior portion of what I have called *ae*. I cannot find a muscle or portion of a muscle in their description corresponding to what I have defined as *pi*. Accordingly, I was tempted to substitute a new name to avoid confusion, but felt that this would require a complete substitution for their names, which form a topographic system. I have found this system to be particularly useful, and so have retained it, completely redefining *pi*.

Pi is easily separated at its insertion from the rest of the muscles, although at its origin it is indistinguishable from both the overlying (*ae*) and underlying (*ai*) muscles.

The deepest and largest of the muscles associated with the nasal passages is the *pars anterointernus* (*ai*). This muscle takes its origin from a broad area of the ascending process of the maxilla, between the origins of *ae* and *pi* and the lateral border of the premaxilla (Figure 8). It is indistinguishable anteriorly from the medial rostral muscle. In order to separate these two, I have arbitrarily drawn a line from the anterior end of the supraorbital crest medially to the premaxilla, and have called everything posterior to this line pars anterointernus. The insertion of this muscle is into the connective tissue mass anterior to the nasal passage, and through it to the contralateral muscle. This muscle is fanshaped, the posterior fibers running anteriorly across the midline, the lateral fibers passing directly medially and the anterior fibers running posteriorly. A few of the deep anterior fibers of *ai*, instead of inserting across the midline anterior to the nasal passage, cross the fibers of insertion of the posterior portion of the muscle and attach to the lateral edge of the nasal passage. This definition represents a fusion of the pars anterointernus and the pars profundus of Lawrence and Schevill (1956:123–126).

The *rostral musculature* consists of an elongate block lying along either side of the rostrum (Figures 8, 9). In transverse section this is seen to consist of fibers radiating from a central area of origin along the maxilla into the tissue of the lip, dermis, and melon. This block of muscle can be divided into two portions, with slightly differing fiber orientation. These are a *lateral portion*, primarily associated with the lip and the connective tissue adjacent to the melon, and a *medial portion*, which inserts into the melon (Figure 9). The separation between these two portions is seen in transverse section as a diffuse zone of connective tissue. If this separation is followed posteriorly, it becomes apparent that the lateral portion is continuous with the superficial musculature of the nasal passage (*pe, i, ae* and *pi*), while the medial portion is continuous with the deep musculature (*ai*). This separation becomes quite striking at the level of the antorbital notch, where there is frequently a strong ridge produced on the maxilla along the line of separation of the two parts.

The separation of the rostral muscle into lateral and medial parts, continuous with different portions of the nasal musculature, raises the question of the homologies of these muscle blocks. Huber (1934) considered the posterior musculature to be homologous with the parts nasalis of the m. maxillonasolabialis, while the rostral musculature was considered to be homologous with the pars labialis of that muscle. The continuity of the rostral musculature with the posterior musculature suggests that if a division is to be made, it is between medial and lateral elements, not anterior and posterior. While this is a question best approached through developmental studies, it seems useful to tentatively designate the lateral rostral musculature and its associated nasal musculature (*pe, i, ae* and *pi*) as

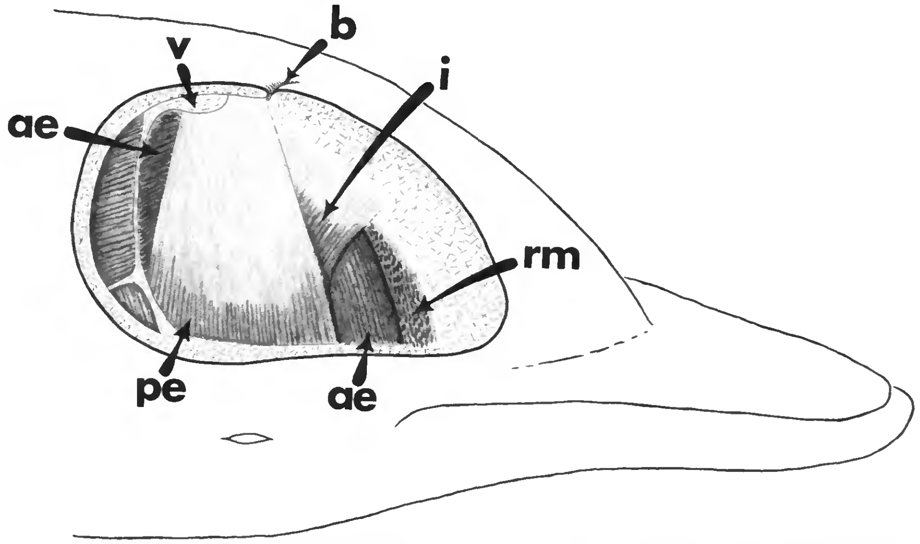

FIGURE 5.—Oblique view of the superficial nasal musculature of *Tursiops truncatus*. (ae=pars anteroexternus, b=blowhole, i=pars intermedius, pe=pars posteroexternus, rm=rostral muscle, v=vertex.)

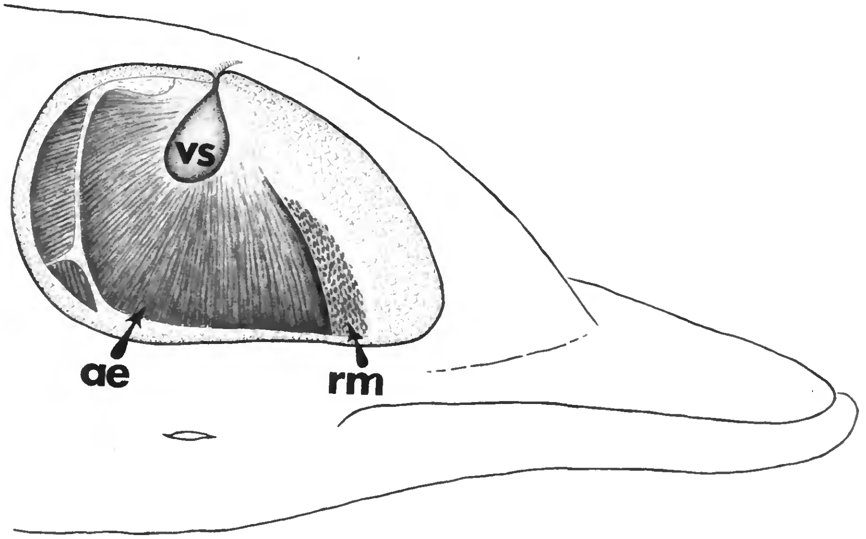

FIGURE 6.—Oblique view of the nasal musculature of *Tursiops truncatus*, at a slightly deeper level than Figure 5. Pars posteroexternus, pars intermedius, and part of pars anteroexternus removed to expose the vestibular sacs. (ae=pars anteroexternus, rm=rostral muscle, vs=vestibular sac.)

derivatives of the pars labialis and the medial rostral musculature and *ai* as derivatives of the pars nasalis of the m. maxillonasolabialis.

These descriptions are complicated and confusing, and a genreal summary may be useful at this point. The most superficial muscle, *pe*, runs from a

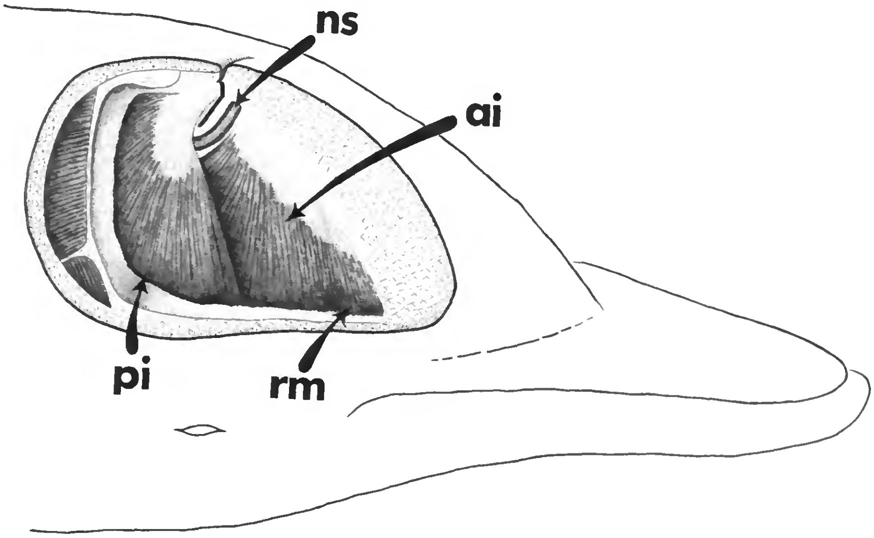

FIGURE 7.—Oblique view of the nasal musculature of *Tursiops truncatus*, at a level intermediate between Figures 6 and 8. Pars anteroexternus completely removed. (ai=pars anterointernus, ns=nasofrontal sac, pi=pars posterointernus, rm=rostral muscle.)

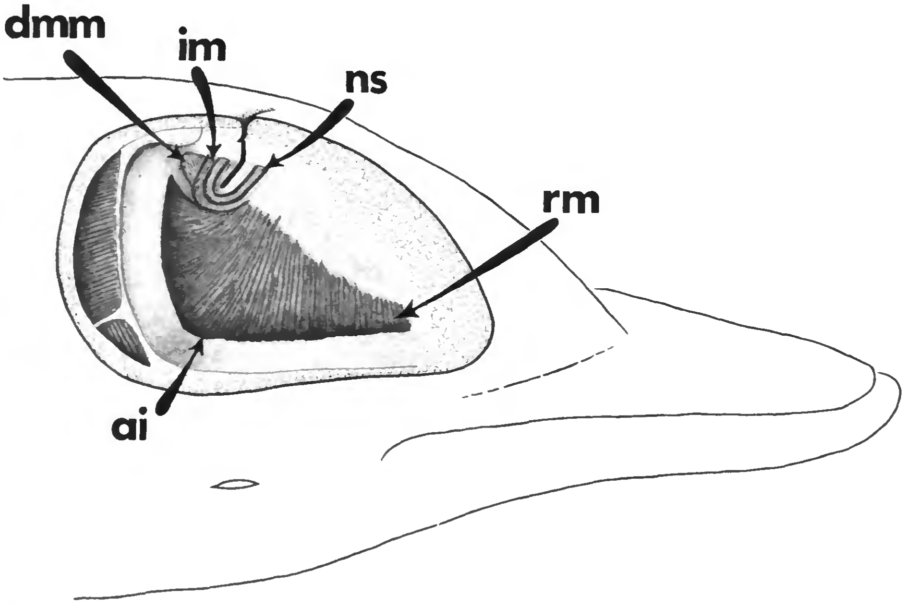

FIGURE 8.—Oblique view of the deep nasal musculature of *Tursiops truncatus*. Pars posterointernus completely removed. (ai=pars anterointernus, dmm=diagonal membrane muscle, im=intrinsic muscle, ns=nasofrontal sac, rm=rostral muscle.)

lateral origin to a medial insertion, posterior to the nasal passage. *Ae* lies immediately under *pe* and consists of fibers converging upon the nasal passage from the margins of the facial region. Between these two muscles, and continuous at its origin with both of them is *i*. This muscle differs from *ae* and *pe* in having a more anterior insertion, and thus a different fiber direction. *Pi* is continuous at its origin with *ae*, but differs in having an insertion entirely posterior to the nasal passage (as does *pe*). *Ai* is continuous at its origin with *pi*, but inserts entirely anterior to the nasal passage, giving it a markedly different orientation. *Ae* and *ai* are continuous anteriorly with each other and with the rostral musculature. Posteriorly *ae* and *ai* are separated by *pi*.

Associated with the vertex and the nasofrontal sacs are a series of small muscles whose relationships are difficult to demonstrate. The muscle fibers are extremely fine and permeated with an equally fine connective tissue matrix which grades into the connective tissue of the adjacent structures. Lawrence and Schevill (1956) refer to this group of muscles as the intrinsic musculature (of the nasofrontal sac). They separate it into a major portion lying posterior and lateral to the nasofrontal sacs, and a minor portion lying anterior. I have found the two to be continuous, and refer to the portions described by them merely as the *intrinsic muscle* (of the nasofrontal sac) (Figure 8).

In *T. truncatus* this muscle originates from the anterodorsal surface of the vertex and the medial end of the nasofrontal sac. It passes laterally, along the anterior, ventral, and posterior aspects of the

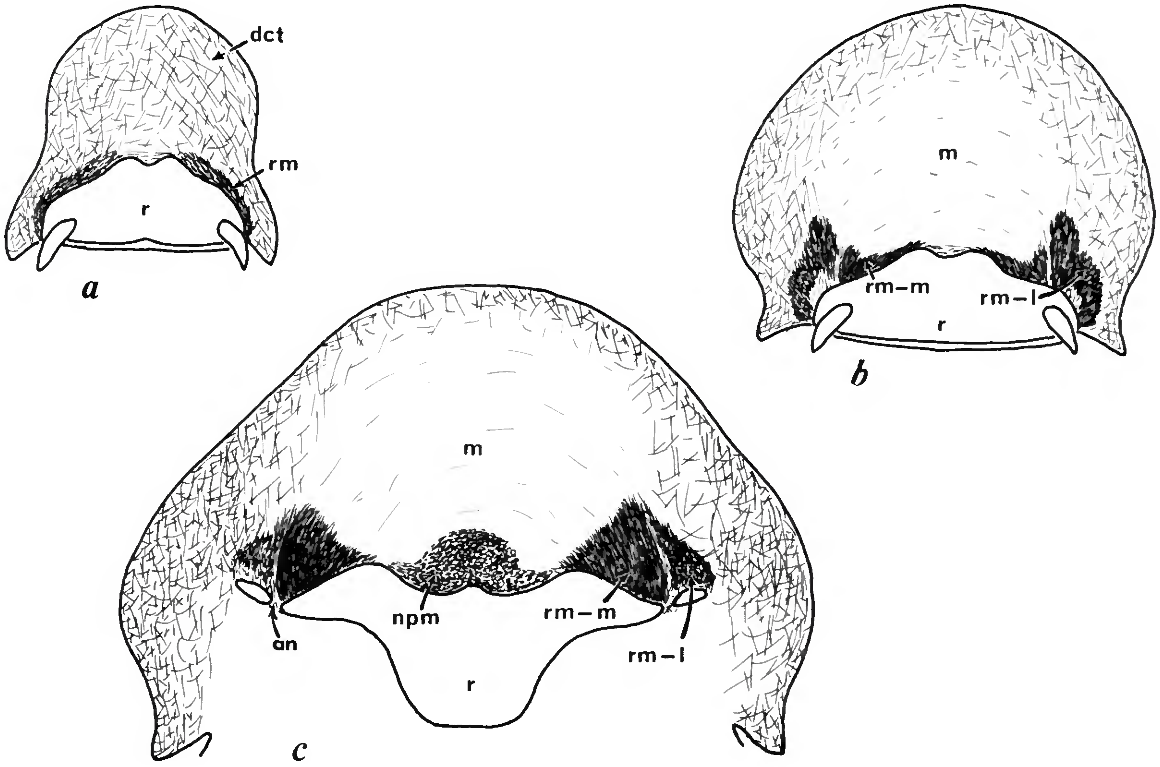

FIGURE 9.—Cross sections of the rostral structures of *Tursiops truncatus* (adult female): *a*, 10 cm posterior to the tip of the rostrum; *b*, 14 cm posterior to the tip of the rostrum; *c*, 18 cm posterior to the tip of the rostrum (at the level of the antorbital notch). (an = antorbital notch, dct = dermal connective tissue, m = melon, npm = nasal plug muscle, r = rostrum, rm = rostral muscle, rm-l = lateral portion of the rostral muscle, rm-m = medial portion of the rostral muscle.)

nasofrontal sacs, occasionally completely encompassing the sac. Throughout its length, its connective tissue matrix is closely associated with that of the adjacent structures, particularly the nasofrontal sac and blowhole ligament. It passes on either side of the communication of the nasofrontal sac with the inferior vestibule, then turns anteriorly, entering the dorsolateral surface of the nasal plug mass and merging with the nasal plug muscle.

Posterior and ventral to the intrinsic muscle lies another small muscle of similar composition. Due to the complexity of this region, this muscle has escaped the attention of earlier workers. It originates from the anterolateral surface of the vertex, lateral and deep to the intrinsic muscle. It then passes anteriorly, ventral to the intrinsic muscle and nasofrontal sac, to insert along the attached margin of the diagonal membrane. Very rarely it sends a few fibers into the free portion of the membrane. Due to the connective tissue in which these muscles are imbedded, it is difficult to ascertain the exact relationship of this muscle to the intrinsic muscle. In some specimens it appears to be sharply delimited from the intrinsic muscle, while in others it seems to be continuous with it. I have designated this the *diagonal membrane muscle*, in reference to its insertion.

MELON.—A frequent problem in the literature dealing with the odontocete nose is the distinction between melon, adipose cushion, spermaceti organ, and case. At one time or another, all of these names have been applied to the adipose connective tissue structure anterior to the nasal passage in delphinids.

"Melon" is a term apparently originating in the whaling industry, referring to the similarity of this mass of tissue, when it is removed from the head of the animal, to a section of melon (particularly in *Globicephala*, where it resembles a section of ripe muskmelon).

"Adipose cushion" is a term coined by Howell (1930), who evidently did not care for the colloquial nature of "melon." He described this structure in some detail and specifically indicated that he was referring to the smaller odontocetes.

The term "case" is another which has originated in the whaling industry, where it was used in reference to the oil-filled cavity in the head of the sperm whale.

Pouchet and Beauregard (1885) apparently originated the term "spermaceti organ" in reference to the structure more colloquially known as the case.

Howell (1930) discussed the possible homology of the adipose cushion (melon) and the spermaceti organ (case), and decided that they were probably unrelated. Raven and Gregory (1933), however, were of the opinion that they were homologous, and applied the term "spermaceti organ" to the structure seen anterior to the nasal passages in *Monodon*. This structure, however, appears to be no different from the adipose cushion (melon) of delphinids. Schenkkan and Purves (1973) examined the anatomy of the nasal complex in physeterids and concluded that the spermaceti organ in *Physeter* and *Kogia* was unrelated to the melon of delphinids.

Despite the rather colloquial flavor of the term "melon," it has been frequently and consistently used in the literature, and I have elected to retain it as applied to delphinids. This is specifically equivalent to the term "adipose cushion" of Howell (1930). I have not used Howell's term because of its functional implications. The functions of this structure are still not well enough understood that we can afford to hamper our reasoning with terms implying a specific function.

The term "spermaceti organ" should be restricted to a distinct fatty body, separated from the other facial structures by a connective tissue wall, as seen in *Physeter*. The free usage of these terms in the past few years has led to considerable confusion as to which animals have a spermaceti organ and which do not.

The *melon* lies approximately in the center of the soft tissue mass of the face (Figures 2, 9). Laterally it grades into the rostral muscle and ventrally into the nasal plug muscle. In some dissections, a sharp distinction can be seen between the dorsal surface of the melon and the adjacent connective tissue of the dermis. This distinction seems to be mainly on the basis of orientation and distribution of blood vessels, the melon being less vascular than the dermis. This is sometimes accentuated upon exposure of a section to the air, the melon and the dermis apparently oxidizing differently. This differentiation continues anteriorly, separating the dermis from the melon. Posteriorly the melon grades into the nasal plug mass, penetrating into the tissue of the right nasal plug.

Litchfield et al. (1973) have demonstrated topographic variation in the lipid content of the melon, while Norris and Harvey (1974) have shown a similar variation in acoustic properties of the melon.

VASCULATURE.—The *vascular supply* of the facial region in *T. truncatus* (as in the other delphinids) is derived from branches of the internal maxillary artery emerging from the infraorbital foramina. Branches from the posterior infraorbital foramina ramify between the layers of the nasal musculature and supply most of the region posterior to the antorbital notch. A bundle of parallel vessels arises from one of the anterior infraorbital foramina, just medial to the antorbital notch, and courses anteriorly on the surface of the maxilla. At intervals these vessels turn dorsally to supply the rostral structures. The facial artery is small and appears to supply only the area around the angle of the mouth and, to a lesser extent, the tissue of the upper lips. There is a prominent vascular system in the superficial fascia over the nasal musculature, which appears to be largely venous. It communicates posteriorly with occipital vessels and laterally with temporal vessels.

None of the facial elements are heavily vascularized, the most prominent vasculature being that of the posterior superficial fascia mentioned above. The melon is markedly avascular, the large vessels seen in its periphery being destined for the skin.

INNERVATION.—The *sensory innervation* of the facial structures is derived from infraorbital branches of the maxillary division of the trigeminal nerve. These emerge onto the surface of the face through the various infraorbital foramina. Posteriorly, large branches of these nerves pass to the nonmuscular structures associated with the nasal passage, particularly the nasal plugs and the deep structures around the vertex. The diverticula do not appear to be heavily innervated, nor does the melon (contra Huber, 1934). Khomenko (1970) reported encapsulated nerve endings in the walls of the diverticula, but did not state that they were particularly abundant. The skin is known to be heavily innervated (Palmer and Weddell, 1964), but the patterns of this innervation could not be determined grossly. Presumably the cutaneous innervation is also derived from the infraorbital branches of the trigeminal nerve, although occipital nerves were seen to extend into the facial area in a fetal *T. truncatus*. There are extensive anastamoses between elements of the facial and trigeminal nerves, particularly between the layers of the nasal musculature near their origins.

So far as is known, all of the *motor innervation* of the nasal muscles is provided by the facial nerve. This nerve passes anteriorly, beneath the orbit, to emerge onto the face through the antorbital notch. The facial nerve is heavily invested with connective tissue throughout its length and is easily mistaken for a tendinous structure. As it passes through the antorbital notch it branches extensively in the dense connective tissue filling the notch. Beyond this point it has a diffuse distribution throughout the layers of the facial muscles.

GLANDULAR STRUCTURES.—Glandular tissue has recently been discovered in the area of the inferior vestibule in *T. truncatus* (Maderson, 1968; Evans and Maderson, 1973). These are small exocrine glands, opening via minute crescentic pores. I overlooked these in my dissections, and it is possible that their distribution throughout the delphinids is more extensive than is now known.

The following descriptions of delphinid genera are based upon comparison with *T. truncatus,* and, in general, only the differences observed are treated in any detail. The genera are treated in an appoximate taxonomic order, with those most similar to *Tursiops* being described first.

Stenella

MATERIALS.—Forty-four individuals of *Stenella attenuata* and *S. longirostris* were dissected, ranging in size from neonates to large adults. Two adult males of *S. coeruleoalba* and one adult male of *S. plagiodon* were also dissected.

The species of *Stenella* examined show very little differentiation from the condition seen in *Tursiops truncatus*, and constitute a relatively homogenous group in their facial anatomy.

NASAL PASSAGES AND DIVERTICULA.—The premaxillary sac in *Stenella* was quite uniform in the species examined, and was similar to that of *T. truncatus* (Figure 24). The only difference noted was a slight increase in the asymmetry of this structure in *S. coeruleoalba.*

The nasal plugs showed little variation in *Stenella,* the right plug always being the larger and having a proportionately larger lateral lip. As with

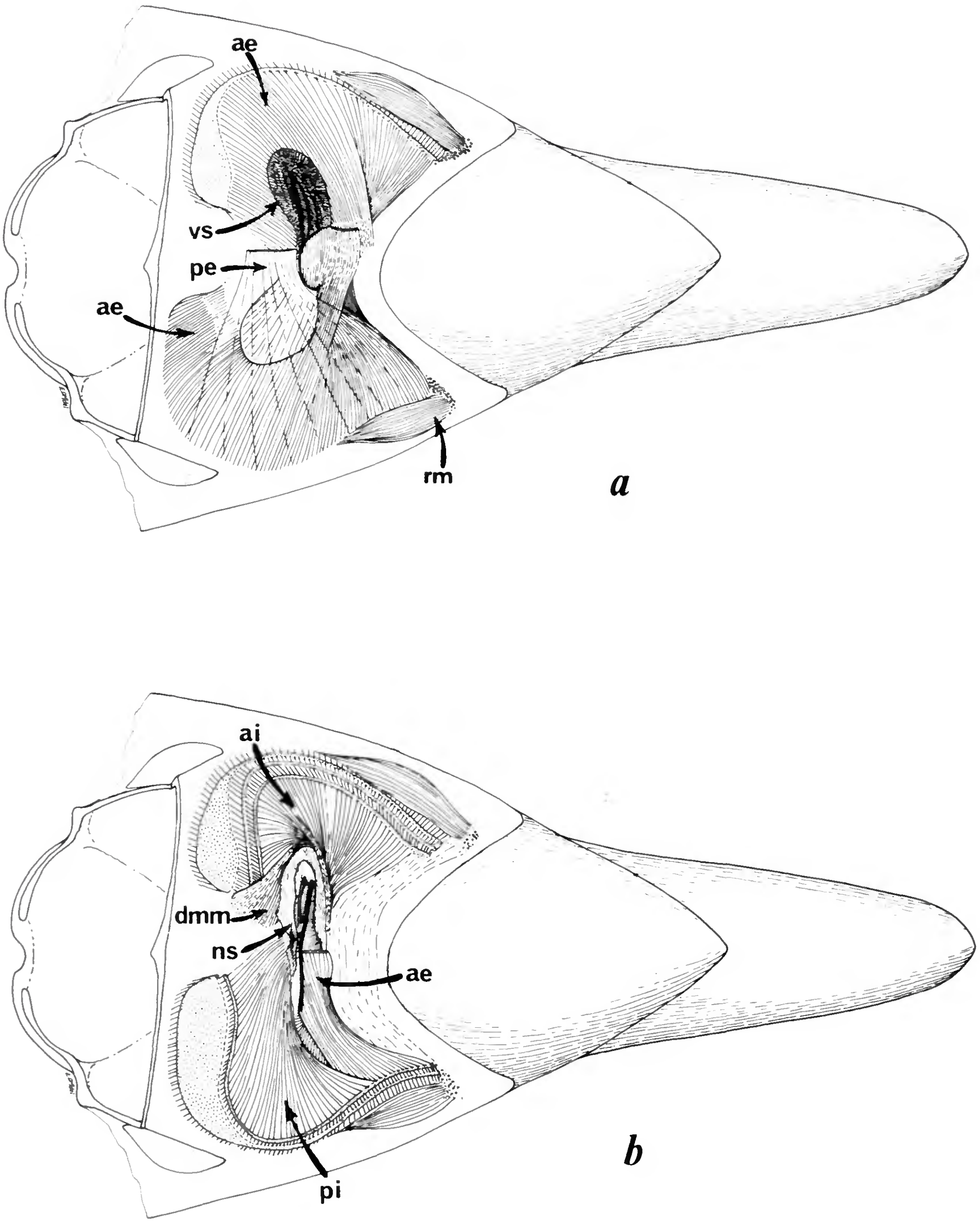

FIGURE 10.—Dorsal views of dissections of the nasal musculature of *Stenella plagiodon* (in each view the structures on the lefthand side are dissected one level below those on the right): *a*, superficial dissection; *b*, deep dissection. (ae=pars anteroexternus, ai=pars anterointernus, dmm=diagonal membrane muscle, i=pars intermedius, ns=nasofrontal sac, pe=pars posteroexternus, pi=pars posterointernus, rm=rostral muscle, vs=vestibular sac.)

a number of characters, this asymmetry was slightly greater in *S. coeruleoalba*.

An accessory sac was present in all of the *Stenella* examined. This sac was quite small, on the order of 5 mm or less in length in all but *S. coeruleoalba*, where it was slightly more than 1 cm long. A posterior branch of the blowhole ligament, passing over the mouth of the accessory sac, was seen in some individuals of all of the *Stenella* species. It was only seen on the left side.

The nasofrontal sac showed some variation in the *Stenella* species. The posterior portions abut against one another at the midline, as in *T. truncatus*. The anterior portions also meet in the midline and actually overlapped by about 1.5 cm in the only specimen of *S. plagiodon* examined. In this instance the right sac lay dorsal to the left. The pigmentation pattern of these sacs is highly variable, and was not seen to fit any particular scheme. The posterior portions are nearly always darkly pigmented, but were light colored in some specimens of *S. attenuata* and *S. longirostris*. The anterior portions are more variable. A common situation was that in which the entire left anterior portion was dark, while the medial portion of the right was unpigmented. In addition to being longer, the right anterior portion was slightly wider than the left, more so in *S. coeruleoalba*.

The vestibular sacs are of moderate size in *Stenella*, the left being somewhat larger than the right in *S. attenuata* and *S. longirostris*. The left sac was also situated more anteriorly than the right in these two species. This was not the case in *S. coeruleoalba* and *S. plagiodon*, where the sacs were roughly equal and both lay slightly more anterior to the nasal passage. The anterior fold of the right vestibular sac was consistently larger than the left in *S. attenuata* and *S. longirostris*, the right usually being 1.0 to 1.5 cm wide, while the left was 0.2 cm or less. The opposite was true in *S. plagiodon*, where the left anterior fold was about 1.5 cm wide, the right 0.8 cm. In *S. coeruleoalba* the right anterior fold was extremely large, 2.0 cm wide, while the left was on the order of 0.2 cm.

MUSCULATURE.—Outside of minor individual variation in the extent of origin of layers of the posterior musculature, and in the relative size of some of these layers, there were no observable differences in the nasal musculature.

The intrinsic musculature of the nasofrontal sac showed no variations within the *Stenella* species, with the exception of being slightly larger in *S. coeruleoalba*.

The diagonal membrane muscle is subject to considerable variation in *Stenella*. It is generally larger on the right side, although the reverse was true in one *S. attenuata*. As it passes ventral to the blowhole ligament, a few fibers may attach to the ligament. There is considerable variation in the extent to which this muscle enters the diagonal membrane. As in *T. truncatus*, it usually does not. However, in one specimen of *S. attenuata* the muscle on the left side extended to the free edge of the membrane, while that on the right did not enter the membrane at all. In another specimen of *S. attenuata* a few of the lateral fibers of both muscles entered the free portion of the membrane. This muscle was extremely large in *S. coeruleoalba*, but did not enter the free portion of the membrane.

OTHER STRUCTURES.—The anterior rostral structures, both the muculature and the melon, showed no noticeable variation throughout the *Stenella* species, nor any appreciable differences from the condition seen in *T. truncatus*.

Delphinus

NASAL PASSAGES AND DIVERTICULA.—The arrangement of the nasal apparatus in *Delphinus delphis* is very similar to that of *Tursiops* and *Stenella*, as shown by Gruhl (1911), Lawrence and Schevill (1956), and Schenkkan (1973). Gruhl's work is particularly useful, as he illustrated the diverticula in a number of individuals, including a fetus.

The vestibular sac is very similar to that of *Tursiops* and *Stenella*, particularly in the presence of a small anterior lobe on the left side.

The nasofrontal sac is virtually indistinguishable from that of *Stenella*, and does not have the lobulations seen on the angle of the right sac in *T. truncatus*. Gruhl's illustration of the nasofrontal sac of a 53.8 cm fetus is of interest, in that it shows a marked asymmetry in the degree of development of the right and left sacs, the right sac developing its anterior portion more rapidly than the left. The accessory sac is similar to that of *T. truncatus*, and is slightly larger than that of all of the *Stenella* species, except *S. coeruleoalba*.

MUSCULATURE.—The musculature appears to be no different from that of *Tursiops*.

OTHER STRUCTURES.—The melon and the rostral structures are similar to those of *Tursiops.*

Lagenorhynchus

MATERIALS.—One juvenile *Lagenorhynchus albirostris* and a juvenile *L. acutus* were dissected.

NASAL PASSAGES AND DIVERTICULA.—The premaxillary sacs of *L. albirostris* differ from those of *Tursiops* and *Stenella* in having a lateral diverticulum on the right side (*lateral premaxillary sac*). This diverticulum opens along the middle two-thirds of the lateral surface of the right premaxillary sac, extends about 1 cm lateral to the edge of that sac, and ends blindly about 1 cm posterior to the posterior margin of its orifice (Figure 14). This structure was either very small or lacking on the left. Nothing similar to this diverticulum has been seen in any of the other dissections, except that of a juvenile *Lagenodelphis hosei.* Schenkkan (1973) did not mention this diverticulum, though he dissected nine specimens of this species. Its presence in the single specimen which I examined might be considered anomolous, were it not also seen in a juvenile *Lagenodelphis hosei.* There was but a trace of it, however, in an adult female *Lagenodelphis hosei,* raising the possibility that it may be a juvenile character which is lost with age. This diverticulum was absent in the single *L. acutus* specimen which I dissected, and is not mentioned in Schenkkan's account of this species. It also seems to be lacking in *L. obliquidens* and *L. obscurus* (Schenkkan, 1973).

The nasofrontal sacs in *L. albirostris* are extremely different from most of the other delphinids. In the specimen examined, these were injected with silastic rubber, so some idea of their distended size was gained. The posterior portion of the nasofrontal sacs is approximately the same size as in *T. truncatus,* but the anterior portion is much larger. The increase in size is confined to the width of the sacs, and the sacs do not overlap one another. In this specimen the anterior portion of the left nasofrontal sac lay on the lateral surface of the nasal plug mass, while that of the right extended onto the anterior surface, crossing the midline. The right sac appeared to be about twice the size of the left, although neither was expanded to its maximum extent. The distension of the sacs was limited more by the adjacent tissues than by the dimensions of the sac itself. Murie (1871) apparently overlooked the nasofrontal sacs in his description of *L. albirostris.* Schenkkan (1973) found the same condition in the *L. albirostris* which he dissected. Hypertophy of the nasofrontal sacs is apparently limited to *L. albirostris,* as those of *L. obscurus* (Gallardo, 1913; Schenkkan, 1973), *L. obliquidens* (Schenkkan, 1973), and *L. acutus* (Schenkkan, 1973) are similar in development to those of *Tursiops.*

The accessory sacs in the specimen of *L. albirostris* which I dissected were relatively large, particularly the right sac, which measured 3 cm long by 1 cm wide. Schenkkan (1973) also noted that these diverticula were large in this species, and described a caudal portion extending posterior to their communication with the inferior vestibule. He noted a similar caudal extension on the right accessory sac in *L. acutus,* though I did not find this in the single specimen which I dissected. The accessory sacs in *L. obliquidens* and *L. obscurus* are essentially similar to those of *Tursiops* (Schenkkan, 1973).

The vestibular sacs of *L. albirostris* presented no pronounced differences from those of *Tursiops.* The anterior folds were large on both sides, that on the right being about 1.5 cm wide, the left 1.0 cm. The folds usually seen in the walls of the vestibular sac were deeper in this specimen than in *T. truncatus,* and some of them seemed to be permanent features (i.e., incapable of distension). Schenkkan (1973) noted that the ventral walls of the vestibular sacs in *L. albirostris* were thickened, which probably correlates with my observations on folding. Schenkkan (1973) described extensive lobulation in the lateral edge of the vestibular sacs in *L. acutus,* and I found a similar condition in the specimen which I dissected. He also noted that their placement was more caudal to the blowhole, which agrees with my dissection. Schenkkan's (1973) specimen of *L. obliquidens* was damaged, but did not appear to present any major differences from *Tursiops.* Schenkkan (1973) noted a reverse asymmetry in the vestibular sacs of *L. obscurus,* the left being larger than the right, though apparently to no great extent, as it is not apparent in his illustration of this species. Gallardo's (1913) comments are too brief to provide a comparison.

MUSCULATURE.—The nasal musculature in *L. albirostris* differed in a few details from that of

T. truncatus. Pe inserted almost entirely across the midline, with only a few fibers attaching to the vertex. There was no discernible *i* on either side. The tendons of insertion of *ae* and *pi* formed more of an aponeurosis than in *T. truncatus,* and were more intimately attached to the connective tissue above the posterior end of the nasal septum. The nasal musculature in *L. acutus* presented no discernible differences from that of *Tursiops.*

The intrinsic muscles, the muscle of the diagonal membrane, and the membrane itself in both species examined presented no differences from those of *T. truncatus.* Nor did the nasal plugs show any unusual features.

OTHER STRUCTURES.—The structures of the rostrum showed a few differences from those of *T. truncatus.* The distinction between the medial and lateral rostral muscles was greater in *L. albirostris.* There was an area of extremely dense connective tissue in the dermis just anterior to the blowhole. The connective tissue in this area is ordinarily slightly denser than in the rest of the dermis, but not as strikingly so as in this specimen.

Lagenodelphis

MATERIAL.—A juvenile male and an adult female of *Lagenodelphis hosei* were dissected.

NASAL PASSAGES AND DIVERTICULA.—The premaxillary sac possessed a small diverticulum on the right side (lateral premaxillary sac) similar to that seen in *Lagenorhynchus albirostris* (Figure 13). This was more pronounced in the juvenile male, hence may be related either to age, sex, or individual variation. Otherwise the premaxillary sacs were similar to those of *Tursiops truncatus.*

The accessory sac was very small on the left, appearing as a slight indentation in the lateral wall of the inferior vestibule. That on the right was quite large, extending 1 cm anterior to the blowhole ligament.

The nasofrontal sacs were similar to those of *T. truncatus.* While the right sac was larger than the left, neither showed any sign of the expansion seen in *Lagenorhynchus albirostris.* The two sacs were darkly pigmented throughout, met anterior to the nasal passage in the juvenile, and overlapped anteriorly by about 1 cm in the adult. The angle of the right sac was slightly lobulated, as in *T. truncatus.*

The vestibular sacs were of nearly equal sizes, the right being possibly a little larger than the left. They did not extend as far laterally as in *T. truncatus,* ending very close to the lateral edge of the nasal passage. The portion of the sacs posterior to the nasal passage was larger than the portion anterior. The anterior fold was quite large on the right, comparable to the condition seen in *Lagenorhynchus albirostris* and *Stenella coeruleoalba.*

None of the deep structures associated with the nasal passage (intrinsic muscles, diagonal membrane and muscle, blowhole ligament, and nasal plugs) were noticeably different from those of *T. truncatus.*

MUSCULATURE.—The nasal musculature of *L. hosei* showed no outstanding differences from that of *T. truncatus. Pe* was well developed and inserted across the midline between the vertex and the nasal passage. Its origin extended further posteromedially than in *T. truncatus,* making it a little more difficult to separate from *ae.* There appeared to be no differentiation of a pars intermedius. The superficial fibers of *ae* had a more anterior orientation than in *T. truncatus,* but this became more medial in the deeper layers. The posterior insertion of *ae* was less well differentiated than in *T. truncatus.*

OTHER STRUCTURES.—The only noticeable difference from *T. truncatus* in the rostral structures was a sharper differentiation of the rostral musculature into medial and lateral portions. The melon showed no unusual features.

Grampus

MATERIALS.—One adult male of *Grampus griseus* was dissected.

NASAL PASSAGE AND DIVERTICULA.—The right premaxillary sac is disproportionately larger than the left in *G. griseus* (Figure 25). This increase has taken place in the posterolateral portion of the sac, where the additional space is occupied by an unusually large lateral lip of the nasal plug. The lateral lip on the right side is about 2 cm wide, while that of the left side is only 0.5 cm. There are no lateral diverticula from the premaxillary sac, and, aside from the lateral lip, the nasal plugs were as in *Tursiops truncatus.*

The accessory sac was somewhat larger than that of *T. truncatus,* the right one being 2.0 cm long, the left 1.5 cm long. None of the previous workers

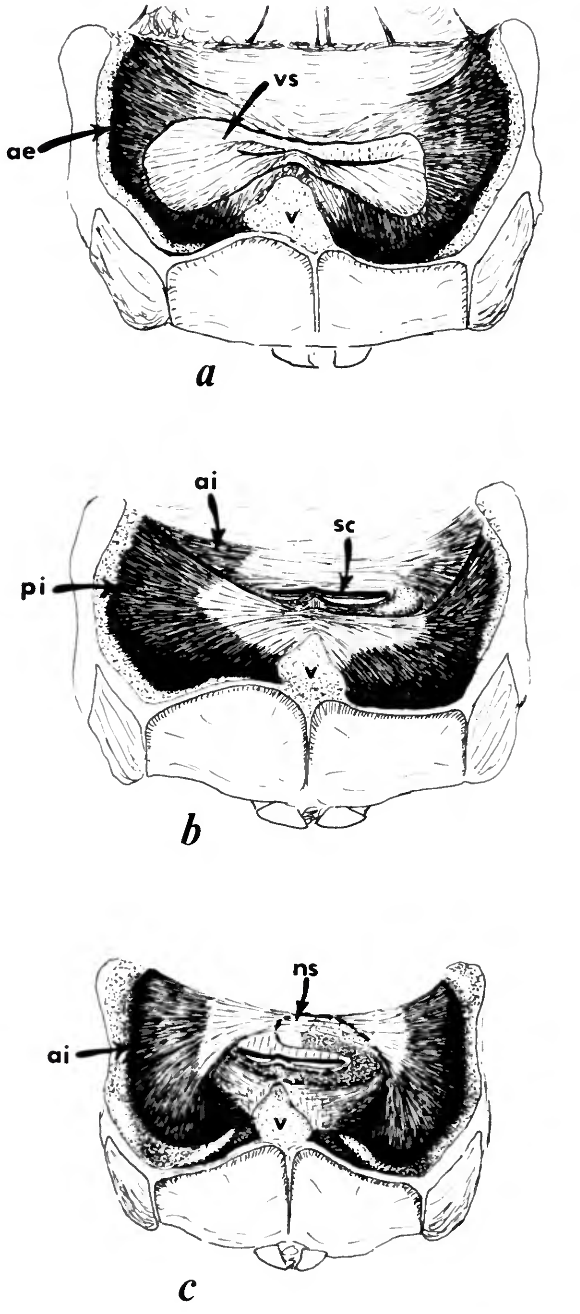

FIGURE 11.—*Grampus griseus* (dissection of the nasal musculature, dorsal views): *a*, superficial muscles removed to level of vestibular sacs; *b*, ae removed; *c*, pi removed. (ae=pars anteroexternus, ai=pars anterointernus, ns=nasofrontal sac, pi=pars posterointernus, sc=spiracular cavity, v=vertex, vs=vestibular sac.)

(Murie, 1870; Bouvier, 1889; Danois, 1911) mention a structure which could be interpreted as this sac.

The nasofrontal sacs present some striking differences from those of *T. truncatus* (Figures 11, 25). The posterior portions of the sacs are similar to those of *T. truncatus*, but the anterior portion of the right sac is considerably larger, though not nearly so much as that of *Lagenorhynchus albirostris*. The greatest difference is seen on the left side, where the anterior portion was lacking, the posterior portion ending about 1 cm lateral to the edge of the nasal passage. Murie (1870) described essentially the same situation in the specimen of *G. griseus* examined by him. His illustration of the diverticula, however, appears to be slightly in error, and gives the impression that the anterior portion of the right nasofrontal sac opens into the inferior vestibule independent of the posterior portion. This gave rise to Bouvier's (1889) mention of a "*sac facial impair*," which added to the confusion surrounding the nasal diverticula.

The vestibular sac of *G. griseus* was unusual in that the left was larger than the right by about 10%, and extended farther laterally (Figure 25). Both vestibular sacs lay more posterior to the nasal passage than in *T. truncatus*. The anterior folds were not particularly unusual, that of the right side being about 0.8 cm wide, while that of the left was barely discernible.

MUSCULATURE.—The intrinsic musculature of the nasofrontal sac was slightly larger than in *T. truncatus*, and its gradation into the lateral portion of the nasal plug muscle was more clearly seen. Along its posteromedial origin some of its fibers interdigitated with fibers of the diagonal membrane muscle. Otherwise the two were quite distinct. The diagonal membranes were of approximately equal size, and neither muscle reached the free edge of the membrane. Murie (1870) seems to have been the only author to notice the difference between the intrinsic muscle and the muscle of the diagonal membrane. The muscle labeled "1" in his figure 1 appears to represent the latter muscle, although he did not discern its insertion into the diagonal membrane.

The pars posteroexternus of *G. griseus* differs markedly from that of *T. truncatus* (Figure 11). It originates from the posterior fourth of the supraorbital process, runs posteromedially along the temporal crest, and inserts upon the lateral portion of the nuchal crest. This muscle was about twice as large on the left as it was on the right. The fibers of *pe* were heavily invested with fat and connective tissue, giving an appearance unlike the rest of the posterior nasal musculature. On its deep surface it was gradational with *ae*. A small superficial slip of muscle on the anterior surface of *ae* may have represented a poorly differentiated *i*. *Pi* was unusual in that there was a deep posterior portion which originated from the lateral surface of the vertex, medial and deep to the posterior origin of *ai*. Normally *pi* originates entirely posterior and superficial to *ai*.

The rostral muscles were considerably different from those of *T. truncatus*. They were larger than in that species, particularly the medial portion (Figure 12). The differentiation between the lateral and medial portions was sharper in *G. griseus* than in *T. truncatus*. This differentiation is associated with a strong crest along the lateral edge of the maxilla, which marked the separation of the two muscle bodies.

OTHER STRUCTURES.—The melon of *G. griseus* is much larger than that of most delphinids (Figures 12, 25). This is particularly true in the posterolateral portions, producing a slightly bilobate, bulbous forehead. The expansion of the forehead is largely due to an increase in the size of the melon, with little corresponding increase in the heavy dermal connective tissue external to it. The result is a very soft mass of tissue, in marked contrast to the other bulbous-headed genera which I have examined.

Aside from some of the points mentioned above, this description agrees with that of Murie (1870). Bouvier (1889) merely compiled data from earlier literature. The description of a 125 cm fetal *G. griseus* by Danois (1911 is confused with regard to the nasal diverticula. He illustrated what appears to be the posterior portions of both nasofrontal sacs, and shows nothing which could be an anterior portion. This might be due to the stage of development of the specimen, although it was relatively large. It will be recalled that the anterior portion of the right nasofrontal sac was well developed in a 53.8 cm fetus of *Delphinus delphis* described by Gruhl (1911).

There is some confusion introduced into the literature by Murie's (1870, fig. 1) illustration of the "maxillary sacs" as lying deep to the nasofrontal

FIGURE 12.—*Grampus griseus*: *a*, sagittal section of the rostral structures, superficial dissection of the nasal musculatue, oblique view; b, parasagittal section of the rostral structures, same view as above, 5 cm lateral to above section; *c*, transverse section of rostral structures at level of antorbital notch. (ae=pars anteroexternus, dct=dermal connective tissue, i=pars intermedius, m=melon, pe=pars posteroexternus, r=rostrum, rm=rostral muscle, rm-l=lateral portion of rostral muscle, rm-m=medial portion of rostral muscle; heavy lines indicate principal orientation of connective tissue fibers in the melon.)

sacs. From this they could be interpreted as being the accessory sacs. Murie also mentioned that the nasofrontal sac opened into the maxillary sac, which would further support this conclusion. However, in his description of *L. albirostris* (1871), the "maxillary sac" is clearly equivalent to the vestibular sac. Danois (1911) follows Murie in his illustration ("inspire de Murie") and shows the "*sacs maxillaires*" as lying deep to the nasofrontal sacs. I am of the opinion that the maxillary sacs are equivalent to the vestibular sacs in both Murie's and Danois' accounts, and that both were in error as to their position. This seems more likely than that both of them had missed the large vestibular sacs and were describing the accessory sacs instead. Further confusion arose as a result of Danois' labeling the spiracular cavity (bony nasal passages) of Murie as spiracular sacs, and describing them as though they were diverticula. It is clear that much of this derives from Danois' misunderstanding of Murie's illustration.

ORCININAE

Orcinus

MATERIALS.—One large adult male and an adult female of *Orcinus orca* were dissected.

NASAL PASSAGE AND DIVERTICULA.—The premaxillary sacs of *O. orca* show no unusual features, and, if anything, are relatively small. The diagonal membrane of the right is slightly larger than that on the left.

The accessory sacs are small, relative to the size of the animal. The right sac was about 3 cm long, the left about half that size.

The anterior portion of the right nasofrontal sac was 2–3 times the diameter of the left. The posterior portions of the nasofrontal sacs were not notably larger in diameter than the left anterior portion and were considerably smaller than the right. Schenkkan (1973) stated that the posterior portions were larger in diameter than the anterior

FIGURE 13.—*Orcinus orca*: *a*, nasal musculature, dorsal view of the superficial dissection; *b*, nasal musculature, dorsal view of dissection to level of vestibular sac. Dorsal wall of vestibular sac removed. (ae=pars anteroexternus, npm=nasal plug muscle, pe=pars posteroexternus, sc=spiracular cavity, tm=temporal muscle, v=vertex, vs=vestibular sac.)

in his material. He also noted that their terminations did not reach the mesial axis of the head, whereas they met anteriorly in both of my specimens. Gruhl (1911) noted that the anterior portions of the nasofrontal sacs developed later than the posterior in a series of *Delphinus delphis* which he examined. Thus the differences between my results and those of Schenkkan may merely reflect age differences.

The vestibular sacs lay considerably posterior to the nasal passage, quite different from their situation in *Tursiops* and *Stenella.* Schenkkan (1973) stated that they lay lateral to the blowhole, although his illustration shows them lying posterior, similar to the situation in my dissections. They were subequal in size, the left being slightly larger. There was a small anterior fold on the left and a very large one (2 cm deep) on the right.

MUSCULATURE.—The nasal musculature of *O. orca* exhibited a few peculiarities. The pars posteroexternus was well defined, inserting across the midline via a series of well-defined tendons (Figure 13), instead of the aponeurosis seen in *T. truncatus.* There was no pars intermedius, nor were there any fibers of *ae* arising posterior to the blowhole and inserting anterior to it. This is in marked contrast to the rest of the delphinids. The posteromedial fibers of *ae* inserted into the heavy posterior wall of the nasal passage, instead of into the blowhole ligament. However, as they were heavily intertwined with the posteromedial fibers of *pi* which did insert upon the blowhole ligament, the functional insertion was unchanged.

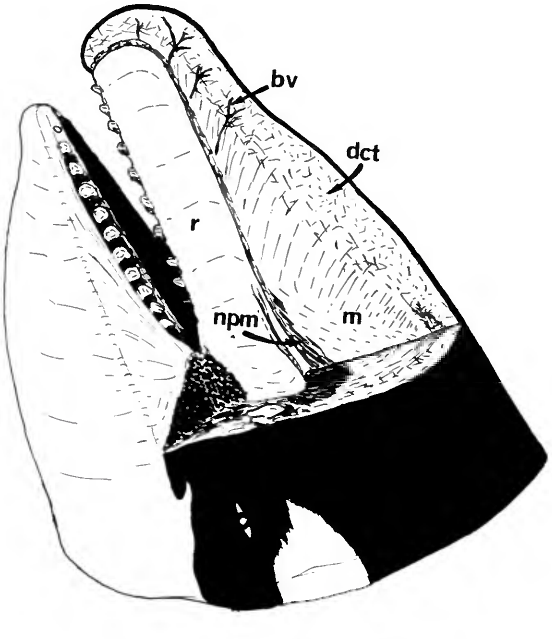

FIGURE 14.—*Orcinus orca,* sagittal section of rostral structures. (bv=blood vessel, dct=dermal connective tissue, m=melon, npm=nasal plug muscle, r=rostrum.)

The anterior portion of the intrinsic musculature ran diagonally across the dorsal surface of the nasofrontal sac, but assumed a more parallel course, grading into the rest of the muscle on the ventral surface. The diagonal membrane muscle was continuous posteriorly with the intrinsic muscle. In the large male the diagonal membrane muscle did not enter the free portion of the membrane, but did in the female.

The nasal musculature of *Orcinus* is generally similar to that of *Tursiops,* and shows no particular resemblance to *Phocoena,* as implied by Schenkkan (1973).

OTHER STRUCTURES.—The rostral structures in *O. orca* were relatively small (Figure 14). The medial and lateral rostral muscles were well differentiated, the latter entering the lips more than in other delphinids. The melon was small and poorly differentiated. Its entry into the nasal plugs was strongly asymmetrical, showing a clear fatty area on the right side.

Pseudorca

MATERIALS.—An adult male and an adult female of *Pseudorca crassidens* were dissected.

NASAL PASSAGES AND DIVERTICULA.—*Pseudorca crassidens* is similar to *Tursiops truncatus* in the anatomy of the facial structures. The premaxillary sacs and nasal plugs present no unusual features, nor do the nasofrontal sacs (Figures 25). The right accessory sac is about 2 cm long, the left is much smaller. A small posterior branch of the blowhole ligament was seen on the right side. The vestibular sacs lie mostly posterior to the nasal passage, and are relatively small.

MUSCULATURE.—The pars posteroexternus of the nasal musculature was poorly differentiated. There was, however, a large pars intermedius. The rest of the musculature was similar to that of *T. truncatus.*

The rostral muscles are relatively small, the lateral rostral muscle entering into the lips more than in most delphinids.

OTHER STRUCTURES.—The melon is surprisingly small, the bulk of the facial mass being made up of coarse dermal connective tissue in a fatty matrix. There is a well-defined connection between the melon and the right nasal plug.

A moderate degree of sexual dimorphism was observed in the shape and size of the forehead in *Pseudorca* (Figure 15). In the male the fatty connective tissue anterior to the melon extended farther anteriorly than in the female. No difference could be seen in the melon, which is not well-defined in this species. A similar situation is seen in the illustrations of a saggital section of the forehead tissues of a male *Pseudorca* presented by Richard (1936, pl. VI: fig. 10). A comparable situation exists in *Globicephala*, where the fatty connective tissue of the forehead is more extensive in the adult males than in the females.

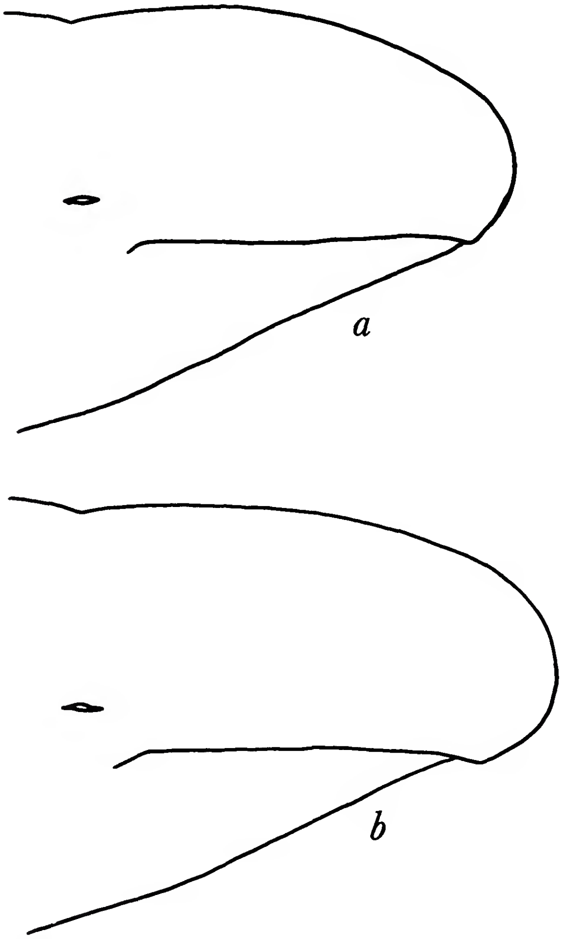

FIGURE 15.—*Pseudorca crassidens*, lateral views of the external appearance of the heads, showing the degree of sexual dimorphism in external head shape: *a*, female; b, male.

Globicephala

MATERIALS.—A large adult male and a neonate of *Globicephala melaena* were dissected.

NASAL PASSAGES AND DIVERTICULA.—The premaxillary sacs and nasal plugs of *G. melaena* are similar to those of *Tursiops truncatus*, as is the diagonal membrane.

The accessory sac on the right side is extremely large, 4 cm long and 2 cm wide (Figures 16, 24), while that of the left side is about 1 cm long by 1 cm wide.

The angle of the right nasofrontal sac in *G. melaena* is extremely unusual (Figure 16). There is a large lateral sacculation, which, when opened, contains a series of trabeculea. These trabeculae are formed by invaginations of the lateral wall of this diverticulum containing slips of the intrinsic musculature. This may allow the intrinsic musculature to compress this sacculation without affecting the rest of the diverticulum. The anterior portion of the right nasofrontal sac is slightly expanded, and is unpigmented in its medial half. The anterior portions of the two sacs abut against one another. The posterior portion of the left nasofrontal sac has an elongate posterior sacculation along its posterodorsal surface. Internally this sacculation is separated from the rest of the sac by a fold of epithelium.

The vestibular sacs are roughly equal in size. They extend a short distance anterior to the nasal passage, where they slope into the anterior lip of the blowhole. Their greatest extent is posterolateral to the nasal passage. The anterior folds are well developed on both sides, the cleft beneath them being about 1 cm deep. The anterior fold overhangs the slit of the nasal passage by 1.8 cm on the left and 1.5 cm on the right. *Stenella plagiodon* was the only other delphinid in which the left anterior fold was larger than the right.

MUSCULATURE.—The general impression obtained from a dorsal view of the nasal musculature of *G. melaena* is that it has been anteroposteriorly compressed (Figure 17). There is a well-developed *pe*, which originates from the posterior third of the supraorbital process and inserts across the midline without attaching to the vertex. The pars intermedius is larger than in *T. trurcatus* and the other delphinids, apparently having incorporated more of the underlying fibers of *ae* into itself. Both *pe* and *i* are heavily invested with fat and connective tissue. *Ai* and *pi* are closely related posteromedially, where they both originate in the fossa lateral to the vertex. The deep posteromedial fibers of *ae* grade into *pi* with no perceptible break. There were several well-differentiated muscle fasciculi in this zone of intergradation, giving the appearance of a series of separate muscles interposed between the fibers of *ae* and *pi* (Figure 17). The tendon of insertion of *pi* is attached to the connective tissue above the posterior end of the nasal septum.

The diagonal membrane muscle is well developed, but does not enter the free portion of either

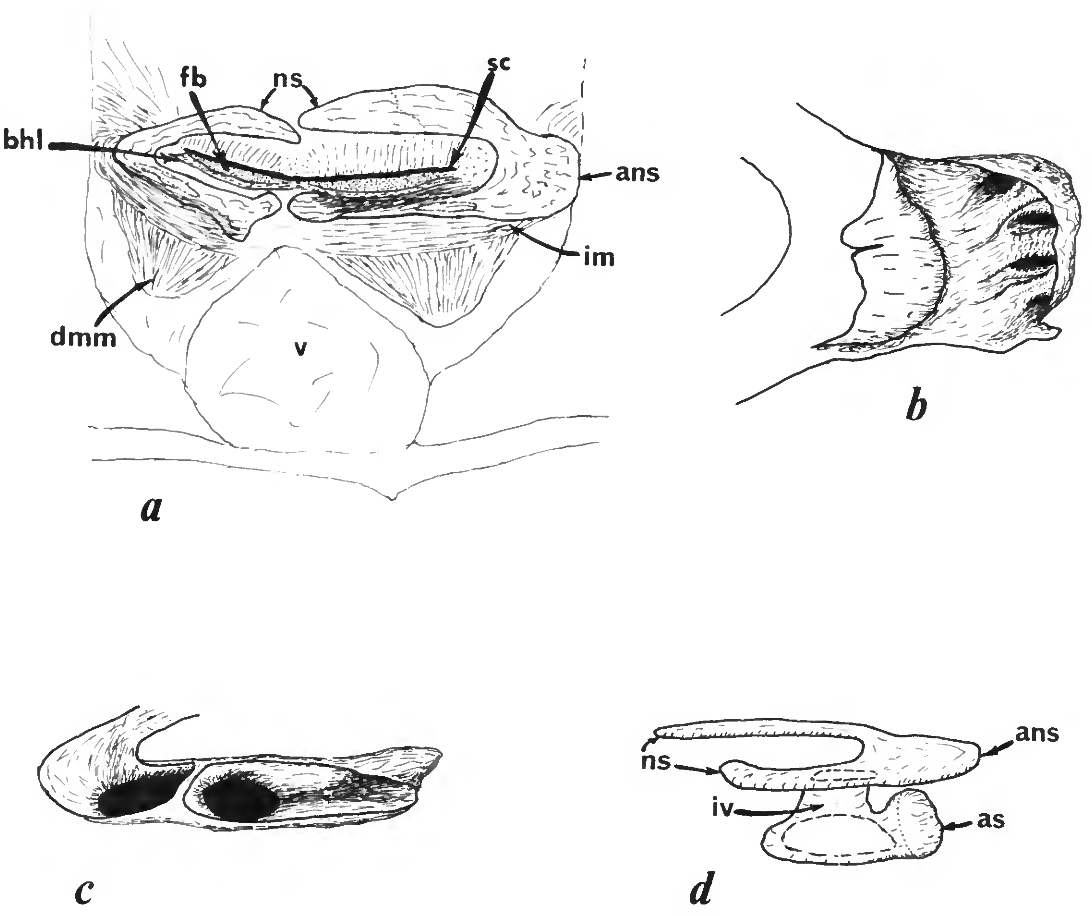

FIGURE 16.—*Globicephala melaena*, nasal diverticula: *a*, dorsal view of nasofrontal sacs and associated structures; *b*, dorsal view of the angle of the right nasofrontal sac, medial portion of the dorsal wall of the sac reflected to show the internal trabeculae; *c*, dorsal view of the posterior portion of the left nasofrontal sac, dorsal wall removed to show the internal partitioning of this portion of the sac; *d*, posterodorsal view of the right nasofrontal sac and associated diverticula. (ans=angle of nasofrontal sac, as=accessory sac, bhl=blowhole ligament, dmm=diagonal membrane muscle, fb=yellow fat body, im=intrinsic muscle of nasofrontal sac, iv=inferior vestibule, ns=nasofrontal sac, sc=spiracular cavity, v=vertex.)

membrane. The intrinsic musculature of the nasofrontal sacs is also well developed but, aside from entering the trabeculae of the angle of the right sac, offers nothing apart from the usual delphinid condition.

The rostral muscles in *G. melaena* are sharply differentiated into lateral and medial portions. They are not unusually large, particularly in relation to the size of the melon, and are not as large relative to the size of the rostrum as in *Grampus*.

Other Structures.—The melon in *G. melaena* is larger than that of any other delphinid examined. It extends dorsally to a level above the vertex, and anteriorly about three quarters of the length of the rostrum (Figures 18, 24). External to the melon is a layer of fatty tissue containing numerous large connective tissue bundles, similar to the condition seen in *Pseudorca crassidens*. Some of these appear to be derived from the rostral muscle, others from the dermis. There is an area of extremely dense connective tissue in the dermis just anterior to the blowhole, as noticed in *Lagenorhynchus albirostris*.

The melon does not pervade the nasal plug muscle as much as it does in the other delphinids. The dorsal surface of the nasal plug mass was uniformly muscular, with no sign of the asymmetrical invasion of the melon usually seen on the right side. *Cephalorhynchus* is the only other delphinid in which this is known to be the case.

As is generally known, there is sexual dimorphism in the shape of the head in *Globicephala* (Figure 19), with the mass of forehead tissue in adult males being larger and projecting farther anterodorsally than in females. As I was only able to examine an adult male, I was unable to determine whether or not this was reflected in the internal structure of this area. I would expect that, as was the case in *Pseudorca*, this dimorphism is limited to an expansion of the fatty connective tissue of the dermis and does not involve the melon. So far as I have been able to determine, *Pseudorca* and *Globicephala* are the only delphinids showing sexual dimorphism in the facial region.

STENINAE

Steno

Materials.—A young male *Steno bredanensis* was dissected. Additional information on this species is available from Purves (1967).

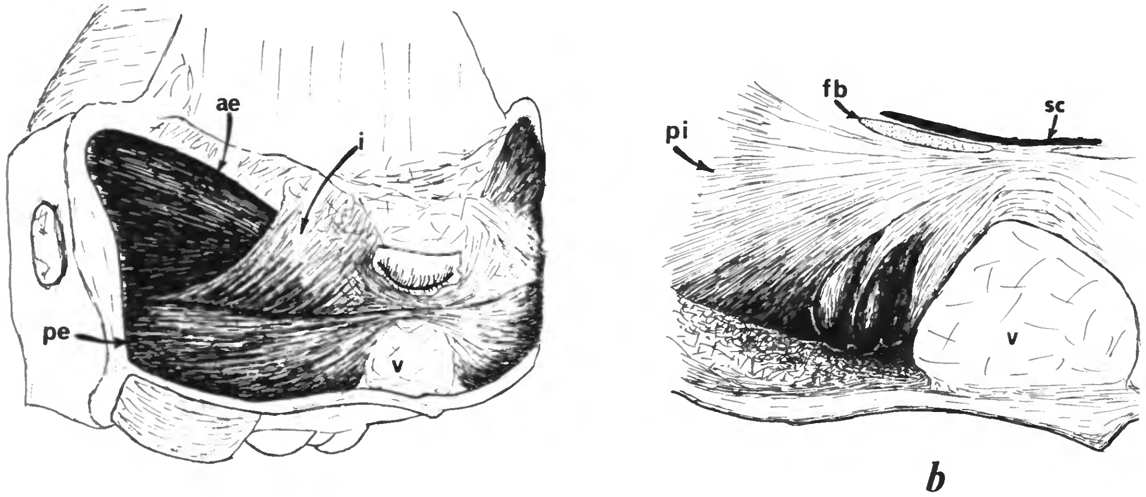

Figure 17.—*Globicephala melaena*, dissections of nasal musculature: *a*, superficial musculature, oblique posterodorsal view; *b*, deep dissection, fasciculi of pi on its posteromedial surface, dorsal view. (ae=pars anteroexternus, fb=fat body, i=pars intermedius, pe=pars posteroexternus, pi=pars posterointernus, sc=spiracular cavity, v=vertex.)

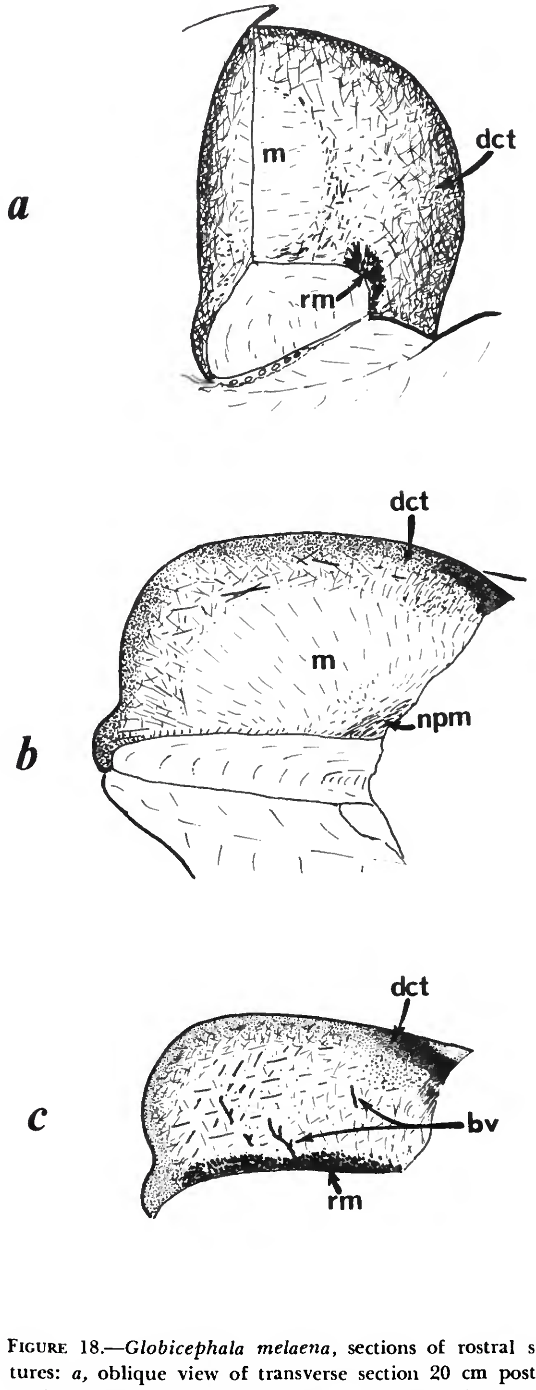

FIGURE 18.—*Globicephala melaena*, sections of rostral structures: *a*, oblique view of transverse section 20 cm posterior to tip of rostrum; *b*, sagittal sections; *c*, parasagittal section, 10 cm lateral to above section. (bv = blood vessels, dct = dermal connective tissue, m = melon, npm = nasal plug muscle, rm = rostral muscle).

NASAL PASSAGE AND DIVERTICULA.—There was a small sacculation on the anterior end of the right premaxillary sac in the specimen when I dissected, but none on the left. This was not mentioned in Purves' (1967) account, and I suspect that it was a developmental anomoly. Otherwise the premaxillary sacs present no unusual features.

The accessory sacs were similar to those of most of the other delphinids, the right being about 2.4 cm long by 1 cm wide, while the left was only about half that size. In both the text and his

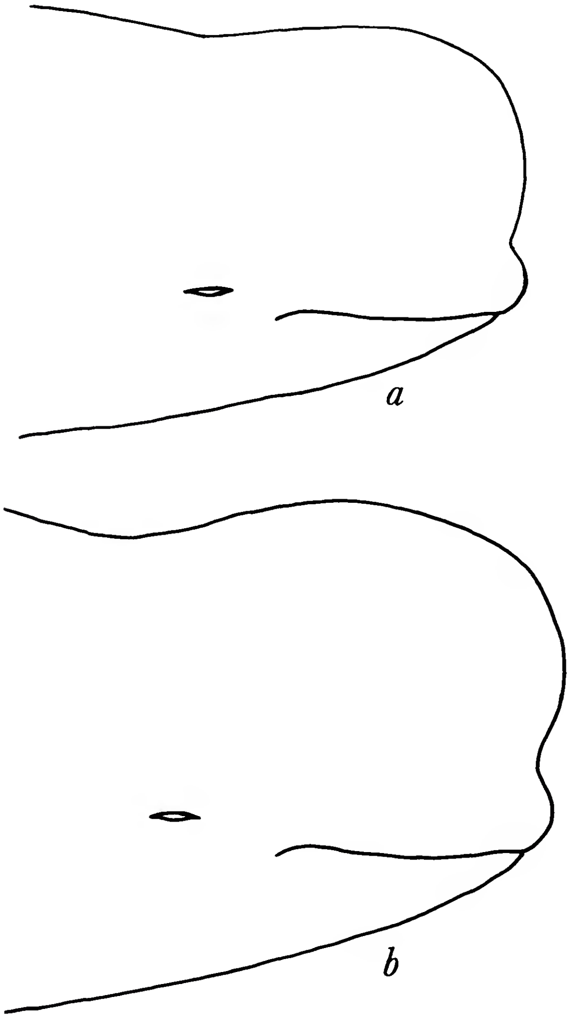

FIGURE 19.—*Globicephala melaena*, lateral views of the external appearance of the heads, showing the degree of sexual dimorphism in external head shape: *a*, female; *b*, male.

figures, Purves (1967) indicated that the accessory sacs formed a communication between the premaxillary and nasofrontal sacs. There has been consistent confusion in the literature over the relationship of these diverticula, and this mistake apparently derives from a misunderstanding of the descriptions of Lawrence and Schevill (1956).

The nasofrontal sacs are similar to those of *Tursiops*, although the angles of both sacs were more lobulated in *Steno*, reminiscent of the condition seen in *Globicephala melaena*, though not nearly as well developed as in that species. The lobulations of the nasofrontal sac were slightly trabeculate when opened, and a few muscle fibers were seen in the larger trabeculae.

The vestibular sacs were subequal, the right being slightly larger than the left, and were somewhat smaller than in most delphinids. There were no indications of anterior lobes on either of the vestibular sacs.

MUSCULATURE.—The nasal musculature of *S. bredanensis* is quite similar to that of *Tursiops*, with only a few minor differences seen in the single specimen examined. *Pe* was very thin and difficult to define, and there was no trace of *i*. Both of these, however, are variable in other delphinids. The rest of the nasal musculature presented no differences from the condition seen in *Tursiops*. Purves (1967) illustrated the nasal musculature, but did not describe it in any detail. However, his illustrations are in agreement with my dissections.

OTHER STRUCTURES.—The melon was similar in development to that of *Tursiops*, and, as in most of the delphinids, entered asymmterically into the right nasal plug. Purves (1967) described an intrinsic muscle of the premaxillary sac, which I was unable to separate from the nasal plug muscle. The diagonal membrane was similar to that of other delphinids, with a moderately developed diagonal membrane muscle which did not appear to enter the free portion of the membrane. The deep structures associated with the blowhole ligament were similar to those of *Tursiops*.

Sotalia

Schenkkan (1972, figs. 1, 2) illustrated the nasal diverticula in *Sotalia guianensis*, and later (Schenkkan, 1973) gave a brief decription of the facial anatomy of this species. The following discussion is based primarily upon his illustrations in the earlier paper.

NASAL PASSAGE AND DIVERTICULA.The degree of asymmetry seen in the premaxillary sacs as shown in Schenkkan's (1972) figure is comparable to that of *Grampus*, and is greater than that seen in other delphinids. The accessory sacs are moderately developed and situated similar to those of other delphinids, as are the nasofrontal sacs. The vestibular sacs, as shown in the earlier paper, are remarkably large, particularly the right sac, which appears to be between two and three times as large as the left. However, in a later paper (Schenkkan, 1973) they are shown as much smaller and nearly symmetrical.

Schenkkan's (1972, fig. 2) mesial view of the nasal diverticula of the right side shows a peculiarity not seen in any other odontocete. This illustration clearly shows a passage originating from the posterolateral edge of the premaxillary sac, just anterior to the accessory sac, and running dorsally to connect with the medial side of the vestibular sac. Unfortunately the text of this paper contains no reference to the nasal diverticula of this species, no information on this structure is given in the labeling of the figure, and the brief description in his later paper (Schenkkan, 1973) contains no information on this structure, so one is at a loss to interpret its significance.

MUSCULATURE.—Schenkkan's (1973) comment that the nasal musculature in *Sotalia guianensis* "was comparable with the situation found in *Delphinus delphis*" does not provide a basis for comparison, but gives no reason to believe that it is any different from the situation seen in *Steno*.

OTHER STRUCTURES.—No data are available for other features of the facial anatomy of *Sotalia*.

CEPHALORHYNCHINAE

Cephalorhynchus

MATERIALS.—A young male (110 cm) *Cephalorhynchus hectori* was dissected. Schenkkan (1973) described a dissection of another male (118 cm) of the same species.

NASAL PASSAGE AND DIVERTICULA.—The premaxillary sacs were relatively short as compared to *Tursiops*. The dorsomedial wall of the left premaxillary sac was produced into a saccular fold, which may have been an individual abnormality, as Schenkkan (1973) noted nothing unusual in this area on his specimen.

The diagonal membranes were small and about the same size on both sides. The accessory sacs, as noted by Schenkkan (1973), were relatively large, with the right sac approximately twice the size of the left (2.6 cm long as opposed to 1.4 cm on the left). There was a small posterior branch of the blowhole ligament passing dorsal to the accessory sacs on both sides.

The anterior portions of the nasofrontal sacs were well developed and were unique among delphinids in that the left sac was much larger than the right. Approximately half of the anterior portion of the left nasofrontal sac extended across the midline, where it was partly overlain by the right. In their relaxed condition in this frozen specimen, the left sac appeared to occupy about twice the area of the right. The angles of both sacs were faintly sacculated, reminiscent of the situation seen in many other delphinids and found in *Globicephala melaena* to an extreme degree. Schenkkan (1973) also noted the reverse asymmetry of the anterior portions of the nasofrontal sacs.

The vestibular sacs were superficially symmetrical and not unusual in size. They lay posterior to the blowhole, similar to the condition seen in *Orcinus*. There walls were heavily wrinkled, indicating considerable distensibility, as in other delphinids. There was a pronounced anterior lobe of the vestibular sac on the left and a somewhat smaller one on the right. The left anterior lobe entered the main portion of the vestibular sacs through a slit just dorsal to the anterior fold, while the right appeared to be an extension of the anterior fold itself. A small, shallow fold just dorsal to the right anterior fold may be the actual homologue of the left anterior lobe of the vestibular sac. Schenkkan (1973) did not note these lobes of the vestibular sacs in his specimen. A similar, though much less pronounced, situation was seen in *Tursiops* and some of the *Stenella*, where there was a slight development of an anterior lobe on the left.

MUSCULATURE.—In general the musculature was similar to that of other delphinids. There was a well-developed *pe*, but no indication of *i* on either side. The portion of *ae* overlying the vestibular sacs was thinner than in *Tursiops* or *Stenella*, but was otherwise similar. The intrinsic musculature of the nasofrontal sacs gave more appearance of being continuous with the nasal plug muscle than it did in *Tursiops* or *Stenella*.

The diagonal membrane muscle was difficult to define, but appeared to enter the membrane to a slight extent. The lateral and medial rostral muscles differed in fiber orientation more than in *Tursiops* or *Stenella*.

OTHER STRUCTURES.—The melon was of moderate size, and was unusual in not extending into the right nasal plug as in most delphinids. The nasal plugs were remarkably asymmetrical, the lateral lip of the right nasal plug being twice as wide (6 mm) as the left (3 mm).

Schenkkan (1973) described a "small bulbous, translucent structure (diameter about ¾ cm) consisting of a tough, unstructurated gelatinous substance" between the medial terminations of the caudal portions of the nasofrontal sacs. I found no trace of such a structure and suppose that this was an individual abnormality, possibly a parasitic cyst, such as the cestode cysts sometimes encountered in small odontocetes.

LISSODELPHINAE

Lissodelphis

Schenkkan (1973) provided a description of the facial anatomy of *Lissodelphis borealis*, upon which the following discussion is based.

NASAL PASSAGE AND DIVERTICULA.—The premaxillary sacs were relatively small, but presented no notable peculiarities. The accessory sacs were well developed and the right sac had a posteriorly directed extension. The nasofrontal sacs were illustrated as being substantially larger than in *Tursiops*, and the angles of the nasofrontal sacs were sacculated, though it is not clear to what extent. The vestibular sacs appear to be relatively larger than in any of the other delphinids, and are situated posterior to the blowhole. Schenkkan's (1974) observation that the nasal passages were displaced caudally as a result of extensive development of the melon is difficult to visualize, and is not supported by his illustrations.

MUSCULATURE.—Schenkkan (1973) commented that "Due to the caudad displacement of the nasal passage, the direction of all muscle fibers was nearly vertical and separation into various layers was therefore fairly difficult." If this is in fact the case, it seems very different from the other delphinids.

OTHER STRUCTURES.—Schenkkan (1973) stated that the melon was relatively large in *L. borealis*, though this is difficult to imagine when considering the external shape of the head.

PHOCOENIDAE

Phocoena, Phocoenoides, Neophocaena

The members of the family Phocoenidae present a number of consistent differences from the Delphinidae, and appear to constitute a very distinct group on the basis of facial anatomy. The nasal apparatus of *Phocoena phocoena* has been described more frequently than that of any other cetacean (von Baer, 1826; Sibson, 1848; Rawitz, 1900; Gruhl, 1911; Moris, 1969; Schenkkan, 1973). Howell (1927) gave a brief description of the nasal complex in *Neophocaena*, and Ridgway (1966) described the vestibular sacs in *Phocoenoides dalli*. Yet it still remains to be described in detail as a functional system. I do not intend to do so at this point, but rather to present a brief description for comparison with the delphinid nasal system. This is based upon the extensive literature listed above and upon my own limited dissections of *Phocoena* and *Phocoenoides*.

MATERIALS.—One adult of *Phocoena phocoena* and one of *Phocoenoides dalli* were dissected.

NASAL PASSAGE AND DIVERTICULA.—The premaxillary sac is relatively small in the phocoenids, as indicated both by my dissections and the literature accounts. The prenasal area of the skull differs markedly from that of the delphinids, in the presence of a strong premaxillary emminence, upon which the premaxillary sac lies.

Schenkkan (1971) found that the accessory sac was small or lacking in the specimens of *Phocoena phocoena* which he examined. This sac had not been reported in the earlier literature, and I was able to find only a very small one on the right side in *Phocoenoides dalli*.

The deep portions of the phocoenid nasal apparatus are more complicated than those of the delphinids, and warrant much more study.

The nasofrontal sacs are large in the phocoenids (Gruhl, 1911; Gallardo, 1913; Howell, 1927; Schenkkan, 1973) and are situated as in the delphinids. I found the anterior portion of the nasofrontal sac in *Phocoenoides dalli* to be lined with a thick, nonpigmented, trabeculate epithelium. This had a glandular appearance, but has not been examined histologically. The illustrations of Gruhl (1911) and Moris (1969) suggest that this condition is also present in *Phocoena phocoena*.

The posterior portion of the deep nasal apparatus is complicated by a diverticulum which arises from the inferior vestibule and passes dorsally, posterior to the nasofrontal sac. This is the "*hintere höhle*" of Gruhl (1911), the "*sac nasal posterieur*" of Moris (1969), and the "*hinter unter höhle*" of von Baer (1826). Schenkkan (1973) refers to this diverticulum as part of the nasofrontal sac, but does not describe it in detail.

The most striking feature of the phocoenid nasal apparatus is the large vestibular sac, which has been thoroughly described in the literature cited above. This diverticulum is on the order of twice the size of those seen in the delphinids. The ventral wall is thrown into a series of folds, 0.5 to 1.0 cm wide, aligned perpendicular to the long axis of the body. The walls of these folds are composed of a thick layer of connective tissue, fixing them in place and precluding distension of the ventral wall. The middle fold of this series is the deepest, clearly dividing the ventral wall into two halves. This fold also appears to form the principal communication with the nasal passage. The vestibular sac is completely enclosed by an intrinsic muscle, and is free to move within the layers of the pars anteroexternus. This situation appears to be common to all three of the phocoenid genera, and is not aproached by any other cetacean.

MUSCULATURE.—The nasal musculature of phocoenids is somewhat different from that of delphinids when examined in detail, yet is still arranged according to the same general plan. The pars posteroexternus appeared to be absent in my dissections. Gruhl's (1911) account of this musculature indicated a similar condition in *Phocoena phocoena*. The pars anteroexternus is arranged in essentially the same manner as in the delphinids. Within this layer, however, a very distinct difference is seen in the structure of the vestibular sac, as described above. The fibers of the musculature of the vestibular sac are oriented perpendicular to those of *ae*. The muscle of the vestibular sac is attached to the maxilla anteriorly, above the surface of the vestibular sac, becoming tendinous on the ventromedial portion of the sac. I have been unable to confirm this in Gruhl's (1911) account, but the illustrations of Gallardo (1913) suggest that this holds for *Phocoena dioptrica*. Howell's account of *Neophocaena* (1927) indicates a similar condition in that genus.

Beneath the level of the vestibular sac, the muscular arrangement is similar to the delphinids. The general impression, however, is that the deeper muscles are relatively smaller in the phocoenids. Unfortunately, I was unable to determine the arrangement of the deep musculature around the vertex (intrinsic muscle, diagonal membrane muscle) in my dissections, and there is no information available from the literature.

MONODONTIDAE

Monodon

Huber (1934) described the facial structures in a large fetal narwhal (*Monodon monoceros*) in sufficient detail to allow comparison with the delphinids.

Nasal Passage and Diverticula.—It is in the nasal passage itself (rather, the spiracular cavity) that *Monodon* appears to be most specialized. Instead of the slitlike passageway seen in delphinids and phocoenids, *Monodon* has a large, spherical cavity. The blowhole opens directly into this cavity on its dorsal surface, and the nasal plugs open from its ventral surface.

Unfortunately, Huber's description was published posthumously, and Howell, who edited it, expressed some doubt as to the exact relationship of the apertures of the diverticula to the spiracular cavity. It appears that the vestibular sac ("lateral sac") opens laterally from this cavity. Huber's figures indicate a complicated nasofrontal sac, opening both into the inferior vestibule and into the spiracular cavity dorsal to the nasal plugs. He also indicates that the anterior portion of the nasofrontal sac opens into the spiracular cavity, just ventral to the opening of the vestibular sac. Schenkkan (1973) found similarities between Huber's descriptions of *Monodon* and his own dissections of *Phocoena*. The degree of complexity of the nasofrontal sac is similar, but more definite comparisons require clarification of some of the uncertainties in Huber's description. There is no indication of an accessory sac.

Scoresby (1823), in his brief description of the nasal passages of the narwhal, illustrated the vestibular sacs, but did not menton any other diverticula.

Musculature.—Huber (1934) concluded, based upon a comparison with *Tursiops*, that the nasal musculature of *Monodon* was derived from the same general plan as that of the delphinids, but differed in detail. The differences appear to be largely due to the extreme modification of the structures with which the musculature is associated. Although Huber did not attempt to define separate layers of the nasal musculature, examination of his illustrations suggest that the same layers as in *Tursiops* can probably be recognized.

The most superficial of these layers of musculature appears to correspond to the pars posteroexternus, but has its origin much more posteromedially than in the delphinids. The configuration of the remaining nasal musculature is more similar to that of the delphinids, at least in terms of origin and general area of insertion. None of Huber's illustrations show the details of insertion of *pi* or *ai*, both of which must differ from the delphinid condition as a result of the modifications in the spiracular cavity of *Monodon*.

Huber's (1934) illustrations give the impression that the nasal plug muscle ("retractor muscle") is continuous with musculature originating from the maxilla to the spiracular cavity (*ai*?). The nasal plugs seem to have a lateral lip, as in delphinids.

Other Structures.—Due to the expansion of the spiracular cavity and the unusual condition of the nasal plug muscle, the relationship of the melon to the nasal plugs must be very different from what is seen in the delphinids. The melon, as indicated by the illustration of Raven and Gregory (1933), is quite large. All told, *Monodon* is a very unusual animal, and certainly warrants detailed investigation.

Delphinapterus

The nasal apparatus of *Delphinapterus leucas* was briefly described by Watson and Young (1879). Their specimen, unfortunately, was in an advanced state of decomposition, and the description suffered accordingly. A more detailed description has been given by Kleinenberg, et al. (1969) in their monograph on this species.

NASAL PASSAGE AND DIVERTICULA.—Watson and Young (1879) were only able to find one pair of nasal diverticula, the premaxillary sacs, which were relatively small. They were familiar with the work of Murie (1870, 1871, 1873) and appear to have spent some time trying to locate all of the delphinid diverticula. The illustration given of the spiracular cavity gives the impression that it is large, as in *Monodon*, but no mention of this was made in the text. The muscles were unsuitable for dissection. One interesting finding was the presence of numerous openings in the walls of the spiracular cavity, which they took to be glandular orifices. Unfortunately, the condition of their specimen renders this suspect.

Kleinenberg, et al. (1969) described the system of nasal diverticula in *D. leucas* in more detail. The vestibular sacs, premaxillary sacs, and nasofrontal sacs are similar to those of delphinids. In addition to these, there is a posterior extension of the inferior vestibule, along the posterodorsal aspect of the nasofrontal sacs, reminiscent of the condition seen in *Phocoena*. These diverticula were termed the accessory cavities of the nasofrontal sacs by Kleinenberg, et al. (1969). No accessory sacs proper were found. In most respects, their description indicates a greater similarity to the delphinid condition than is seen in *Monodon*. In their figure 51, however, which illustrates the possible action of the diverticula during ventilation, they show a large spiracular cavity immediately dorsal to the nasal plugs. This would correspond to the expansion of the spiracular cavity described in *Monodon*. The other figures of Kleinenberg, et al. do not, however, support this idea. No mention is made of any glandular structures similar to those described by Watson and Young (1870), nor are the diverticula described as being asymmetrical.

MUSCULATURE.—No data is available on the musculature of *D. leucas*.

OTHER STRUCTURES.—The melon in *D. leucas* appears to be quite large, judging from the external appearance of the head, but no descriptions of its structure are available.

PLATANISTIDAE

Platanista

The anatomy of the nasal complex in this interesting cetacean was briefly described by Anderson (1878), and has been more recently covered in detail by Purves and Pilleri (1973). The blowhole of *Platanista* is unusual in being a longitudinal slit instead of the transverse crescent seen in the delphinids. The mechanics of such a structure are very different from those of the delphinid nose, and the anatomy differs accordingly. There are no vestibular sacs, a condition otherwise seen only in *Hyperoodon* (Schenkkan, 1973; Purves and Pilleri, 1973) (excluding the Physeteridae in which structural homologies are unclear). The "maxillary" sacs described by Anderson (1878) are not homologous to the maxillary sacs (=vestibular sacs) of Murie (1870), but to one of the deeper diverticula. The nasofrontal sacs in *Platanista* are grossly similar in form to those of delphinids, but differ markedly in that the distal portion (comparable to the anterior portion of delphinids) extends dorsally rather than anteriorly. Purves and Piller (1973) described an additional diverticulum originating from the area of the inferior vestibule (which appears to be reduced in *Platanista*) and lying posterodorsal to the nasofrontal sacs. They treated it as a branch of the nasofrontal sac and did not assign it a separate name. Although the relationship is far from clear, this condition seems comparable to that seen in *Phocoena*, where there also was a diverticulum lying posterodorsal to the nasofrontal sacs. The accessory sacs are absent and the premaxillary sacs are relatively small.

The most striking features of the facial region in *Platanista* are the extensive maxillary crests. Purves and Pilleri (1973) described these in detail and demonstrated that they contain an extensive system of air cavities derived from the pterygoid air sinus system. In this respect *Platanista* is remarkably different from any other cetacean.

The nasal musculature is quite different from that of the delphinids, as necessitated by the extreme modification of the other facial structures, making comparison with that group difficult and beyond the scope of this paper.

Purves and Pilleri (1973) described the topographic homologue of the melon as a dense mass of fibrous tissue. This seems quite different from the condition seen in other odontocetes. However, they ascribe a similar condition to *Inia* and *Pontoporia*, both of which I have examined and found to have considerable fatty differentiation in this area. I suspect the differences are partly due to their using formalin fixed material, in which the connective tissue becomes more conspicuous, partly to actual difference in relative amount of fat and connective tissue, and partly to semantic differences in usage of descriptive terms.

The nasal plugs lack a lateral lip, as seems to be the general situation in the platanistids. An item of some interest is Anderson's (1878) mention of a glandular recess around the ventral portion of the nasofrontal sac. I have seen such a structure in *Inia*, which may well be homologous to the glandular structures described by Evans and Maderson (1973) in *Tursiops*.

Lipotes

The anatomy of the nasal region in the Chinese river dolphin, *Lipotes velixifer*, has been very briefly commented upon by Hinton and Pycraft (1922) and Hinton (1936). The blowhole is peculiar in being a longitudinal rectangular opening. In the lateral margins of the blowhole are two small bones, one on either side. Various slips of musculature are attached to these, and Hinton and Pycraft (1922) felt that the bones were instrumental in effecting blowhole closure. Hinton (1936) mentions that they also occur in *Pontoporia*, the La Plata river dolphin, though Schenkkan (1972) does not mention them in his description of this species, and I did not find them in the fetus which I dissected. Hinton and Pycraft (1922) described two pairs of superficial diverticula, an anterior one dorsal to the bones, and a posterior one ventral to them. The posterior one is of considerable extent on the right side, covering the whole of the "dilator naris," while that of the left side is concealed beneath the small bone. Both of these diverticula are at the level of the vestibular sac, and one of them (probably the posterior) is homologous to it. Hinton (1936) said that the same configuration of diverticula was found in *Pontoporia*, but that the degree of asymmetry was less. None of the other facial structures were described in the above works.

Pontoporia

Burmeister (1867) briefly described parts of the nasal system in *Pontoporia blainvillei*, while more recently, Schenkkan (1972) described the nasal complex in some detail. The discussion of this species is primarily based on the latter work. In addition, I have made a preliminary dissection of a near-term fetus of this species, confirming much of Schenkkan's description.

As opposed to the two preceding genera, the blowhole is a crescentic slit, as in delphinids. The deeper nasal diverticula in this species, as apparently in all of the platanistids, are relatively small. The premaxillary sacs are comparable to those of delphinids, differing primarily in size, while the accessory sacs are absent. A small caudal portion of the nasofrontal sac is present, but the anterior portion is missing. The vestibular sacs, in striking contrast to the other diverticula, are extremely large and complex, covering much of the dorsal and lateral surface of the facial region. As in most of the delphinids, the right vestibular sac was larger than the left, though to a much greater degree.

The nasal musculature appears to be more comparable to delphinids than that of *Platanista*, but detailed comparisons remain to be made. The melon is moderately developed and situated similar to that of delphinids. Schenkkan (1973) indicated that the nasal plugs were relatively simple, without lateral lips.

Inia

I have made some preliminary dissections of the facial region of *Inia geoffrensis*, which are of use in comparing it to the other river dolphins. The blowhole is of the type normally seen in delphinids, crescentic with the concavity facing anteriorly. There were no bony elements in the margins of the blowhole, nor did I find two pairs of superficial diverticula. The vestibular sac is extremely large, much more so on the right, and covers the whole of the posterolateral portion of the nasal musculature. The nasofrontal sacs are moderately developed and, as in *Platanista*, are associated with a glandular structure, the exact nature of which has yet to be determined. The anterior portions of the nasofrontal sacs are lacking, the posterior portion extending to a point just lateral to the nasal passage. The accessory sacs are well developed, and situated as in delphinids. I have not attempted to work out the pattern of the musculature in *Inia,* which appears to be very different from that of the delphinids. The melon is well developed, though it appears to contain a greater amount of connective tissue than any of the delphinids examined.

Summary of Descriptive Anatomy

Nasal Passage and Diverticula

Delphinidae.—This is the most variable portion of the delphinid nasal complex. Of the delphinines, the group comprised of the genera *Tursiops, Stenella,* and *Delphinus* appears to represent the most generalized condition and the included forms show few differences among themselves.

Lagenorhynchus albirostris differs from this group of genera in the extreme expansion of the nasofrontal sacs and the development of a lateral diverticulum from the right premaxillary sacs. *Lagenodelphis* is similar to *Lagenorhynchus albirostris* in having a lateral diverticulum from the premaxillary sac, but does not show any expansion of the nasofrontal sacs.

Grampus is also distinctive in the morphology of its nasofrontal sacs. The anterior portion is absent on the left side and is greatly enlarged on the right.

Of the orcinines, only *Globicephala* shows any notable modifications of the diverticula. Again, it is the nasofrontal sac which is specialized, having an unusual trabeculate sacculation on the angle of the right sac.

The Steninae and the Lissodelphinae show no outstanding modifications of the nasal diverticula, while the only member of the Cephalorhynchinae examined, *Cephalorhynchus hectori,* shows a striking enlargement of the anterior portions of the nasofrontal sacs, and is further unusual in that the left sac is larger than the right.

The vestibular, accessory, and premaxillary sacs are relatively conservative in the delphinids, the nasofrontal sac being the most variable portion of the system.

Other Families.—The nasal diverticula are extremely variable in the other odontocete families. The vestibular sacs in the phocoenids have rigid, heavily folded ventral walls. In some of the platanistids these sacs are extremely large, covering most of the posterior facial region. They appear to be relatively small in the monodontids.

The nasofrontal sacs of the phocoenids are more complicated than those of the delphinids, and possess a trabeculate anterior portion. The posterior portion is also more complicated, with an additional diverticulum arising from the inferior vestibule and lying posterior to the nasofrontal sac. In the monodontids, the nasofrontal sacs are relatively complex, and are in some ways reminiscent of those of the phocoenids. These diverticula are relatively small in the platanistids, most of whom appear to lack an anterior portion. They are somewhat more complicated in *Platanista,* which has a diverticulum lying posterodorsal to the nasofrontal sacs, somewhat similar to the condition seen in phocoenids.

Musculature

Delphinidae.—Within the delphinids the nasal musculature is relatively conservative. *Pe* and *i* are the most variable elements, the former being particularly so in the Orcininae. The deeper portions of the musculature are more constant.

Other Families.—Outside of the Delphinidae, this portion of the anatomy shows considerable variation. The phocoenids are probably closest to the delphinid pattern, differing mainly in the arrangement of the superficial portions of the musculature. The reverse seems to be true in *Monodon,* where the deep musculature is most divergent from the delphinid pattern. None of the other odontocetes have been examined in sufficient detail to draw comparisons.

Melon

Delphinidae.—In most of the delphinines, the melon is relatively small. In *Grampus,* however, it becomes quite large, but without the proliferation of dermal connective tissue seen in some other delphinids.

In the orcinines this structure is more variable. In *Orcinus* and *Pseudorca* it is relatively small. In the latter, however, the dermal connective tissue superficial to the melon has become thick, giving a bulbous appearance to the forehead, particularly in the male. In *Globicephala* both the melon and the connective tissue have hypertrophied, again, more so in the male than in the female. The bulbous-headed genera *Grampus, Pseudorca,* and *Globicephala* are compared in more detail in a later section.

OTHER FAMILIES.—In the phocoenids the melon is relatively small, with the possible exception of *Neophocaena,* which has a bulbous forehead. In the monodontids the melon is relatively large, apparently without a thickening of the dermal connective tissue. The melon in the platanistids is relatively small.

OTHER STRUCTURES

The rest of the nasal complex shows little variation in the delphinidae. The platanistids stand out as an unusual group in many ways, one of the more important of which may be the lack of lateral lips on the nasal plugs in this group. Glandular structures are apparently present in all of the families, but are not well enough known to permit general comparisons.

FUNCTION OF THE FACIAL COMPLEX

Introduction

The facial complex is potentially involved in a variety of functions. This complex has differentiated around the external nasal passages, and most of its possible functions involve movement of air in these passages. The functions can be broken down into two general categories, those associated with respiration and those associated with sound production. Respiratory functions are of undoubted importance, but do not account for the degree of morphologic specialization seen in this area, suggesting that sound production may be of considerable importance in this region. In this context sound production is meant to include not only the generation of acoustic energy, but also modification of that energy, such as modulation, reflection, and refraction.

In this chapter the possible roles of the facial structures in respiration are considered first. The facial structures are discussed in the same order as in the descriptive section, and the possible function of each element is considered separately. Following this, the questions of sound production are considered in detail, with a review of the literature pertinent to this problem. In the next section of this chapter, the functional significance of cranial asymmetry is gone into in a similar manner. Finally, a summary section is given, presenting the most likely of the functions in which this region is involved.

Respiratory Considerations

One of the general functions proposed for the elaborate nasal apparatus of odontocetes has been the exclusion of water. While this is of undoubted importance to a diving animal, I believe that it has been overemphasized with respect to odontocetes. It has been commonly thought that the deeper an animal dives, the greater will be the tendency for water to enter the nares or for air to be lost. This would only be the case if a pressure differential existed at the point of closure of the nasal system. In general, it can be assumed that the air within the respiratory system of a diving animal will be compressed by collapse of the lungs, thus equalizing the internal and external pressures upon the system. A problem exists only if the air available in the collapsible portions of the respiratory system is not sufficient to raise the pressure within the noncollapsible portions of the system to a level equal to that of the external pressure. It has been suggested that this is compensated for in cetaceans by expansion of vascular tissues into the rigid air spaces (e.g., the middle ear), thus reducing their volume and equalizing the pressure. In any event, this is only a problem in structures deep to the fleshy nasal passages, as this sort of pressure differential would tend to force the nasal plugs more firmly into the bony nares, effectively tightening the seal. Pinnipeds, with relatively simple nasal passages, have been reported to dive to depths of 600 meters (Kooyman and Anderson, 1969), substantiating the idea that deep-diving does not demand an extremely specialized nasal apparatus.

A different sort of question involving the entry of water into the nasal passages has also been raised. This is the possibility of water entering the passages during breathing. Cuvier (1797) thought that the diverticula in the delphinid nose served as traps to prevent inspiration of water. Lawrence and Schevill (1956) noted that water frequently entered the vestibular sac if the animal started to submerge with the blowhole partially open. This appeared to present no problems to the animal, and the water was expelled in the next breathing cycle. They also noted that one of their experimental subjects experienced no difficulty if the blowhole was manually forced open underwater. Consequently they suggested that the vestibular sacs function as a water trap. This would, however, be effective only if the nasal plugs were seated and water penetrated no farther than the spiracular cavity. If, however, the vestibular sacs were absent, water would merely be forced out by closure of the nasal passage. Thus, although the vestibular sacs will hold water, this ability seems to be merely a consequence of their presence and does not provide any particular advantage to the animal.

Lawrence and Schevill (1956) were of the opinion that there is no mechanism for removing water once it got into the deeper portion of the respiratory system. The normal respiratory cycle of these animals, however, is sufficiently rapid that every expiration is essentially a cough, and should be sufficient to clear small amounts of water from the passages. Tomilin (1967) described a series of experiments in which water was introduced into the respiratory passages of dolphins, sometimes in considerable quantity. This seemed to present no problem to the animals and was expelled in subsequent expirations.

Schenkkan (1973) suggested that the vestibular sacs were filled with air from the nasofrontal sacs immediately before surfacing to breathe, and that this provides a "pneumatic cushion beneath the superficial fascia of the vestibular sections of the m. maxillonasalis, facilitating the rapid opening of the blowhole. . . ." It is not clear how this would facilitate opening of the blowhole, nor is it evident that it actually occurs. Blockage of the entrance of water to the nasal passage by the initial outflow of air from the vestibular sacs, as suggested by Schenkkan (1973), would seem to be of negligible importance when compared to the outflow of respiratory air from the lungs. Water may, in fact, enter the vestibular sacs, but it is difficult to see how the "small particles enclosed in the epithelial lining of the vestibular sacs in some species" relates to this question. Much of Schenkkan's material was derived from stranded animals, as was mine, in which it is not uncommon to find sand and detritus as far back in the respiratory tract as the terminal bronchioles, either washed in post mortem, or, in the more extreme cases, inspired when the animals were thrashing about in the surf.

The observation that "in general a living dolphin seems to be unable to open its blowhole unless the vestibular sacs have been previously expanded" is apparently based upon a misunderstanding of the observation by Anderson (in Purves, 1967) on a dead *Phocoena*. Schenkkan (1973) interpreted the statement to mean that "when the air was expressed from the (vestibular) sacs of a specimen, it died in a motionless condition as the head and indeed the entire animal sank beneath the surface." The statement in Purves (1967) is as follows: "Recently dead animals have been observed to sink below the surface when the vestibular sacs have been punctured." This observation does relate to Purves' (1967) discussion of the vestibular sac as a buoyancy regulator, but not to Schekkan's (1973) speculations.

Thus, the complexity of the odontocete nose cannot be accounted for by the obvious demands of an aquatic existence. Movement of air during sound production, however, may require particularly tight closure of the nasal passages. It may also be advantageous to be able to control the passages at different level, isolating some of the diverticula. The layered structure of the nasal musculature supports such an idea.

Nasal Passage and Diverticula

A great variety of suggestions have arisen for the functioning of the nasal diverticula. It was first suggested (Ray, 1671) that they were part of the olfactory system, later (Sibson, 1848) that they were filled with air to maintain the head of the animal near the surface while it was sleeping. The olfactory hypothesis has long been abandoned in view of the lack of olfactory innervation in these animals. The idea of buoyancy regulation by the diverticula appears in a number of later papers (e.g., Purves, 1967), but has not been demonstrated experimentally.

Norris (1964) suggested that the vestibular sacs serve as reflective elements, directing sound emitted from the region of the external bony nares anteriorly. If these sacs are air-filled during vocalization, then they would certainly be effective reflectors of sound energy. Their situation with respect to the surrounding muscles allows them to expand primarily in a horizontal plane, increasing their reflective surface. As these sacs are capable of distension, the area of reflective surface could be modified, thus altering the shape of the emitted sound field. The variation in morphology of these diverticula suggests that there may be considerable variation in the shape of the sound field between different species.

The *anterior folds,* as pointed out by Lawrence and Schevill (1956), provide a tight closure of the nasal passage at the level of the vestibular sacs.

Lawrence and Schevill (1956) proposed that the *nasofrontal sacs* formed a pneumatic seal around the nasal passage. This certainly appears to be the mechanism functioning to produce closure of the nasal passage in a dead animal when air is introduced into the nasal system through the larynx, not action of the lateral lips of the nasal plugs as stated by Schenkkan (1973). While this is a possible function for the nasofrontal sacs, it is also possible to achieve the same end with the two large muscle masses, *pi* and *ai,* which encircle the passage at this level. In *Grampus* the anterior portion of the left nasofrontal sac is absent, precluding pneumatic closure of that side. In *Lagenorhynchus* the nasofrontal sacs have been greatly enlarged, beyond what would seem to be useful for pneumatic closure. These modifications suggest a role in addition to or other than closure of the nasal passage.

At the moment, however, it is difficult to assign a primary function to these sacs. Certainly any cavities connected with the nasal passage can serve as reservoirs for recycling of air during phonation. If they contain air, they are going to be effective reflectors of sound. The large nasofrontal sacs of some species suggest that one of these functions might be relatively important.

The *accessory sacs* are more of a puzzle than are the nasofrontal sacs. Lawrence and Schevill (1956) proposed that they served to conduct air from the posterolateral edge of the premaxillary sacs into the nasofrontal sacs. But as Schenkkan (1971) has pointed out, the accessory sacs are blind diverticula, unsuited for the conduction of air between other cavities. He also noted that they are extremely variable and suggested an inverse relationship between their size and that of the posterior portion of the nasofrontal sacs. As with any of the diverticula, air storage and sound reflection are likely possibilities. Air can pass into them without passing through many other structures, arguing for their usefulness as reservoirs in laryngeal sound production. The intrinsic musculature surrounding them would be able to return the air to the respiratory passages without involving manipulations of the rest of the nasal complex. Their small size, of course, is a point against their being effective in this role.

Of all of the diverticula, the *premaxillary sacs* are probably the best situated for storage and recycling of air for sound production (particularly for laryngeal sound production). They are larger than the other diverticula, and open directly into the bony nasal passage. Fibers of *ai* which run from the maxilla over the nasal plug mass could easily provide the compression necessary to recycle air back into the nasal passage. At the same time this would firmly seat the nasal plugs posteriorly and block the escape of air into the dorsal parts of the nasal tract. Purves (1967) is a strong proponent of this view and thinks that the premaxillary sacs are the primary reservoirs of air during phonation. They are also effectively situated to contribute to reflection of sound anteriorly.

Musculature

The *pars posteroexternus* (*pe*) of the nasal musculature, as defined in this paper, appears to be a compressor of the underlying structures (Figure 20). This is certainly the case where its insertion is upon the vertex, and thus fixed with respect to its origin. Compression would limit vertical expansion of the vestibular sacs, and in so doing would serve to increase lateral expansion. The same function could be performed by the pars anteroexternus, but since it also has a large insertion upon the nasal passage, its contraction might produce other, possibly undesirable, effects.

The *pars intermedius* (*i*) has no immediately obvious function. Lying as it does, it could produce compression as well as posterior displacement of the structures deep to it. These functions could also be performed by the pars anteroexternus (*ae*) (Figure 20). The functional differentiation between *i* and *ae* will have to await experimental evidence.

The most posterior of the superficial fibers of the *pars anteroexternus* (*ae*), which insert upon the posterior wall of the blowhole, act to draw the posterior lip backward, facilitating opening of the blowhole aperture. The superficial fibers originating just anterior to this, however, run from an origin posterior to the nasal passage to an insertion anterior to it. These perform the antagonistic function of drawing the anterior lip posteriorly, thus acting to close the blowhole aperture. As the anterior lip is more mobile than the posterior, simultaneous contraction of all the superficial fibers of *ae* would probably result in maintaining blowhole closure, drawing the aperture slightly posteriorly and compressing the underlying structures. The fibers of *ae* which lie adjacent to the vestibular sacs are loosely attached to them and could possibly serve to draw the sacs posteriorly. The greater part of *ae* passes beneath the vestibular sacs, where its fibers converge radially upon the walls of the nasal passage. At this level *ae* is a strong dilator of the nasal passage.

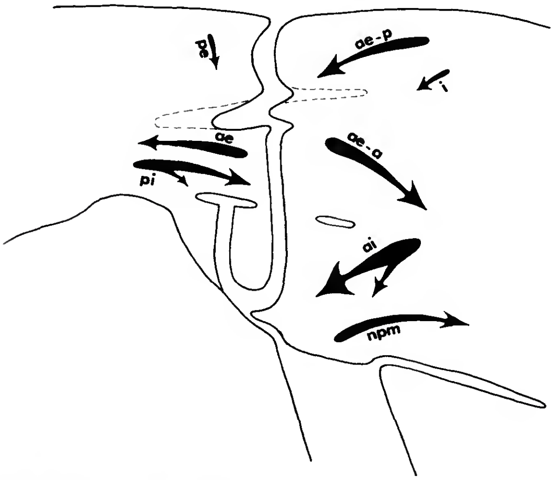

FIGURE 20.—Diagramatic view of the actions of the layers of the nasal musculature. (ae=pars anteroexternus; ae-a=pars anteroexternus, anterior fibers; ae-p=pars anteroexternus, posterior fibers; ai=pars anterointernus; i=pars intermedius; npm=nasal plug muscle; pe=pars posteroexternus; pi=pars posterinternus).

The *pars posterointernus* (*pi*), inserting via a tendinous sling around the posterior wall of the nasal passage, draws the posterior wall anteroventrally, opposing the action of the posterior fibers of *ae* (Figure 20). *Pi* is certainly one of the main agents of passage closure at this level. In drawing the posterior wall ventrally it also serves to bring the blowhole ligament to bear upon the lip of the nasal plug, facilitating closure of the bony nasal aperture.

The *pars anterointernus* (*ai*) is the largest and the most powerful of the nasal muscles. Its principal function is closure of the nasal passages, both by drawing the anterior wall posteriorly and by compressing the nasal plug mass, forcing the plugs back over the bony nares (Figure 20). The anterior portions of *ai*, which insert upon the nasal passage could, however, be functional in dilation of the passage. As suggested by Purves (1967), *ai* could also compress the premaxillary sac and recycle air from that sac to other parts of the system. In addition, Purves suggested that *ai* compresses the accessory sac, a function which may be better performed by parts of the intrinsic musculature.

Purves (1967) contended that the separate layers of nasal musculature (*ae*, *pi*, etc.) could not operate independently, owing to the disposition of the nerves and blood vessels among them. His observations were based on studies of specimens in which the vasculature had been injected with latex or polyester resin. He found that the innervation and vasculature "which supply the major groups of muscles spring each from a separate main trunk and pass from layer to layer within the group, branching only within the 'layer' of the muscle." He concluded that shearing stresses produced by independent action on the muscle layers could cause ruptures of the vessels. I found the same distribution of vessels and nerves in my dissections, and did not consider it remarkable, as it is the normal pattern for innervation and vascularization of skeletal musculature. One has only to examine an injected preparation of the human forearm, where the same pattern can be seen in the musculature controlling the fingers, to realize that this arrangement can permit considerable independence of muscle action.

It is difficult to assign a discrete function to the *intrinsic musculature* of the nasofrontal sac. Its disposition along the posterior portion of this diverticulum, around the communication of the nasofrontal sac with the inferior vestibule, and around the accessory sac puts it in a position to produce a variety of actions upon these structures. It probably provides partial isolation of these diverticula, allowing independent emptying and filling of their cavities. It can also provide constriction of these diverticula, altering their shape and capacity. Purves (1967) suggested that it draws the nasofrontal sacs laterally, assisting in pneumatic closure of the nasal passage. I do not see how this would work and think that it must be a minor function at best.

As pointed out by Lawrence and Schevill (1956), the *nasal plug muscle* withdraws the nasal plugs from the bony nares. This muscle may also be involved in complex movements of the nasal plugs during phonation.

The *rostral musculature* is difficult to interpret functionally. Lawrence and Schevill's (1956) contention that it serves to "keep the melon under tension and makes a strong connection between it and the rostrum" is difficult to accept. This could be performed equally well by the connective tissue of the rostrum.

The melon is known to have considerable mobility in the beluga (*Delphinapterus leucas*). This has not been demonstrated in any other odontocetes, and the relationship of the beluga to the delphinids is not well understood. It is possible, nevertheless, that the rostral musculature may produce slight changes in the shape of the melon in delphinids.

There is a possibility that the rostral musculature may play a role in sound projection. Recent work by Norris and Harvey (1974) has demonstrated gradients in sound velocity in the melon, which they feel may be of importance in shaping the sound field. The rostral musculature, lying immediately adjacent to the melon, may be involved in this system, and may be capable of altering its effect upon the sound field through changes in its acoustic properties upon contraction.

The lateral portion of the rostral musculature is partly associated with the upper lip. The lips of cetacea are generally considered to be immobile, but in view of the great expanse of lip surface in animals such as *Globicephala* and *Grampus* and the relatively large mass of muscle inserting into the connective tissue of the lips in these forms, a certain amount of mobility may be present and may be important in feeding. It is interesting to note that a greater portion of the rostral musculature was concerned with the lips in *Orcinus* and *Pseudorca* than in other delphinids. This may be part of their specialization for feeding on large prey.

At least one of the functions of the nasal plugs, that of closing the nasal passage at the level of the bony nares, seems relatively clear. These plugs fit tightly over the surface of the premaxillae, sealing the nasal passage at that point. It is possible, as suggested by Lawrence and Schevill (1956), that air could be forced around the plugs from below. This would involve unseating the plugs at some point determined by the pattern of compression of the muscles dorsal to the plugs, and could allow air to flow into either the premaxillary sacs or the inferior vestibule. From the inferior vestibule air would be free to enter both the accessory and nasofrontal sacs.

Evans (1973) provided a new suggestion on the role of the nasal plugs in sound production. According to his theory, movement of the plugs against the margin of the bony nares would set up relaxation oscillations, "much the same mechanism that causes chalk to screech when pushed across a blackboard." This hypothesis was later amplified (Evans and Maderson, 1973), taking more anatomical details into consideration.

The *lips of the nasal plugs* have been implicated in sound production, a function which will be discussed in detail later in this paper. They also appear to provide a more effective seal over the bony nares by projecting posteriorly beneath the blowhole ligament.

The function of the *diagonal membrane* is probably more complex than has been suggested. Lawrence and Schevill (1956) thought that it facilitated closure of the nasal passage by the nasal plugs. Norris (1969) suggested that it may form part of an air metering system for sound production. It is also possible that these membranes may be directly involved in sound production. Now that it is known that they are under muscular control, it seems likely that they play a more active role than was previously thought.

The *blowhole ligament* and the fat body associated with it maintain stability in the complex area around the inferior vestibule. The blowhole ligament prevents the mouths of the accessory and nasofrontal sacs from collapsing, and provides a surface against which the nasal plugs fit in closing the nasal passage. The fat body maintains the shape of the posterior fold.

Melon

The melon has constituted one of the most enigmatic portions of the nasal complex. One suggestion as to its function was that of Howell (1930), who thought it might be a buffer to reduce the effect of water pressure on the skull. While the role of water pressure in influencing the shape of the cetacean head has been exaggerated, the idea of the melon as a buffer is fairly plausible. It is suitably constructed for such a purpose, having a soft, almost fluid core contained within a tough sheath of dermal connective tissue. It seems likely that in some of the bulbous-headed delphinids (particularly *Globicephala*) the melon actually serves this purpose. It seems less likely, however, that this is of primary importance in other, less specialized delphinids.

Huber (1934) was of the opinion that the melon serves as a special sensory organ to detect changes in pressure "when the animal accelerates, when it dives to greater depths, or approaches unyielding objects. . . ." This seems to have been based on its presumed rich innervation. I attempted to follow this innervation, and believe that most of it runs to the area around the nasal passages and to the skin. The skin is known to be highly innervated (Palmer and Wenddell, 1964) and could better accomplish some of the functions suggested by Huber. The detection of changes in hydrostatic pressure requires a different sort of mechanism. Since animal tissues are relatively incompressible, this function is likely to be performed by sensors in air-containing structures which are subject to compression with changes in depth.

Another group of suggestions has been that the melon served as a reservoir for dissolved gases. Howell (1930) suggested that the melon and other fatty structures might absorb carbon dioxide, but felt that this was more possible than probable. Kooyman and Andersen (1969) suggested that fatty structures in diving mammals might serve as nitrogen buffers during serial deep dives. The lack of vascularity in the melon makes it unlikely that it is involved in any sort of gas exchange.

Raven and Gregory (1933) thought that the lesser density of the melon served to buoy up the anterior end of the animal, making breathing easier. This has been recently revived by Clarke (1970), with respect to the extreme situation seen in the sperm whale. In the case of the sperm whale, as in the bulbous-headed delphinids, the amount of energy required to push this structure through the water is likely to more than make up for the small advantage conferred in raising the head to the surface. It must also be borne in mind that, while a slightly positive buoyancy may be of some advantage in rising to the surface to breathe, it is of a corresponding disadvantage in diving. Clarke (1970) has hypothesized that the spermaceti organ in *Physeter* is cooled by drawing water into the nasal passage, thus altering the density of this mass when the animal is ready to dive. Lawrence and Schevill (1956), however, note that cetaceans seem to be able to rapidly alter their buoyancy, probably through altering lung displacement. Ridgway (1971) further discussed Clarke's hypothesis from a physiological standpoint and concluded that it was unlikely.

Raven (1942) thought that the melon served as a cushion upon which the nasal musculature acted to compress the nasal plugs against the bony nares. While this may occur in the most posterior portions of the melon, the greater portion of it lies anterior to the insertion of this musculature.

Recently, with the increased knowledge of echolocation in delphinids, the melon has been examined with respect to possible acoustic roles. The shape and position of the melon led to the suggestion (Lilly, 1961) that it is an acoustic lens, a theory which has received considerable acceptance. The principal objections to this theory have been that the melon is not shaped like a lens and that there was no evidence that its acoustic properties differ sufficiently from those of the surrounding tissues to make it effective as an acoustic refractor.

Kleinenberg et al. (1969) subscribed to the idea of the melon as an acoustic lens, although with no new evidence along this line. They also suggested that the melon may be able to focus sufficient acoustic power to enable prey to be stunned at a "considerable distance." It seems highly unlikely that the animals would be capable of generating enough power to do this without disrupting their own tissues.

Norris (1968) has suggested that the melon serves as an acoustic waveguide, offering a path of minimum resistance through the forehead tissues. This, of course, can be countered by the suggestion that there would be even less acoustic resistance if there were no tissue there at all. However, assuming that the elevated vertex and the posterior nasal apparatus are important to the animal, removing the tissue of the melon would result in a concave forehead, producing more drag than a convex forehead as the animal moves through the water. The conclusion from this line of reasoning is that the melon is merely filler to produce a particular external form. While this may have been important in the early evolution of the melon, it is probable that other functions are presently more important.

The work of Bullock et al. (1968), in which areas of sensitivity to sound were mapped on the head of a live animal, suggested that the melon might be involved in acoustic reception. They found two general areas of sensitivity: a ventral one over the posterior end of the lower jaw and a dorsal one anterolateral to the blowhole. Norris (1968) suggested that an acoustic waveguide may extend from the dorsal area through the antorbital notch to the lower jaw and thence to the ear. The antorbital notch is occupied by dense connective tissue through which the facial nerve runs and seems unlikely as a route for sound conduction. Experimental work by Norris and Harvey (1974) did not demonstrate acoustic transmission in this area. The alternative is conduction through the bones of the skull, which is contrary to the present theories of cetacean hearing. However, of these two alternatives, I would tend to support the latter theory, rather than the idea of an antorbital waveguide. More work needs to be done to demonstrate the paths of sound reception, and to clarify the possible role of bone conduction in hearing.

Ackman et al. (1971) noted that the lipids of the melon and mandibular fat bodies (which are suspected of playing a role in sound transmission) were similar and that they differed from the lipid content of the blubber. They speculated that these differences may reflect differing physical properties advantageous for high frequency sound transmission.

Recent experiments by Norris and Harvey (1974), utilizing tissues from freshly dead specimens, have demonstrated a gradient in sound velocity in the melon tissues. They found that the center of the melon possessed relatively slow transmission velocities, while peripheral areas were somewhat faster (ca. 10%). These differences may be due to variations in lipid composition or lipid content, as described by Litchfield et al. (1973). Unfortunately, it is not possible to make a precise comparison between Norris' sound velocity data and Litchfield's lipid data, as the exact correspondence between the sites measured cannot be determined. This would be of great interest, as the greatest velocity difference (in Norris' section C, about 30%) does not appear to correspond to any of the lipid differences described by Litchfield, nor to any anatomical differences known to me.

Unfortunately, no data is available on the in vivo acoustic properties of any of the tissues of the facial complex. Until this is available, the acoustic functioning of the structures will remain unclear.

Glandular Structures

Glandular structures have been described in the nasal passages of *Delphinapterus leucas* (Watson and Young, 1879), *Platanista gangetica* Anderson (1878), and *Tursiops truncatus* (Maderson, 1968). I have found tissue which appeared to be glandular in *Phocoenoides dalli* and *Inia geoffrensis*. The observation of Watson and Young (1879) may be in error, as their specimen was in an advanced state of decomposition. Such structures were not mentioned by Kleinenberg et al. (1969) in their extensive monograph on *D. leucas*.

Glandular tissue in *I. geoffrensis* and *P. gangetica* was located around the nasofrontal and accessory sacs and the inferior vestibule. I could not discern any ducts or openings into the nasal passage, leaving the functional relationships of the glands unclear.

In *P. dalli* the anatomical situation is much different. Here the anterior portion of the nasofrontal sac itself is modified into what appears to be a glandular structure.

Glandular tissues have recently been discovered in the area of the inferior vestibule in *T. truncatus*

(Maderson, 1968; Evans and Maderson, 1973). They are described as compound acinar, exocrine glands, opening onto the surface via small crescentic pores. The secretion of these glands is not mucinous and is suggested to contain a lipid, possibly for lubrication of adjacent structures.

Functional Basis of Sound Production

REVIEW

Odontocetes have long been known to produce sounds and there is a relatively voluminous literature dealing with this subject. With the discovery of echolocation in odontocetes, there has been a tremendous increase of activity relative to cetacean sound production. In the last ten years, by far the bulk of the literature dealing with odontocetes has been concerned with acoustic problems. Unfortunately the problems are complex and much remains to be resolved.

The mechanism of sound production in Cetacea is poorly understood and the literature pertaining to it is full of confusion, errors, and misunderstanding. Norris (1969) lists the following as being the only definitely known sources of sound production in odontocetes: the lips of the blowhole (external), movements of the jaws, and slaps of the body, flippers, or flukes against the water. None of these mechanisms accounts for the variety of complex sounds which these animals have been observed to produce.

In the following pages I will review first the nature of the sounds and the sound field, then the theories of the site and mechanism of sound production. Following this, I will consider these problems in the light of the present study.

The nature of the sounds themselves has received the greatest attention, as this has been the most accessible part of the problem. Norris (1969) and Evans (1973) have provided summaries of the descriptive information on odontocete sounds. Unfortunately the state of our knowledge is not such that detailed comparisons of delphinid sounds can be made. An extremely wide variety of equipment has been used to record these sounds, limiting the frequencies which could be analyzed in many cases. The relatively recent discovery that the sound field is highly structured (Evans and Prescott, 1962; Norris and Evans, 1967; Schevill and Watkins, 1966; Evans, 1973) has made it imperative that the orientation of the animal with respect to the receiving apparatus be precisely known. This has seldom been the case. Norris (1969) presented evidence that there may be considerable individual variation in echolocation, further complicating the situation. Caldwell et al. (1965) have demonstrated individual variation in the low frequency components of delphinid vocalizations. Thus it is impossible at present to make any correlations between anatomical differences and differences in sound production.

Odontocetes are known to produce sounds from within the audible range of humans to over 250 kHz (Norris and Evans, 1967). Within this frequency range there is a variety of sound types. Two general types of sounds are important for consideration of sound production mechanisms: (1) whistles or squeals, which are within the audible range of man and which seem to be primarily communication signals; and (2) clicks, which are broad-band pulsed sounds extending well above the audible range. The latter are usually considered to be primarily important for echolocation.

As noted above, the sound field produced by delphinids has been shown to be highly directional. The shape of this field has been described for a few animals and had been shown to vary with the frequency of the emitted sound. Most measurements of this field have been made in the horizontal plane and indicate an asymmetry in the shape of the field. In general, the greatest amount of energy is radiated directly anterior to the animal, with the field strength dropping laterally and posteriorly. This is particularly true of the higher frequencies. Norris and Evans (1967) presented data based upon work with live animals (*Steno*). Their data indicate that the sound intensity 20 degrees to the left of the midline is 1–2 db greater than that 20 degrees to the right of the midline (frequency unspecified). Evans et al. (1964) obtained essentially the same results with an artificial sound source implanted "in the area of the nasal sacs" in an infant *Stenella microps* (= *S. longirostris*) cadaver. Their tests ranged from 20 to 60 kHz and indicated that the asymmetry increased with an increase in frequency. The sound field observed by these workers was less directional than that measured by Norris and Evans (1967) with live *Steno*.

Evans et al. (1964) also measured the sound field in the vertical plane (under the same conditions) and found slightly more energy dorsally in the low range, changing to ventrally at 60 kHz. Evans (1973) presented further data based upon work with a live *Tursiops truncatus*. He noted a double pulse waveform with maximum energy at 30 kHz and a striking right-left asymmetry in relative strength of the two pulses. Measurements of the shape of the sound field indicated a rapid loss of energy below the horizontal plane of the animal. These measurements were apparently based on the 30 kHz pulses, although the frequency or bandwidth of the measurements is not given.

Evans et al. (1964) conducted tests on dry skulls of *Tursiops* and found that for the lower portion of the range (20–40 kHz) more energy was radiated laterally than anteriorly. At 60 kHz, however, this changed and the anterior portion of the sound field was about 10 db above the lateral portion. Their data also indicated that for the skull alone, the asymmetry becomes less at higher frequencies.

Evans and Prescott (1962) produced sounds by forcing air through the upper respiratory system (including larynx) of a severed head of *Stenella graffmani* (= *S. attenuata*), as well as by forcing air through the excised larynx alone. They stated that the sounds produced in both cases were similar, although the production of "echolocation clicks" was dependent upon inflation of the nasal sacs. They measured the sound field around the head (all frequencies) and found that it was stronger on the right side in both the horizontal and vertical planes. They also found a substantial ventral element to the sound field.

The statement that there is no significant ventral portion of the emitted sound field (i.e., that sound is emitted "above the level of the mouth") has appeared in the literature as an argument against the larynx as a sound source (Norris, 1968). This is based upon the findings of Norris et al. (1961), who stated that when their experimental animal presented the ventral surface of the head to the hydrophone, "the volume decreased markedly." No frequency specific measurements were made and the type of sound (whistle or click) was not specified. The text implies that this concerned the audible sound range only. Since the data of Evans et al. (1964) indicate that the strength of the ventral portion of the sound field increases with frequency, the implications of Norris et al. (1964) may not hold for the higher frequencies of the echolocation sounds.

At this point I would like to review the arguments concerning the site of sound generation in odontocetes. These are concerned with two areas, the larynx (which is somewhat removed from the area of my work) and the upper portion of the nasal passage.

At the moment there is no direct evidence relating to the mechanism of sound production, and relatively little indirect evidence.

The diverticula of the nasal passage have frequently been implicated in sound production (Lilly and Miller, 1961; Lilly, 1961, 1962; Evans and Prescott, 1962; Norris, 1964, 1968; Norris and Evans, 1967), a possibility originally suggested by Lawrence and Schevill (1956). Lilly and Miller (1961) speculated that the cavities of the nasal tract are "shock excited." I have trouble following their arguments, but it seems that shock excitation is by means of sound (specifically, clicks) produced elsewhere. This is in accordance with the view expressed by Lilly (1961) that the clicks were produced by the larynx. He does, however, state that the nasal plugs and sacs are used to produce sound, but does not produce any evidence for this statement. Lilly's other work (1962) merely contains a reference to his book (1961). Thus, the work of Lilly, which is frequently cited as supportive of nasal sac sound production, contains no evidence and, in fact, expresses the view that the larynx is the source of the "echolocation clicks."

In their work on severed heads of *Stenella graffmani* (= *S. attenuata*), Evans and Prescott (1962) noted that production of "echolocation clicks" ceased if the nasal diverticula were deflated by depressing the anterior surface of the head (over the melon). This could be interpreted as evidence that the nasal sacs were involved in sound production (as the authors suggested). It is also possible that such manipulation more firmly seats the nasal plugs, slowing the flow of air through the entire system.

Another line of evidence which has been brought forward as implicating the nasal diverticula is that the sound field is stronger on the dorsal surface of the animal. As noted earlier, the evidence for this is scanty and indicates that this is true principally for low frequencies. Even if this were demonstrably the case, it does not preclude laryngeal sound production.

One of the underlying problems of this question concerns the anatomy of the nasal diverticula. Lawrence and Schevill (1956:114) described the accessory sac (connecting sac) in such a way that it is possible to get the impression that it has two openings, one into the nasal passage and one into the nasofrontal sac. This is further implied by the name ("connecting sac") which they used for this diverticulum. Their illustrations, however, do not show this to be the case. I think that this has resulted in a number of people believing that the accessory sac forms an alternate pathway for air to reach the nasofrontal sac. This view is implicit in several papers of Norris (1964, 1969) and is explicit in van Heel's (1970) illustration of the nasal passages. Norris (1964) postulated that air is forced from the vestibular sacs into the nasofrontal sacs, passing around the lateral lips of the nasal plugs and producing clicks. According to him the air passes from the nasofrontal sacs through the accessory sacs to the nasal passage below the level of the nasal plugs. The plugs remain seated throughout this procedure. When the supply of air in the vestibular sacs is depleted the nasal plugs withdraw from the nares and air is passed to the vestibular sacs, allowing a new cycle to start. Neither Schenkkan (1971) nor I have found any anatomical basis for the idea of a continuous passage for air past the lateral lips of the nasal plug.

The lateral lips of the nasal plugs rest within the common orifice of the accessory and nasofrontal sacs (the inferior vestibule), but both of these sacs (as described by von Baer, 1826; Gruhl, 1911; and Lawrence and Schevill, 1956) are in fact blind. This limits the amount of air which can be passed through this system without pausing for recycling.

Kleinenberg et al. (1969) discussed the role of the nasal diverticula in sound production, basing their observations on the beluga. According to them, the sound source could be located by ear in the upper part of the nasal passages of belugas examined on land. Tampering with the nasal apparatus by hand affected sound production. These observations, of course, dealt with sound in the human audible range, apparently of the whistle type. They suggested that sound is produced by the movement of air between the diverticula (with the nasal plugs seated). This general idea has appeared in the work of many people, usually, however, involving recycling of the air between the upper and lower respiratory passages. The explanation of Kleinenberg et al. (1969) involves only the supracranial portion of the respiratory system. The details concerning the operation of this mechanism were not discussed.

Purves (1967) discussed sound production in cetaceans at great length and concluded that the larynx is capable of producing the sounds used for echolocation by odontocetes. His initial argument is that of Occam's Razor, whereby the larynx should be assumed to be used in sound production unless there is some compelling reason to believe otherwise. He eliminated the lack of "true vocal chords" as an argument against laryngeal sound source in cetaceans by noting their absence in most mammals other than man. Mammals generally employ modifications of the thyroarytenoid fold, artiodactyls utilizing the aryepiglottic folds (Negus, 1949). Purves carried out a series of experimental investigations on the larynx and concluded that it was capable of producing the sounds recorded from odontocetes. He also concluded that coupling of sound to the skull via the palatopharyngeal muscles would result in the observed pattern of the emitted sound field. His data do not, however, eliminate the possibility of nonlaryngeal sound production, as he did not investigate this aspect of the problem in his experiments.

Evans (1973) argued against Purves' theories of laryngeal sound production on a variety of points. His observation that a "closed tube" model could not produce the observed sounds may be correct, but probably does not apply to the cetacean larynx, which is a complex, flexible structure, nor does the argument that the lack of demonstrated differences in the laryngeal anatomy of whistling and nonwhistling species carry much force. The observed differences in sound production may be limited by behavior rather than anatomy, and, definitive anatomical studies of the larynx remain to be done.

The hypothesis proposed by Evans (1973), that sound is produced by movement of the nasal plugs against the edge of the bony nares and not through airflow past apposed surfaces, has several advantages. It removes the questions of complex airflow and the problem of sound production at great depth, where the air volume is very limited. Although it is not explicit in his papers (Evans, 1973: Evans and Maderson, 1973), it is presumed that this explanation is meant to cover production of high-frequency clicks and not the lower frequency whistles.

Recently Norris et al. (1971) have presented an analysis of low frequency "chirp" production based upon cineradiography of the head of a live *Stenella longirostris.* They demonstrated complex movements in the nasopharynx and nasal diverticula concurrent with production of squeals or chirps, and concluded that the most probable site for production of these sounds was the left nasal plug. Briefly, the sequence of events described by them consisted of movement of air (recycling) from the nasal diverticula into the nasopharynx, closure of the nasal plugs and posterior nasopharynx, movement of air past the nasal plugs into the premaxillary sacs, then pulsation of the tissues around the left nasal plug, with air movement into the spaces above the plug. The last part of this sequence was correlated with production of squeals. This activity was observed only in the left naris.

One of the critical factors in this experiment was the determination that there was no airflow through the larynx during sound production. Although their arguments are convincing, the question may be raised of the adequacy of the resolution of the cineradiography equipment to demonstrate this conclusively. If there remains a possibility of air movement through the larynx, the events observed above may be correlated with movement of air into reservoir space rather than sound production per se. As noted by the authors, their evidence relates to production of low-frequency squeals and not to clicks.

Schenkkan (1973) raised a series of objections to the hypothesis of Norris et al. (1971). His statement that "no one has disputed that dolphins can produce sounds with their nasal passages when the head is above water" is irrelevant, as the authors were not dealing with the familiar noises produced by trained animals with their blowholes open, but rather with sounds apparently identical to the squeals produced underwater with the blowhole closed. The nasal plugs are not essential to preclude water from being taken into the internal nares, as stated by Schenkkan (1973), since closure can be effected both by the blowhole and between the level of the vestibular sacs and the nasal plugs by tissue elasticity and muscular control. The nasopalatine sphincter is capable of movement anterodorsally, contra Schenkkan's statement, as can be readily demonstrated by manual pressure in a fresh specimen. This muscle is very loosely attached to the periosteum of the nasal passage and moves quite readily over it. Schenkkan's (1973) views concerning the loss of any air which passes distal to the nasal plugs is based upon the assumption that the nasal plugs cannot be unseated underwater, which has been partly discussed above. Anatomically the plugs appear capable of complex movements, and there is no reason to assume that air cannot be moved around them without losing it out the blowhole or allowing water to enter.

Schenkkan (1973) presented a rather elaborate description of the functions of the nasal diverticula and associated structures during phonation. Unfortunately he appears to have adopted fairly rigid ideas of the possible relative movements of air and of the anatomical structures, without sufficient allowance for the complexity of the system. His functional observations are further clouded by the derivation of a sequence for the evolution of the cetacean nasal complex based upon an arrangement of the highly specialized living forms into a supposedly phylogenetic series.

Schenkkan (1973) argued heavily against many of the current theories of sound production. His observation that ziphiids produce echolocation clicks but do not possess lateral lips on the nasal plugs is certainly an argument against those structures being used for sound production in that group, and clearly suggests that echolocation clicks can be produced by some other mechanism. It does not necessarily apply, however, to the somewhat distantly related and structurally different delphinids. Nor would it be necessary, as he postulates, for the entire nasal plug mass to vibrate in order to produce sound in the absence of lateral lips. His argument that air expanded in vibrating the lateral lips of the nasal plug could not be recovered is unlikely and is in contradiction to most of his earlier statements about airflow, particularly in and out of the nasofrontal sacs. The further argument that clicks would be confined to the right side and as such could not be produced into a beamed transmission, since such transmissions are only produced through interference between two or more sources, is incorrect. This is indeed one way to produce a beamed pattern, which can also be produced by reflection, refraction, attenuation, or any combination of these.

Schenkkan's arguments for laryngeal sound production suffer similar deficiencies. As stated in his paper, production of relaxation oscillations through a constricted aperture is efficient, but can be applied equally to all of the suggested sites of sound production, not just the larynx. His concept of "matched loads" equally fits all other areas of the system. The fact that the lips of the nasal plugs are nonmuscular has no bearing on the theories involving their action in sound production, all of which postulate vibration between apposed surfaces, not freely in an air cavity as stated by Schenkkan. His calculations of the potential power output of this musculature (based upon Gray's (1936) estimate of the power output of dolphin axial musculature) suffers from the consideration that the visceral musculature associated with the larynx probably differs considerably in physiological characteristics from the skeletal muscles used in locomotion.

In short, Schenkkan's (1973) functional discussions of sound production seem to have little actual bearing on the problems involved.

The fact that odontocetes can produce both "whistles and clicks" simultaneously, starting and stopping one without affecting the other, and with no indication of one modulating the other, has been cited as an indication that two separate sound sources were active (Lilly and Miller, 1961). This is circumstantial evidence for both the larynx and the nasal apparatus being active in sound production. Following the suggestions of Evans (1967) and Schevill (1964), among others, that the larynx is responsible for whistles, this would leave the nasal apparatus responsible for the "echolocation clicks." It is also possible, as suggested by Norris et al. (1971), that the left nasal plug produces whistles while the right produces clicks.

One thing which must be borne in mind in any discussion of sound production is the possible differences between apparent and actual sources of sound. Sound may be conducted from its actual source to another point at which it becomes apparent to the observer. The evidence to date suggests that sound radiates from a point external to the skull, but deep within the facial complex. This does not, however, preclude a laryngeal sound source, as sound could easily be conducted from the larynx to the external bony nares.

ANATOMICAL CONSIDERATIONS

Purves (1967) discussed the nature of the sounds produced by odontocetes and concluded that they were of the relaxation oscillation type, produced by the approximation of the walls of some portion of the nasal passage, forming an aperture through which air is forced. This mode of sound production has also been variously referred to as "raspberry" or "Bronx cheer" sound production. If this is the case, only those portions of the nasal apparatus which can be approximated to form suitable apertures are likely to be involved in sound production.

Unfortunately, there are a great many structures of this description within the nasal passages and diverticula. Thus, while it is not possible to conclusively delimit the site of sound production on an anatomical basis, it may be possible to decide which structures are most likely to be involved and which are least likely. In production of sounds of this sort, it would seem that relatively small apertures would be advantageous, as they would permit higher velocities of airflow with the restricted amount of air available. For the same reason, structures which can be tightly appressed are more suitable than those which can only be loosely approximated. It is also advantageous to have a large reserve volume on either side of the site of sound production to minimize the necessity for recycling the air.

The juncture of the spiracular cavity with the vestibular sacs, while under considerable muscular control, is quite wide and thus probably not involved in sound production. The apertures of both the nasofrontal and accessory sacs are held open by the blowhole ligament and are thus incapable of sound production by themselves. The lateral lip of the nasal plug, however, may be inserted into the apertures of these diverticula to form an appropriate mechanism for sound production. This is the prevalent theory at the present time. The principal objection to this theory is that in most species the volume of the nasofrontal and accessory sacs is quite small. There is not, as was sometimes supposed, a connection between the distal portion of the nasofrontal sacs and the rest of the nasal passage via the accessory sac. This limited volume would impose serious limitations on the duration of individual cycles of phonation.

The nasal plugs are capable of being apposed to a great variety of surrounding surfaces to create apertures, some of which are suitable for sound production. These include the bony aperture of the nasal passages, the posterior wall of the spiracular cavity, and the diagonal membrane. If air is passing from the bony nasal passages into the distal portion of the nasal system, the nasal plugs must be partly unseated. Depending upon the movements of the nasal plugs, air could escape upward via several routes. It could pass anteriorly into the premaxillary sacs, but the surface between the nasal plugs and the anterior edge of the bony nares does not seem particularly suitable for sound production. Air could also pass between the nasal plug and the diagonal membrane, entering anteriorly where the membrane slopes ventrally into the bony nasal passage. It could then pass posterolaterally into the inferior vestibule, and from there into the accessory and nasofrontal sacs. If the nasal plugs were not closely appressed to the posterior wall of the nasal passage, air could then pass dorsally into the vestibular sacs. Along this route are several structures which seem capable of sound production. The most likely of these are the diagonal membrane, where it lies against the nasal plug, and the lateral lip of the nasal plug, where it is in contact ventrally with the wall of the inferior vestibule. Either of these sites would probably allow passage of air into the spiracular cavity and vestibular sacs.

The above ideas have presumed movement of air from the bony nasal passage into the supracranial portion of the nasal system. There is also the possibility of involvement within the supracranial system between the diverticula or movement from the supracranial system ventrally into the bony nares.

If the vestibular sacs are involved in the movement of air during sound production, it is most likely that they serve as reservoirs to receive air, rather than as sources of air. This is due to the arrangement of the anterior fold, which would probably not allow passage of air toward the deeper structures without the spiracular cavity being opened fairly widely.

The premaxillary sacs are better suited to serve as sources for air during phonation. With the nasal plugs seated, air could pass from the premaxillary sacs posterolaterally, ventral to the lateral lips. The insertion of *ai* is suitably placed to compress the premaxillary sacs, providing the pressure necessary for high air velocity.

An interesting possibility is the movement of air from the premaxillary sacs into the bony nasal passage past the apposed surfaces of the nasal plug and diagonal membrane. This seems like an admirable site for sound production, except that air movement in this direction would probably interfere with production of sound by the larynx. It might, however, be possible for air to flow between the nasal plug and the posterior wall of the nasal passage. The arrangement of musculature within the nasal plug is reminiscent of the intrinsic musculature of the tongue, suggesting that it might be capable of complex movements.

A principal consideration in the functioning of the nasal structures is the levels at which the various portions of the system can be isolated. The vestibular sacs can certainly be isolated from structures ventral to them through the combined actions of the anterior folds and the nasal musculature. The interaction of the deeper structures is more complex. As noted earlier, the apertures of the accessory and nasofrontal sacs are held open by the blowhole ligament, and it is only through movements of the lateral lip of the nasal plug that these diverticula might be closed. The nasal plugs would also be the critical factor in isolation of the premaxillary sacs. In view of their possible plasticity, it is possible that they may be able to isolate many of the deeper structures, allowing complicated airflow in this area.

As noted above, the nasal plugs are capable of being apposed to a variety of structures, and are probably capable of complex muscular activity. This agrees well with Evans' (1973) theory of sound production by movements of the nasal plugs independent of any airflow. As he noted (Evans and Maderson, 1973), the premaxillary sacs may function as clefts allowing free anteroposterior movement of the nasal plugs for this type of sound production.

In summary, it appears that the structures most likely to be involved in sound production are those in the vicinity of the nasal plugs. The discovery of musculature associated with the diagonal membrane renders it more likely than previously supposed that it is involved in sound production. All of the available evidence, particularly that of the asymmetry (to be discussed later), implicates the nasal plugs in sound production.

Functional Aspects of Cranial Asymmetry

Review

One of the striking peculiarities of the delphinid skull is the asymmetry of the facial elements. The entire area of the external nares is shifted slightly to the left. This primarily involves the elements bordering the nares, the premaxillae and the nasals. The frontals and the maxillae are distorted to a lesser degree. This sinistral displacement is most pronounced along the median sutures between the premaxillae, nasals, and the posterior portion of the frontals. The lateral sutures, between the premaxillae and maxillae, and the maxillae and frontals are much less affected (Figure 1). The rostrum is usually free from this distortion. Correlated with the displacement of the bones bordering the nares is an enlargement of the right-hand elements. This is most pronounced in the premaxillae, where the ascending process of the right premaxilla is sometimes half again as wide as that of the left. Only the facial elements are involved in this asymmetry. The internal nares and nasal passages are symmetrical.

All living odontocetes show this cranial asymmetry to one degree or another. It seems to be least in some of the river dolphins and is greatest in the sperm whale (Ness, 1967). Mysticetes, however, are completely unaffected by this phenomenon.

The question of the origin and functional significance of this asymmetry has been treated extensively in the earlier literature, which is reviewed in the following pages.

Pouchet (1886) ascribed the cranial asymmetry in odontocetes to a process which he termed "pleuronectism," derived from a comparison with the flatfish, *Pleuronectes*. This term was applied to symmetry modifications resulting from swimming on one side. Pouchet pointed out the advantages of the dorsal situation of the blowhole, arriving at the conclusion that the blowhole will tend to seek the dorsal surface. Thus, if the animal preferentially swims on one side, the blowhole will migrate to the other side. He presented very little evidence for the relevance of this theory to odontocetes, merely citing the old tale of handedness in the sperm whale (see Scammon, 1874). He did note that mysticetes swim on their sides as well, and attributed the asymmetrical pigmentation of *Balaenoptera physalus* to pleuronectism. He did not, however, explain why this had no effect on the blowholes of mysticetes.

Weber (1886) briefly mentioned the cranial asymmetry of odontocetes and considered it in comparison with asymmetric variation seen in pinniped crania without arriving at any conclusions.

Beddard (1900) discussed the phenomenon of asymmetry in odontocete crania. He correlated it with the presence of a specialized nasal apparatus, but was unable to proceed further.

Abel (1902a, 1902b) provided one of the more extensive overlooks of the question of odontocete cranial asymmetry. Noting the fundamental differences between mysticetes and odontocetes in the narial region, Abel correlated cranial asymmetry in the latter with posterodorsal displacement of the nares. He ascribed the immediate cause of the asymmetry to the development of the nasal and interparietal bones during ontogeny, but was unable to arrive at any functional or phyletic conclusions. He did state that the asymmetric pigmentation of the finwhale was not related to the cranial asymmetry of the odontocetes, thus implicitly contradicting Pouchet's (1886) theory of pleuronectism. He also felt that Kükenthal's (1893) ideas about the relationship of the flukes to cranial asymmetry were incorrect.

Lahille (1908) examined a skull of *Balaenoptera acutorostrata* in which there was a slight asymmetry of the nasal bones. He correlated this with lack of a hypoglossal canal on one side, which he felt might have produced a physiologic asymmetry, and suggested that cranial asymmetry in cetaceans in general might be connected with similar asymmetries in soft structures. The lack of a hypoglossal canal on one side (the hypoglossal nerve then exiting through the posterior lacerate foramen) is relatively common and not connected with any other manifestations of asymmetry. The cranial asymmetry of odontocetes is certainly correlated with soft part asymmetries, but not as far removed as the ventral surface of the head.

Kükenthal (1908) was of the opinion that Cetacea progressed through the water with a spiral motion of the flukes. This was based partly on the observations of earlier writers (Beddard, 1900) of animals at sea, where the motion of the flukes seemed more complex than a simple up and down stroke. It was also based on Kükenthal's own observations on fetal material (1893), where the flukes are folded in a spiral fashion. Kükenthal felt that this mode of locomotion produced a torque, bending the head to the left, and that the cranial asymmetry was produced by the difference in water pressure on the two sides of the head as the animal swam.

The principal defect in Kükesthal's theory is that the evidence applies equally to mysticetes, in which there is no cranial asymmetry. Slijper (1936) suggested that the folding of the flukes in the fetus may play a role in the uterus. The question of movements of the flukes in locomotion is very complex. However, there is no sound evidence for any asymmetry in their movements (Parry, 1949).

Lillie (1910) noticed that the larynx in two specimens of *Physeter* examined at a whaling station was situated on the left side of the pharynx. He concluded that this had developed to facilitate passage of food through the gullet and that it has resulted in asymmetric development of the nares (the idea being implicit that differential use of the nares in respiration resulted in the asymmetry). One would expect on the basis of his hypothesis that the left naris would be the larger of the two. This, however, is the opposite of what actually occurs. Lillie noted that Pouchet and Beauregard (1892) found the larynx to be situated on the right in *Physeter.* I would suspect that the larynx is mobile, and that the position in which it lies depends upon postmortem manipulation of the carcass. Purves (1967:299) commented further on this:

> To complete the general description of the nasopharynx, it must be stated, that, as with the larynx, this part of the respiratory tract is perfectly bilaterally symmetrical and in marked contrast with the upper narial region, which in the odontocete is noted for its asymmetry. Even in the sperm whale *Physeter catodon,* in which one of the upper nares is from five to seven times greater in diameter than the other, there is not the least trace of asymmetry in the posterior narial region.

I would agree with this. However, on page 259 of the same paper Purves stated:

> In most odontocetes the left bony narial aperture is larger than the right and the naris follows a more vertical course. The epiglottic spout is bent slightly to the left (markedly so in the Ziphiidae and Physeterida) and when the larynx is pushed upward into the nasopharynx the glottis moves towards the left posterior naris.

It is difficult to decide what Purves had in mind. The narial passages of the odontocetes which I have examined were symmetrical, except for the area immediately adjacent to their exit from the skull. As for *Physeter,* the narial asymmetry is considerable and apparently extends well down the bony nasal passage. Hosakawa (1950) noted that one of the intrinsic laryngeal muscles was asymmetrical in *Physeter,* as was the relationship of the esophagus to the larynx. He did not, however, mention that the larynx itself was asymmetrical.

Houssay (1912) agreed with Kükenthal's correlation of cranial and caudal asymmetry, but thought that the cause and effect were somewhat different. According to his theory, the early cetacea were unstable, tending to capsize. This resulted in the cranial asymmetry. Subsequently the caudal asymmetry developed to correct for the instability problem.

Steinmann (1912) followed the theory of Kükenthal (1908), but went beyond it in attempting to explain the origin of the asymmetry in the flukes. According to this theory, cetaceans are descended from ichthyosaurs and the horizontal flukes of the former are derived from the vertical tail of the latter. He noted that the vertebral column of ichthyosaurs extended only into the lower lobe of the tail, which is larger than the upper lobe. As the tail rotated to assume a horizontal position, the vertebral column regressed, but the former lower lobe remained larger and the flukes retained an ontogenetic vestige of this rotation in the form of the spiral folding observed by Kükenthal.

Howell (1925) discussed cranial asymmetry only in noncetaceans and concluded that, when developed to an appreciable extent, it was due to disease or injury.

Howell (1930) reviewed a few of the early theories on cranial asymmetry and dismissed them as unconvincing. He stated that he and Ernst Huber had suspected the nasal musculature, but upon examining it found it to be symmetrical, and was unable to shed further light on the question.

Richard (1930) described an asymmetrical bending of the hemal arches in several specimens of the sperm whale. From this he concluded that unequal forces were being applied by the caudal musculature originating from them, and that these were producing the asymmetry of the skull. He applied this theory to cetaceans in general, and suggested that cranial asymmetry was not produced in the mysticetes because the elastic jaw joints and the large mass of the tongue acted as cushions to absorb the forces applied by the tail. Slijper (1936), however, stated that he could not find the consistent caudal asymmetry upon which Richard based his theory.

Slijper (1936), in his monograph on cetacean anatomy, gave considerable attention to the question of cranial asymmetry. Building upon the wealth of theories advanced by earlier workers (largely Abel, 1902b; Houssay, 1912; and Pouchet, 1886), Slijper arrived at a phyletic and functional interpretation of odontocete cranial asymmetry. He accepted Pouchet's (1886) pleuronectism theory as the immediate cause of the cranial asymmetry, and looked for the cause of the swimming instability postulated by that author. Slijper's extensive examination of the relationships of the viscera (which are normally asymmetrically disposed in vertebrates) resulted in the observation that the Cetacea were uncommonly symmetrical in this area. He countered this observation by supposing that, in the transition from terrestrial forms, there must have been an ancestral form which had the viscera (mainly the lungs) asymmetrically arranged, and that the cranial asymmetry became fixed during that stage of phylogenetic development. Subsequently Slijper (1958) discovered that the apparent organ symmetry documented earlier (Slijper, 1936) was in error, and that the viscera of cetaceans are as asymmetrically disposed as those of terrestrial mammals.

Sleptsov (1939) investigated the state of cranial asymmetry in fetal specimens of *Delphinus, Delphinapterus*, and *Phocoena* with regard to Kükenthal's (1908) theory. Sleptsov found asymmetry to be present at an early stage and strongly criticized Kükenthal's ideas. He also measured a series of flukes and found no consistent asymmetry. Sleptsov suggested that the cranial asymmetry resulted from more rapid ontogenetic reduction of the olfactory nerve on the left. He also suggested that the asymmetry is useful in breathing without, however, providing any basis for this.

Purves (1967) presented the most recent discussion of the problem of cranial asymmetry in odontocetes. He considered asymmetry of the narial diverticula to be related to hydrostatic problems. This was based on the argument that lateral displacement of the blowhole is advantageous during ventilation, to reduce the amount of expired air and water vapor taken in on inspiration. It is difficult to imagine that the observed displacement of the blowhole laterally (on the order of 1 to 2 cm in a large *Tursiops*) has an appreciable effect on the pattern of flow of air and water vapor during expiration. At any rate, one might expect the pattern of flow in expiration and inspiration to be similar (i.e., if expired air is expelled laterally, then inspired air should be drawn from that direction as well).

Displacement of the blowhole, along with the associated diverticula would, according to Purves (1967), result in a shift in the center of buoyancy of the head, tending to return the blowhole to a middorsal position. In order to counteract this, the diverticula have become larger on the right. This disparity of size in the diverticula is true for the deeper diverticula, but not for the vestibular sac, to which Purves assigns a particular hydrostatic importance. The vestibular sac is slightly larger on the right in some animals, equal in others, and larger on the left in some. In some genera, such as *Stenella*, this sac is consistently larger on the left than on the right.

Purves (1967) further argued that paired nasal passages of equal size are less efficient (in terms of airflow) than if one is increased in size and the other correspondingly decreased. His argument in terms of surface/volume ratio is quite plausible. However, it also follows that efficiency would be even more drastically improved if both nasal passages were increased in size, and thus is not an argument in favor of asymmetry, but of increased diameter alone. It would seem that if the factors controlling the diameter of the nasal passages would allow an increase in the size of one, then they might also allow an increase in the other. The same net increase in efficiency gained by increasing the size of one passage, while decreasing the size of the other, could be gained by a relatively small increase in the size of both passages. The above arguments aside, it does not appear that the bony nasal passages, in delphinids at least, differ in diameter at any point other than their immediate exit from the skull. As for the fleshy portion of the passages, the right is much larger than the left, contra Purves' arguments.

To summarize the discussion thus far, the early theories attempting to explain the functional basis of the cranial asymmetry fall largely into two categories: (1) those based upon the assumption of asymmetrical locomotory forces (Kükenthal, 1908; Steinmann, 1912; Richard, 1930; Borri, 1931) produced by a screwlike movement of the flukes; and (2) those based upon a buoyancy-related instability or some unspecified lopsidedness (Pouchet, 1886; Houssay, 1912; Slijper, 1936). Slijper (1936, 1961) presented anatomical and observational data sufficient to indicate that the first group of theories has no basis in fact and concluded that the folding of the flukes observed in fetal material could be related to problems of gestation and birth. He also concluded that the axial musculature showed no asymmetrical development and that there was no observational basis for asymmetrical movements in swimming. In addition, it is obvious that those theories apply equally well to the mysticetes. Richard (1930) had countered this argument by suggesting asymmetrical forces were absorbed by the elastic joints and tongue of mysticetes. But, according to this reasoning, *Physeter*, with its enormous mass of connective tissue and fat on its head, should be the least affected of all whales, whereas it is the most asymmetrical in its facial anatomy.

The second group of theories can also be criticized on the basis that it applies equally well to both suborders (as well as to other aquatic mammals) and, in fact, would apply most strongly to archaeocetes, which show no signs of cranial asymmetry. In addition, these theories rest upon Pouchet's (1886) hypothesis that the blowhole will tend to migrate dorsally. Thus, it would be expected that the blowhole would be the most asymmetrically situated element in the system. While the blowhole is placed slightly laterally, its relations are not nearly as asymmetrical as those of the deeper elements.

This brings us to the observation (Howell, 1930; Abel, 1902; Beddard, 1900) that asymmetry of the skull is correlated with the development of a complex nasal apparatus. This is based upon the facts that (1) the blowhole apparatus is more complex in all odontocetes than it is in any mysticete, and (2) that the most complicated nasal complexes, those of the physeterids, are associated with the most asymmetrical skulls.

Norris (1964) discussed cranial asymmetry as it might relate to sound production and suggested that it might be instrumental in producing the observed asymmetrical sound fields. He also suggested that the sound field asymmetry might be more complicated than it seems, particularly with respect to frequency distribution. In a later paper (Norris, 1968), he noticed that the melon entered only the right nasal plug in *Delphinus*, but did not seem to connect this with the rest of the cranial asymmetry.

Wood (1967), in a discussion of the nasal passages of *Kogia*, made the following observation: "I think this asymmetry in the skull reflects the evolutionary development of sound producing mechanisms and the utilization of one narial passage primarily for sound production, and the other for breathing."

This is the conclusion at which I have arrived through examination of the delphinids, and which I think can be applied to odontocetes in general.

ANATOMICAL CONSIDERATIONS

I have approached the problem of cranial asymmetry by first assuming that it is probably not the bones which are primarily asymmetrical, but the soft tissues associated with them. This working hypothesis is based upon the generalization that bony elements of a complex system are likely to be more strongly influenced by the soft tissues which they support than the other way around (Moss and Salentijn, 1969). Accordingly, I have attempted to ascertain which soft structures exhibited the greatest degree of asymmetry, as an indication of where the primary source of asymmetry might lie.

This approach was largely confined to specimens of *Stenella*, which provided the only sample large enough to take individual variation and dissecting errors into account. The small amount of data collected from other genera show the same trends as the *Stenella* data. My data on muscle weights confirms the observation of Howell (1930) that the musculature is relatively symmetrical (Table 3). While a number of the weights of individual muscles were markedly asymmetrical in some of the specimens, the combined weights of all of the muscles for the specimens were less so. There is considerable variation in the muscle weight ratios, some of which is, no doubt, due to factors of dissection. These factors are substantially reduced by lumping the weights for all the muscles on each side of a specimen (total muscle weight ratio). This ratio shows a consistent asymmetry, on the order of 5 to 10 percent. If anything, I feel that this is due to inclusion of more connective tissue in the muscle samples from the right sides. The tendon of insertion of these muscles is larger and, even though I attempted to remove it consistently on both sides, probably accounts for some of the asymmetry. At any rate, this asymmetry is much less than that seen in the relative widths of the nasal passages, which is on the order of 50 percent. The asymmetry of the deep diverticula, as estimated visually, is on this order as well, as is the width of the lateral lip of the nasal plug. The vestibular sac did not appear to fit into this pattern, so it was dissected and the epithelium of the sac weighed to obtain relative size. The data of Table 3 indicate that for the *Stenella* sample, the vestibular sacs are equal in size, or slightly larger on the left, in contrast to the deeper diverticula, which are larger on the right. As with many other characters, *Stenella coeruleoalba* was an exception, the right vestibular sac being 50 percent larger than the left.

Having seen that the primary asymmetry probably lies in the fleshy portion of the nasal complex between the levels of the premaxillary and vestibular sacs, we can attempt to interpret it functionally. As discussed earlier in this paper, these structures are apparently concerned with the production and/or manipulation of sound.

Since the larynx normally occupies an intranarial position, all of the theories of sound production necessitate movement of air through the cranial portions of the respiratory tract. Observations on living animals indicate that most sounds are produced without loss of air from the system, the advantages of which are obvious to a diving animal. This means that air must be stored in the distal portions of the system and recycled for sound production. Since the diverticula are larger on the right, it may be suggested that more air is cycled through the right-hand portions of the system. This is equally applicable, whether the sound is produced by the larynx, around the nasal plugs, or in both places. In any case, it suggests that greater acoustic activity takes place on the right side. The same logic applies if the diverticula are considered as reflective structures.

If the melon functions as an acoustic pathway, then its posterior extension into the right nasal plug supports both the idea of the nasal plug as a sound source and the idea of greater acoustic activity on the right side.

As noted above, these arguments work equally well for laryngeal or nasal sound production. If, however, sound production by the lateral lip of the nasal plug is considered separately, some interesting possibilities appear. The lip of the nasal plug and the adjacent structures are larger on the right, which might render them more suitable for sound production.

Lawrence and Schevill (1956) presented some interesting data relevant to the functioning of the large nasal plug on the right side. They observed an asymmetry in the opening and closing of the blowhole, with the left side opening earlier than the right. Their sequential photographs of blowhole movements also indicate that the left passage opens wider than the right. In some of their photos it is possible to see straight down into the bony nasal passage on the left side, while the right side is always slightly occluded by the nasal plugs. I would suggest that this is due both to the greater size of the lips of the nasal plug on the right, and to the invasion of the nasal plug muscle by the melon on that side, rendering it less effective as a retractor of the plugs. It does seem clear that the right nasal passage is less effective than the left during ventilation. This implies that the modifications on the right side must be of sufficient functional importance to offset the respiratory disadvantage incurred.

Norris et al. (1971) noted asymmetric activity in the blowhole during production of squeals in *Stenella longirostris*. In this case, the left side was active, while the right side appeared quiet. They suggested the possibility that the left side is primarily involved in low-frequency sound production, while the right side may be specialized for the production of clicks. However, if movement of air through the larynx is involved in low-frequency sound production, as suggested by several workers, it would be reasonable to expect movement of air primarily through the less specialized left naris, as in respiration.

Taking all of the preceding arguments into account, I believe that at some point in cetacean evolution, the nasal plugs, which probably originally developed as valves, became involved in sound production. As a result of the mechanism of sound production it became advantageous to increase their size. This, however, had an adverse effect on ventilation, so that one passage became specialized for vocalization, while the other remained as a respiratory pathway. Consequently the blowhole was shifted slightly, to lie more directly over the respiratory side.

A larger nasal plug requires a larger posterolateral area in the premaxillary sac to accommodate it. As the premaxillary sac is intimately related to the ascending process of the premaxilla, this accounts for that portion of the bony asymmetry. This also explains the shift to the left in the aperture of the bony nasal passage. The increase in the size of the other deep diverticula may be related to their function as air reservoirs, reflecting elements, or to direct involvement in sound production.

It must be borne in mind that the acoustic functioning of the structures in the odontocete head is still poorly understood. While I have emphasized the possible role of asymmetry in differences in sound quantity, it may equally well be involved in differences in sound quality (e.g., sound of a higher frequency may be differentially produced on one side, or the asymmetry may affect generation of harmonics).

Summary of Facial Complex Function

NASAL DIVERTICULA

The nasal diverticula probably function both as air reservoirs during phonation and as sound reflectors serving to direct the sound field anteriorly. The exact relationships of these functions are not known, but it seems likely that the vestibular sac serves as both a receptable for air and as one of the principal reflectors. The premaxillary sac may serve as a source of air during phonation.

The nasofrontal sac is more of a problem. In most delphinids it appears to be too small to be particularly important as either a reservoir or a reflector. In these animals its primary function may be that suggested by Lawrence and Schevill (1956), as a partial pneumatic seal of the nasal passage above the level of the nasal plugs. In *Lagenorhynchus* this diverticulum has been greatly enlarged and may be of considerable importance as both a reservoir and a reflector. In *Grampus*, where the anterior portion of the nasofrontal sac is absent on the left, its effectiveness as a pneumatic seal is impaired. The enlarged right-hand portion, however, may be more effective as a reservoir or reflector.

The function of the accessory sac is difficult to ascertain, as it appears to be inconsequential due to its small size. If the source of sound is close to this diverticulum, as is hypothesized, then it may be important as a reflector of sound which would otherwise radiate laterally.

The lateral premaxillary diverticulum of *Lagenorhynchus* and *Lagenodelphis* probably serves principally to increase the volume of the premaxillary sac, substantiating the role of the latter as an air reservoir.

The pronounced directionality observed in the delphinid sound field necessitates the presence of an effective focusing mechanism. At the moment it seems likely that this is accomplished at least in part by reflection from the nasal diverticula.

NASAL MUSCULATURE

The larger nasal muscles (*pe, i, ae, pi*, and *ai*) open and close the nasal passage at various levels, a function important both in respiration and sound production. The more superficial of these muscles (*pe, i, ae*, and to a certain extent *pi*) effect closure above the level of the nasal plug. *Pi* and *ai* also serve to seat the nasal plugs in the orifice of the bony nasal passage. *Ae* and a small anterior portion of *ai* are functional in opening the nasal passage. This is in marked contrast to the interpretation of Schenkkan (1973), that the musculature functions only to open the nasal passages.

The nasal plug muscle serves both to withdraw the nasal plugs from the aperture of the bony nasal passage during respiration and possibly to effect complex movements of the nasal plugs during phonation.

The role of the intrinsic musculature is very poorly understood. It is capable of altering the configuration of the posterior portion of the nasofrontal sac, but in which functions this would be important is unknown. The diagonal membrane muscle is possibly active during phonation, serving to change the tension of the diagonal membrane and thus to alter its contact with the nasal plug.

OTHER STRUCTURES

Both the nasal plug and the diagonal membrane have been implicated in sound production. They also serve to close the nasal passage at the lower of the bony nares. The blowhole ligament provides stability in the relationships of the deep structures, principally the apertures of the nasofrontal and accessory sacs. It is also important in providing a surface against which the nasal plug fits to close the nasal passages.

The melon is probably an acoustic channel, providing a path of minimum resistance for sound passing in an anterior direction. The rostral musculature may be involved in movements of the lips or may be related in some obscure way to sound transmission.

Experimental Approaches

As stated earlier in this paper, none of the experimental data currently available allows correlations to be made between structure and function. It is most important to obtain comparative data which will allow such parameters as shape of the sound field to be correlated with differences in anatomy of the facial complex. This will provide information of the structures important in shaping the sound field. It should also be ascertained whether the shape of the sound field is capable of being actively altered by the animal. To a lesser extent, comparative data on the frequency range of sound production may allow correlations to be made with anatomical differences.

The nasal complex appears to be suitable for investigation by electromyography. Simultaneous synchronized recording of muscular activity and both vocalization and respiratory movements would provide evidence on the function of the various components of this complex. These techniques could also be useful coupled with cineradiography, such as used by Norris et al. (1971).

To a lesser extent, the nasal structures may be modified experimentally in order to see what effect this would have on sound production. Perhaps the most useful approach here would be to fill the various diverticula with some inert substance, such as silicone rubber, which would alter both their functioning as reservoirs and reflectors. Surgical alteration of these elements has the drawback of introducing the element of trauma and thus rendering the conclusions suspect.

In any of these approaches it would be useful to obtain information from as wide a morphologic range as possible. Data on the phocoenids would be of particular interest, as their nasal structure is considerably different from that of the delphinids.

PHYLETIC RELATIONS OF THE DELPHINIDAE

Relationships within the Delphinidae

The classification of odontocetes used in this paper is essentially that of Simpson (1945), with the suprageneric groupings of Fraser and Purves (1960). *Peponocephala* has been placed in the Delphininae on the basis of osteological resemblances of Lagenorhynchus, but its position here is still subject to question. *Peponocephala electra* was formerly placed in the genus *Lagenorhynchus* (True, 1889). Within the family Delphinidae, as used here, there are five subfamilies: Delphininae, Orcininae, Lissodelphinae, Cephalorhynchinae, and Steninae. On the basis of osteological characters the Delphinidae is generally felt to constitute a coherent assemblage. The arrangement of Delphinids into subfamilial groups is a fairly recent development. Slijper (1936) made one of the better attempts to establish groups of genera within the Delphinidae, and recognized that a distinction needed to be made between the delphinines and the orcinines. Fraser and Purves (1960) provided the most well-founded grouping of delphinid genera, based upon characters of the ventral portion of the skull.

I have found that, in general, the delphinids are fairly conservative in their facial anatomy. Thus, I have found no characters which consistently separate the Orcininae and the Delphininae, the only two subfamilies for which I have had extensive material. Nor do the subfamilies Steninae and Lissodelphinae, for which there is comparative data, present any major differences from these delphinids. The Cephalorhynchinae, as represented by *Cephalorhynchus hectori*, seem quite distinct from the other delphinids in terms of facial morphology. In the following discussions involving the relationships of various genera, it must be borne in mind that in some of these all of the species have not been examined and the conclusions are therefore somewhat tentative.

Within the Delphinidae, *Tursiops* appears to be a conservative, generalized animal, and can be related with equal facility to all but the most divergent species. Within the subfamily Delphininae it is structurally most similar to *Stenella* and *Delphinus*. The relationships of the species in this group of three genera have been examined by Fraser and Purves (1960) and Mitchell (1970). They agree that *Tursiops* is the most generalized of this series, and *Delphinus* is the most specialized. The interrelationships of the numerous species of *Stenella* are uncertain at this time. Mitchell (1970) has suggested that *S. attenuata* and *S. longirostris* are the most generalized of this group, so far as external pigmentation is concerned, and that the other species may represent divergent specializations. The data from facial anatomy indicate that the *Stenella* species form a closely related group, with only one of the species examined being unusual. *Stenella coeruleoalba* differs from the other *Stenella* species in a number of features of the nasal diverticula. It thus appears to be the only member of the *Tursiops-Stenella-Delphinus* group which has diverged on the basis of nasal specializations.

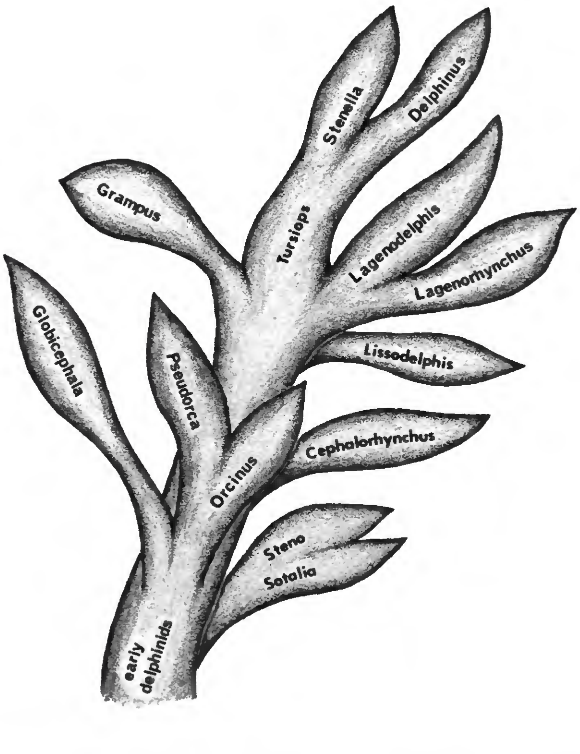

Figure 21.—Phyletic relationships of the delphinid genera examined in this study, based upon both data from the facial anatomy and from the literature.

In addition to the *Stenella* species group, there is a large group of species gathered into the genus *Lagenorhynchus*. Of the four species for which information is available, three (*L. acutus, L. obliquidens,* and *L. obscurus*) are essentially similar to *Tursiops* in facial morphology, while the fourth (*L. albirostris*) differs in development of the nasal diverticula. A number of authors (True, 1889; Fraser, 1966; Fraser and Purves, 1960; Mitchell, 1970) have suggested that *L. obscurus* is similar in many ways to *Stenella,* and it may be the most generalized of the *Lagenorhynchus* species, while *L. albirostris* may be the most specialized.

Lagenodelphis should probably be grouped with the *Lagenorhynchus* species, as it shows a resemblance to *L. albirostris* in its facial anatomy, and differs from the rest of the delphinids in this point. Fraser (1956), in the initial description of *Lagenodelphis,* suggested not only a relationship to *Lagenorhynchus,* but also to *Delphinus* and *Stenella.*

Grampus seems to be closely related to *Tursiops* in osteological characters, structure of the pterygoid air sinuses (Fraser and Purves, 1960), and the existence of possible hybrids (Fraser, 1940). It is quite different from *Tursiops* in its facial anatomy, and I would be tempted to put it in a subfamily by itself if not for the data relating it to *Tursiops.*

There is no anatomical information available for *Peponocephala,* which seems to represent a development toward a bulbous-headed form from the *Lagenorhynchus* group.

The Orcininae appear to form a natural group on the basis of development of the pterygoid air sinuses (Fraser and Purves, 1960), but specific relationships within this subfamily are not clear. Fraser and Purves suggested that *Pseudorca, Orcinus,* and *Orcaella* formed a "natural sequence of specialization," while *Feresa* and *Globicephala* showed certain resemblances to one another and to *Orcinus.* Mitchell (1970) suggested a slightly different arrangement, with *Feresa* and *Orcinus* forming one group, *Globicephala, Orcaella,* and *Pseudorca* forming another. Anatomical data is available only for the three genera which I dissected, *Orcinus, Pseudorca,* and *Globicephala. Orcinus* appears to be a very generalized delphinid, which has attained a large size and has become specialized for feeding on large prey. The melon is relatively small and structures posterior to it show no specializations. *Pseudorca* is similar to *Orcinus* (and to *Tursiops,* for that matter), except in the development of a large, elongate connective tissue mass on the forehead external to the melon. As described earlier, there is no increase in the size of the melon, and it is thus quite different from both *Grampus* and *Globicephala. Globicephala* has developed a similar layer of thick dermal connective tissue, but has greatly enlarged the melon as well. In addition, *Globicephala* shows some specializations in the nasal diverticula, separating it from the rest of the orcinines.

Information is available for only one species of the Cephalorhynchinae, *Cephalorhynchus hectori.* The anterior portions of the nasofrontal sacs are extremely large, somewhat similar to the condition seen in the *Lagenorhynchus albirostris* specimen which I dissected. *Cephalorhynchus hectori* differs markedly, however, in that the left nasofrontal sac is by far the larger, whereas the right is larger in all other delphinids for which there is information. *Cephalorhynchus hectori* was also unusual in that the fatty tissue of the melon did not penetrate the right nasal plug as it does in most delphinids.

Cephalorhynchus is clearly different from the other delphinids in a number of other characters, such as details of the skull, postcranial skeleton, and external body form. In some of these it shows resemblances to phocoenids, and may in fact be somewhat convergent upon them.

The Lissodelphinae (consisting only of the two species of *Lissodelphis*) show no particular specializations from the general delphinid facial morphology and are separated on the basis of their peculiar elongate body form. In general cranial characters they are perhaps most similar to *Lagenorhynchus* and may represent a locomotory specialization from an origin near that genus.

The data available for the Steninae indicate a generalized facial morphology, essentially similar to that of *Tursiops.* Dohl et al. (1974) reported a viable hybrid between *Tursiops* sp. and *Steno bredanensis,* suggesting a fairly close genetic relationship between these genera.

Relationships to Other Families

In the structure of the face the Phocoenidae are as different from the delphinids as are any of the nonphyseteroid odontocetes. This is manifest in the form of the vestibular sac and the greater complication of structures around the inferior vestibule.

The Monodontidae also represent a divergent group, with *Monodon* appearing to be more specialized facially than *Delphinapterus.* In some respects the monodontids resemble the phocoenids, and may actually be more closely related to that group than to the delphinids. The details are unclear, however, and more work is needed to establish the degree of relationship of these two genera to one another and to the other delphinoid families.

The data available for the Platanistidae suggest that this is a very heterogeneous grouping of genera. They have been grouped in a variety of ways in different systems of classification, perhaps the most soundly based being that of Fraser and Purves (1960) in which *Inia* and *Lipotes* are grouped together. There is some indication, however, that *Lipotes* and *Pontoporia* are related in facial structure (Hinton, 1936). There seems to be general agreement that *Platanista* is not particularly related to the other genera, largely on the basis of facial characters. The relationship of the Platanistidae to the Delphinidae is uncertain, but does not appear to be very close.

Very little data is available for the Physeteridae, and that which exists is sometimes contradictory. *Physeter* and *Kogia* are very different from one

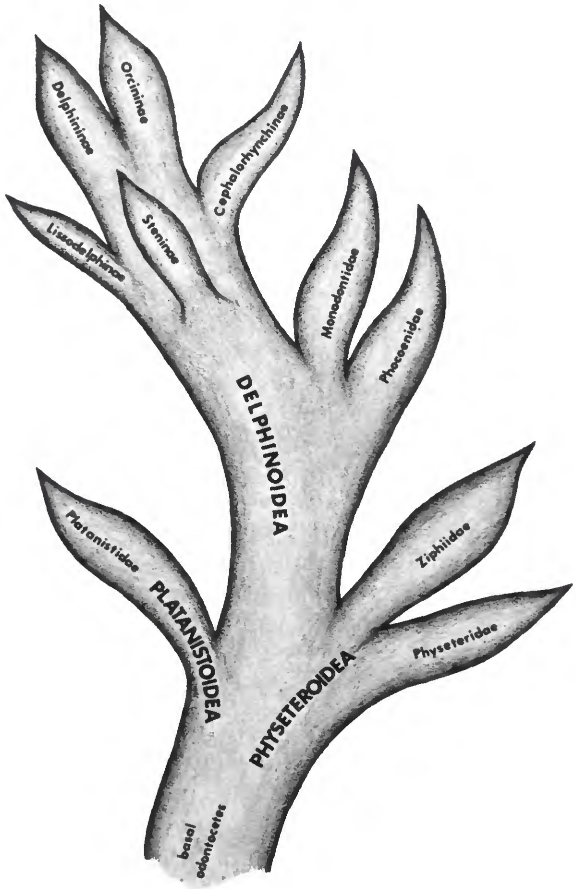

FIGURE 22.—Phyletic relationships of the suprageneric groups of odontocetes. (Based upon both data from the facial anatomy and from the literature.)

another, but appear to be even more different from the rest of the odontocetes, and bear no particular relationship to the delphinids.

The Ziphiidae are another unusual group whose relationships are not clear. They are commonly grouped with the Physeteridae, though the evidence for this relationship is tenuous. The scanty information on ziphiid facial anatomy (Schenkkan, 1973) indicates a morphology more comparable to delphinids than to physeterids, but still quite different from either. Relationships within the Ziphiidae are equally unclear.

Relationships of Bulbous-headed Delphinids

GENERAL CONSIDERATIONS

Bulbous-headed species have developed independently in a number of odontocete groups. In these animals some portion of the facial apparatus has become hypertrophied, resulting in a bulbous appearance of the forehead.

In the delphinines, *Grampus* represents an extreme development of this type, while *Peponocephala* shows a slight hypertrophy of this area. Hypertrophy of the facial structures is common in the orciniines, all members of this subfamily except *Orcinus* showing it to a certain extent. In none of the other delphinids, however, is this condition developed.

Among the nondelphinid odontocetes, several groups show hypertrophy of the facial elements. The monodontids are quite bulbous-headed, as are some of the ziphiids (*Hyperoodon* and *Berardius*). Although facial structures in the platanistids appear to be extremely complicated, none of them have developed a bulbous forehead. One phocoenid, *Neophocaena*, should probably be included in the category of bulbous-headed animals. Both of the physeterid genera show extreme hypertrophy of this area, but in a manner totally unlike that of the other odontocetes.

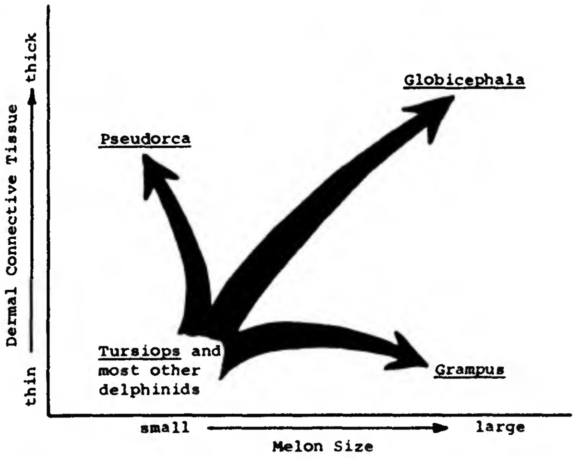

FIGURE 23.—Structural relationship of the bulbous-headed delphinids, according to which portion of the rostral tissues has become hypertrophied.

Of the bulbous-headed odontocetes, I have examined material of three of the delphinids, *Grampus, Globicephala,* and *Pseudorca.*

If the structures of the facial region are examined, two principal elements are seen to be involved in this hypertrophy: (1) the melon and (2) the dermal connective tissue overlying the melon. A coordinate system can be devised, as in Figure 23, in which the relative degree of hypertrophy of these elements can be presented graphically. In this graphic system the bulk of the delphinids, in which the facial structures are not hypertrophied, fall near the origins of the axes. Any displacement in a positive direction along these axes represents development toward bulbous-headedness. It can be seen from this graph that the three animals examined represent the three possible extremes of development of these characters. Presumably, when the other bulbous-headed odontocetes are examined they will occupy intermediate positions in this system. Physeterids must be excluded from these considerations, as they do not appear to be comparable to other odontocetes in these characters.

COMPARISON OF *Pseudorca, Globicephala,* AND *Grampus*

The general shape of the head differs considerably among these animals. In *Pseudorca* (Figure 26) the facial mass is enlarged anteriorly, retaining a more or less streamlined configuration. In *Globicephala* (Figures 18, 26) the enlargement takes place both anteriorly and dorsally, producing an extremely protuberant forehead (hence the common name "pot-head," which is sometimes applied to this animal). In *Grampus* (Figures 12, 25), enlargement is mainly in a dorsal direction, resulting in a high forehead, which slopes steeply down to the tip of the rostrum. In addition, there is a median sulcus on the anterior portion of the forehead of *Grampus* (Figure 12), resulting in a distinctly bilobed external surface.

As is indicated in Figure 23, the relative degree of hypertrophy of the anterior facial elements differs among these three animals. In *Pseudorca* only the dermal connective tissue is hypertrophied, while in *Grampus* only the melon is involved. In *Globicephala,* which has by far the largest forehead mass, both of these elements have increased in size. As a result, the consistency of the forehead is different in these animals. In *Pseudorca* and *Globicephala,* in which the dermal connective tissue is very thick, the forehead mass is extremely firm and resilient. In *Grampus,* on the other hand, the forehead is quite soft. In this connection it is interesting to note that a prominent feature of the behavior of *Globicephala* is head-butting (Kritzler, 1952; Brown, 1962). This appears to be connected with mating behavior. Comparable data are not available for *Pseudorca* and *Grampus,* but it might be expected on the basis of anatomical similarities that *Pseudorca* would engage in this behavior, while *Grampus* would not.

The nasal diverticula present some interesting modifications in these animals. The vestibular sacs are not remarkably different from those of the other delphinids, but lie consistently somewhat more posterior to the nasal passage. The nasofrontal sacs of *Pseudorca* are similar to those of *Tursiops,* while *Grampus* and *Globicephala* are markedly different. In *Grampus* the anterior portion of the right nasofrontal sac is extremely large, while that of the left is absent. In *Globicephala* the general size and shape are not peculiar, but there is an unusual trabeculate sacculation on the angle of the right sac. None of these modifications of the nasofrontal sac, however, appear to be related to the hypertrophy of the anterior structures. The remainder of the diverticula in all three animals are not notably different from those of *Tursiops.*

In the musculature, as in the diverticula, *Pseudorca* is similar to *Tursiops,* while *Grampus* and *Globicephala* present what appear to be independent specializations. In *Grampus, pe* is different from the condition seen in *Tursiops,* while in *Globicephala* it is *pi* which has been modified.

The degree of cranial asymmetry does not appear to be related to development of a bulbous forehead. In fact, *Globicephala* is unusual in being one of the two known delphinids in which the melon does not invade the right nasal plug.

These three animals clearly represent independent developments of enlarged facial structures In most respects *Pseudorca* is conservative, while *Grampus* and *Globicephala* represent extreme conditions. Very little information is available on the natural history of these animals, making it difficult to correlate facial hypertrophy with behavior or ecology. It is interesting to note that both *Globi-*

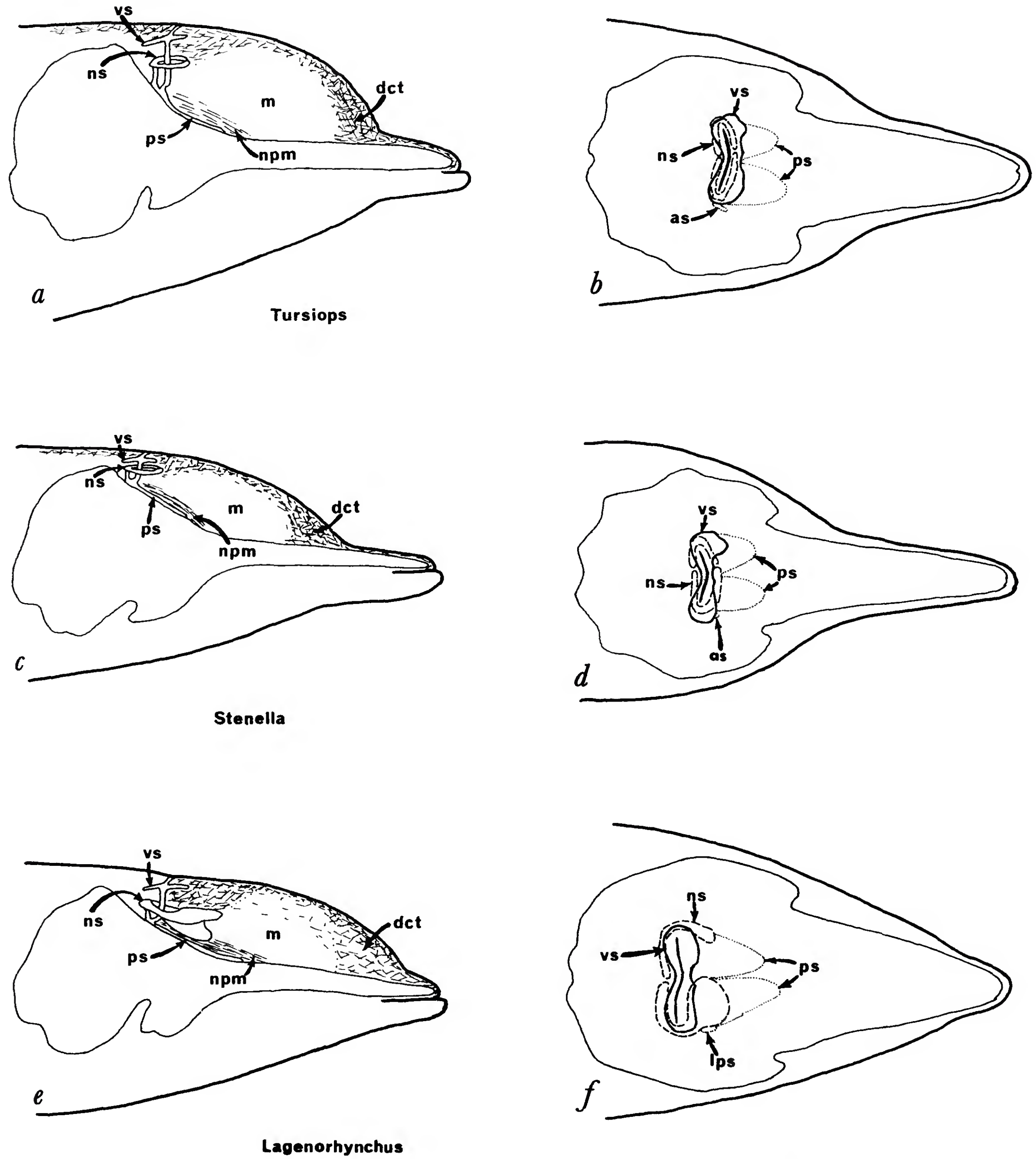

FIGURE 24.—Diagrammatic views of the nasal diverticula and melon. *Tursiops truncatus*: *a*, lateral view; *b*, dorsal view. *Stenella attenuata*: *c*, lateral view; *d*, dorsal view. *Lagenorhynchus albirostris*: *e*, lateral view; *f*, dorsal view. (as=accessory sac, dct=dermal connective tissue, lps=lateral premaxillary sac, m=melon, npm=nasal plug muscle, ns=nasofrontal sac, ps=premaxillary sac, vs=vestibular sac).

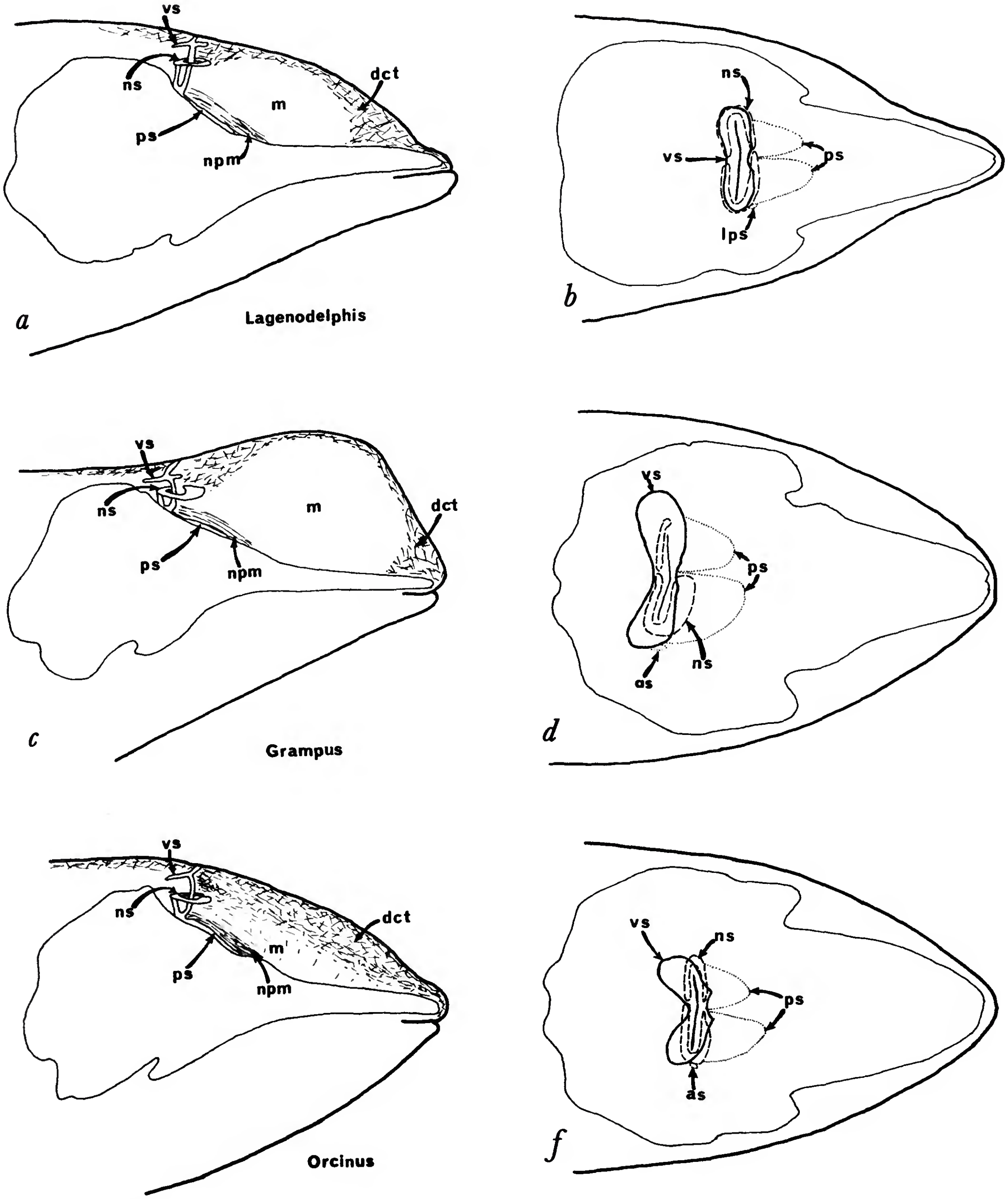

Figure 25.—Diagrammatic views of the nasal diverticula and melon. *Lagenodelphis hosei*: *a*, lateral view; *b*, dorsal view. *Grampus griseus*: *c*, lateral view; *d*, dorsal view. *Orcinus orca*: *e*, lateral view; *f*, dorsal view. (as=accessory sac, dct=dermal connective tissue, lps=lateral premaxillary sac, m=melon, npm=nasal plug muscle, ns=nasofrontal sac, ps=premaxillary sac, v=vestibular sac.)

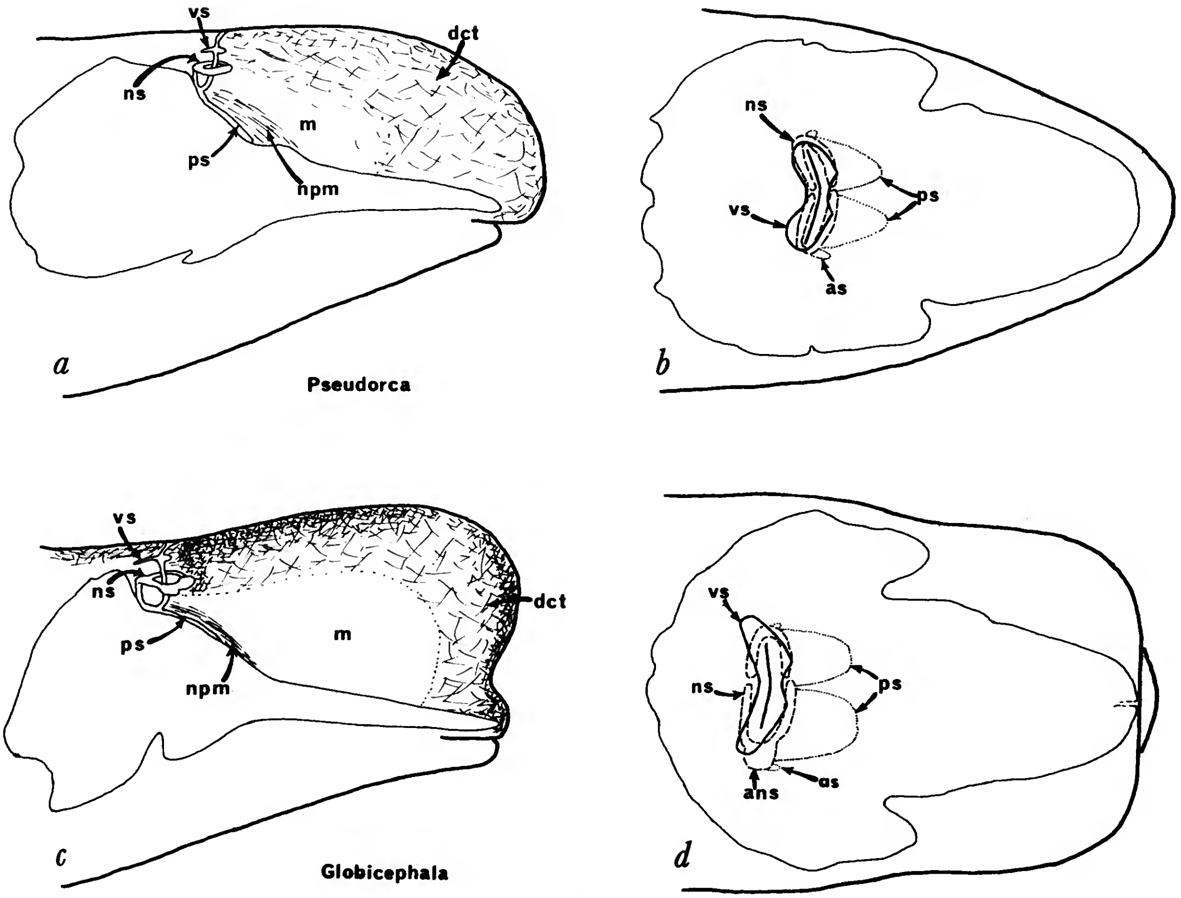

FIGURE 26.—Diagrammatic views of the nasal diverticula and melon. *Pseudorca crassidens*: *a*, lateral view; *b*, dorsal view. *Globicephala melaena*: *c*, lateral view; *d*, dorsal view. (as=accessory sac, dct=dermal connective tissue, lps=lateral premaxiliary sac, m=melon, npm=nasal plug muscle, ns=nasofrontal sac, ps=premaxillary sac, vs=vestibular sac.)

cephala and *Grampus* feed preferentially on squid, as do a number of other bulbous-headed animals (ziphiids, physeterids, and *Monodon*) (Tomilin, 1967). *Pseudorca* frequently feeds on cephalopods, but it also takes large quantities of fish, while *Delphinapterus* differs from the above forms in feeding predominantly on fish. The extreme hypertrophy of the anterior facial elements may be in some way correlated with a cephalopod diet, or it may merely be due to coincidence.

ORIGIN OF THE ODONTOCETE NASAL APPARATUS

The nose of most mammals is a relatively complex organ, and there is no reason to assume that the nose of the terrestrial ancestor of the cetaceans was any less complex than that of an ordinary dog or cat. It was probably provided with a series of muscles (of the maxillonasolabialis group) capable of constriction and dilation of its orifice according to the ordinary needs of terrestrial animals. During the course of evolution from such a terrestrial ancestor to the completely aquatic Cetacea, there should have been little difficulty in adapting the nose to fit the altered needs of an aquatic existence. Mere exclusion of water from the nasal passages appears to present very little problem, and has been accomplished many times by aquatic and semiaquatic vertebrates. The skull of the early archaeocetes does not indicate any special modifications in the nasal apparatus.

Elaboration of the soft tissues of the nose in cetaceans seems to have occurred after the separation of the lines leading to mysticetes and odontocetes. As noted in the introduction, the nose of the former is relatively simple and presents little in the way of modification from what was probably the primordial mammalian plan. Odontocetes, however, have drastically modified the structure of the nose. If such modifications are not necessary to exclude water from the nasal passages, as is evident from their absence in other aquatic mammals, then they are connected with some other function of the respiratory passages, in this case probably sound production.

The production of sound in mammals normally involves movement of air through the larynx. If this takes place underwater, where the animal cannot replenish its air supply, provisions must be made to prevent the loss of air through the nostrils. This movement of air results in an increase of pressure in that portion of the respiratory system distal to the larynx, proportional to the ratio of the volume of air used in phonation to the volume of the distal portion of the respiratory system. The pressure thus produced tends to force air through the nostrils, and poses a problem entirely different from that of excluding water from the nasal passages. One approach to this problem is to increase the capability of the nostrils to retain air under pressure, the other is to increase the volume of the distal air reservoir (assuming that the means of sound production has not altered in order to utilize a smaller volume of air in the production of sound).

Odontocetes appear to have approached this problem from both ways. The nasal musculature has greatly increased in size, making it possible for the animal to close the nasal passages effectively, and at several different levels. They have also developed a series of diverticula, expanding the volume of the reservoir available for storage of air. The mammalian nose seems to readily develop such diverticula in response to changing needs of the animal, as they are seen in a great variety of modern mammals. Anthony (1926) discussed the question of the homology of the nasal diverticula in cetaceans with those of other mammals, and concluded that they are most comparable to those of perissodactyls. Cetacea, however, seem to bear no other particular resemblance to perissodactyls, and there seems to be no reason to assume that the odontocete nasal diverticula were not developed de novo (particularly in consideration of their absence in mysticetes). It is easy to imagine that any increase in the volume of the distal portion of the nasal passage would prove of value to the early odontocetes and might lead to the development of a diverticulum. Norris (1968) has also suggested that the diverticula were an early development related to sound production.

The point might be raised that, since mysticetes are known to utilize underwater sound production, such a system would be advantageous to them, but is seen to be lacking. The difference between the two major divisions of living whales, in the structure of the noses and the larynx, suggest that specialized underwater phonation was probably developed independently by each. Mysticetes have always been large animals, and it may well be that the initial volume of the nasal passage was sufficient for retention of air during vocalization.

Once the nasal diverticula have developed, for whatever initial reasons, they will become effective reflectors of sound when filled with air. It seems likely that this has been utilized to some advantage by the odontocetes, and may now be one of the principal functions of these diverticula. This same line of reasoning is applicable to the possible function of the nasofrontal sac in pneumatic closure of the nasal passage.

The origin of the melon is a more difficult problem. Schenkkan (1972) stated that the melon is a "degenerate, hypertrophied part of the musculus maxillolabialis." Purves and Pilleri (1973) elaborated this view somewhat, suggesting that the melon was initially a fibrous structure derived by "hypertrophy of the tendinous origin of the maxillolabialis," and that the fatty melon seen in most odontocetes represents a degeneration of this condition.

One of the critical problems in understanding the origin of the melon is our lack of understanding of its function. It seems clear that it is structurally related to the insertion of the medial portion of the rostral muscle (which is equivalent to part of the m. maxillolabialis as used by the above authors), but its functional relationship to this muscle is uncertain. At this point it is not possible to decide whether the musculature as such was once more extensive and the melon developed through fibrous or fatty degeneration of the muscle, whether it developed as a fibrous or fatty addition to the muscle, or whether in fact the medial portion of the rostral muscle was absent primitively and developed along with a fibrous or fatty structure in this area.

The possible relation of cranial asymmetry to sound production raises some interesting evolutionary possibilities. If extra-laryngeal sound production in modern odontocetes is connected with cranial asymmetry, as suggested earlier in this paper, this gives us a functional character which can be traced back into the fossil record. A cursory examination of the data available for fossil odontocetes indicates that many of the Miocene forms show cranial asymmetry similar to that of the living delphinids, and they may therefore have possessed a similar acoustic system. The nature of the fossil material is such, however, that a detailed study is necessary to demonstrate the extent of the cranial asymmetry in the early forms.

There is, however, a comparative anatomical approach to the question of the origin of the modern odontocete acoustical system. The fact that the cranial asymmetry in all of the odontocetes involves a displacement of the nares to the left suggests that this cranial asymmetry was present in a common ancestor. This raises the possibility that some of the very early odontocetes utilized the nasal apparatus for sound production and had reached a level of specialization where one passage was dominant in this role. Whether or not echolocation was involved is something which we probably can never determine. It does suggest, however, that sound production was important and formed one of the bases for the differentiation of the odontocetes from the mysticetes and from the more archaic cetaceans.

Appendix 1

CLASSIFICATION OF THE ODONTOCETES (TOOTHED WHALES)

- Order Cetacea Brisson, 1762
  - Suborder Odontoceti Flower, 1867
    - Superfamily Physeteroidea Gill, 1872
      - Family Physeteridae Gray, 1821
        - Subfamily Physeterinae Flower, 1867
          - *Physeter* Linnaenus, 1758 [sperm whale]
        - Subfamily Kogiinae Gill, 1871
          - *Kogia* Gray, 1846 [pigmy sperm whales]
      - Family Ziphiidae Gray, 1865
        - *Mesoplodon* Gervais, 1850 [beaked whales]
        - *Ziphius* Cuvier, 1823 [Cuvier's beaked whale]
        - *Tasmacetus* Oliver, 1937 [Shepherd's beaked whale]
        - *Berardius* Duvernoy, 1851 [giant bottlenose whales]
        - *Hyperoodon* Lacepede, 1804 [bottlenose whales]
    - Superfamily Platanistoidea Simpson, 1945
      - Family Platanistidae Gray, 1863
        - Subfamily Platanistinae Flower, 1867
          - *Platanista* Wagler, 1830 [Susu]
        - Subfamily Iniinae Flower, 1867
          - *Inia* D'Orbigny, 1834 [Boutu]
          - *Lipotes* Miller, 1918 [white flag dolphin]
        - Subfamily Stenodelphininae Miller, 1923
          - *Pontoporia* Gray, 1846 [franciscana]
    - Superfamily Delphinoidea Flower, 1864
      - Family Monodontidae Gray, 1821
        - *Monodon* Linnaeus, 1758 [narwhal]
        - *Delphinapterus* Lacepede, 1804 [beluga]
      - Family Phocoenidae Bravard, 1885
        - *Phocoena* Cuvier, 1817 [harbor porpoises]
        - *Phocoenoides* Andrews, 1911 [Dall's porpoise]
        - *Neophocaena* Palmer, 1899 [finless porpoise]
      - Family Delphinidae Gray, 1821
        - Subfamily Delphininae Slijper, 1936
          - *Delphinus* Linnaeus, 1758 [common dolphin]
          - *Stenella* Gray, 1866
          - *Grampus* Gray, 1828 [Risso's dolphin]
          - *Tursiops* Gervais, 1855 [bottlenose dolphin]
          - *Lagenorhynchus* Gray, 1846
          - *Lagenodelphis* Fraser, 1956 [Fraser's dolphin]
          - *Peponocephala* Nishiwaki and Norris, 1966 [melon-headed whale]
        - Subfamily Orcininae Slijper, 1936
          - *Orcinus* Fitzinger, 1860 [killer whale]
          - *Pseudorca* Reinhardt, 1862 [false kiler whale]
          - *Globicephala* Lesson, 1828 [pilot whale]
          - *Orcaella* Gray, 1866 [Irrawaddy dolphin]
          - *Feresa* Gray, 1870 [pygmy killer whale]
        - Subfamily Steninae Fraser and Purves, 1964
          - *Steno* Gray, 1846 [rough-toothed dolphin]
          - *Sotalia* Gray, 1866 [tucuxi]
        - Subfamily Lissodelphinae Fraser and Purves, 1964
          - *Lissodelphis* Gloger, 1841 [right whale dolphins]
        - Subfamily Cephalorhynchinae Fraser and Purves, 1964
          - *Cephalorhynchus* Gray, 1846

Appendix 2

TABLES

TABLE 1.—*Nomenclature of nasal structures*

Present study	Lawrence and Schevill, 1956	von Baer, 1826	Murie, 1870, 71, 73	Gruhl, 1911	Anthony, 1926	Huber, 1934	Moris, 1969
vestibular sac	vestibular sac	spritzsäcke	maxillary sac	spritzsäcke	diverticule lateral	lateral sac	sac paranasal superieur
nasofrontal sac	tubular sac	hintere obere höhle; vordere obere höhle	nasofrontal sac	haupthöhle	diverticule	nasofrontal	sac paranasal
accessory sac	connecting sac	------------	------------	blindsäcke	------------	------------	sac paranasal moyen?
premaxillary sac	premaxillary sac	vordere untere höhle	premaxillary sac	vorderd untere höhle	diverticule anterieur	premaxillary sac	sac nasal anterieur
inferior vestibule	------------	------------	------------	------------	------------	------------	sac paranasal moyen?
spiracular cavity	nasal passage (constriction, slit)	gemeinschäft-liche höhle	nasal passage	------------	------------	------------	------------
pe	pe	------------	occipito-frontalis	pars superficials	------------		muscle evental, plan superieur
i	i	------------			------------		
ae	ae, pi	------------	several muscles*		------------	pars nasalis	muscle evental, plan moyen
pi	------------	------------	?pyramidalis	pars profunda	------------		
ai	ai, pr	------------	depressor ali nasi		------------		

*Levator labii superioris alaeque nasi, zygomaticus, levator superioris proprius.

TABLE 2.—*Muscle weight ratios (right/left) for species of Stenella* (pe = pars posteroexternus; ae = pars anteroexternus; pi = pars posterointernus; ai = pars anterointernus; vest. sac = vestibular sac; total musc. = total musculature; $\bar{x}$ = mean)

Species	Sex	Specimen No.	Pe	Ae	Pi	Ai	Vest. Sac.	Nasal Passage	Total Musc.
S. attenuata	M	WFP 48	0.87	-	-	-	1.0	1.47	1.32
	M	WFP 49	1.37	0.92	0.72	1.24	0.83	-	1.07
	M	WFP 51	1.17	0.94	1.31	1.09	0.86	1.26	1.05
	M	WFP 56	1.31	0.82	2.34	1.15	0.82	1.38	1.08
	M	WFP 77	1.10	0.86	1.22	1.01	1.04	1.68	0.99
	M	WFP 81	1.18	0.82	1.44	1.18	0.94	1.56	1.08
	M	JSL 91	0.96	0.94	0.82	0.97	0.95	1.47	0.95
	M	JSL 92	1.11	1.07	1.04	1.08	0.89	1.50	1.08
		$\bar{x}$ =	1.13	0.91	1.27	1.10	0.92	1.47	1.08
S. attenuata	F	WFP 55	1.37	1.08	1.08	1.03	0.85	-	1.07
	F	WFP 66	1.24	0.93	0.92	1.12	0.95	1.67	1.09
	F	WFP 73	1.54	0.85	1.09	1.03	0.93	1.26	1.04
	F	WFP 78	2.09	0.79	1.55	1.09	1.02	-	1.07
	F	JSL 96	1.42	1.14	0.71	0.86	1.02	1.37	0.98
		$\bar{x}$ =	1.53	0.96	1.07	1.03	0.95	1.43	1.05
S. longirostris	M	WFP 47	0.78	0.94	1.27	1.08	1.22	-	1.01
S. longirostris	F	WFP 54	0.72	1.00	0.70	1.26	0.87	1.38	1.04
	F	WFP 57	1.19	1.08	1.35	1.10	1.00	-	1.10
	F	WFP 58	1.44	1.08	2.63	0.96	1.11	1.64	1.13
	F	WFP 74	1.22	0.95	0.66	1.18	1.12	1.47	1.03
	F	WFP 79	0.97	0.91	1.14	1.22	0.96	-	1.08
	F	WFP 80	0.99	0.87	0.78	1.20	0.93	-	1.02
		$\bar{x}$ =	1.09	0.98	1.21	1.15	1.00	1.50	1.07
S. plagiodon	M	EDM 844	-	0.95	1.55	1.03	1.03	1.28	1.04
S. caeruleoalba	M	EDM 845	0.91	1.01	1.21	0.88	1.47	1.51	0.90
	M	WFP 50	0.86	1.23	0.64	1.23	1.93	-	1.13

TABLE 3.—*Data on specimens examined* (measurements in size column are total lengths; specimen catalog numbers are from collection of Division of Mammals, National Museum of Natural History)

Species	Sex	Size	Field Number	USNM Catalog Number
Cephalorhynchus hectori	m	110 cm	WAW 142	500864
Globicephala melaena		near-term fetus		
" "	m	575 cm	0180-71	
Grampus griseus	m	335 cm	0160-71	
Inia geoffrensis	f	adult		
Lagenodelphis hosei	m	110 cm	LR23	396079
" "	f	adult		
Lagenorhynchus acutus	m	198 cm		
Lagenorhynchus albirostris	f	177 cm		
Orcinus orca	m	755 cm	0119-71	
" "	f	618 cm	0118-71	
Phocoena phocoena		adult		
Phocoenoides dalli		adult		
Pontoporia blainvillei	f	near-term fetus	AO 42	
Pseudorca crassidens	m	adult		485827
" "	f	adult		501200
Stenella attenuata	m	128 cm	JSL 87	
" "	m	145 cm	JSL 88	
" "	m	146 cm	JSL 91	
" "	m	156 cm	WFP 59	396037
" "	m	157 cm	WFP 81	396175
" "	m	160 cm	WFP 77	396171
" "	m	163 cm	JSL 92	
" "	m	165 cm	JSL 94	
" "	m	167 cm	WFP 56	396034
" "	m	168 cm	WFP 62	396038
" "	m	172 cm	JSL 90	
" "	m	186 cm	JSL 93	
" "	m	190 cm	WFP 48	396027
" "	m	192 cm	WFP 51	396029
" "	m	197 cm	WFP 49	396028
" "	f	105 cm	JSL 86	
" "	f	108 cm	JSL 97	
Stenella attenuata	f	122 cm	WFP 63	
" "	f	138 cm	JSL 95	
" "	f	145 cm	WFP 72	396024
" "	f	161 cm	WFP 66	396018
" "	f	165 cm	WFP 73	396025
" "	f	167 cm	WFP 78	396172
" "	f	179 cm	WFP 67	396019
" "	f	185 cm	JSL 96	
" "	f	191 cm	JSL 89	
" "	f	200 cm	WFP 55	396033
" "	f	201 cm	WFP 70	396022
Stenella coeruleoalba	m	214 cm	WFP 50	
" "	m	236 cm	EDM 845	
Stenella longirostris	m	136 cm	WFP 75	396169
" "	m	154 cm	WFP 68	396020
" "	m	164 cm	WFP 65	396017
" "	m	166 cm	WFP 71	396023
" "	m	169 cm	WFP 53	396031
" "	m	174 cm	WFP 76	396170
" "	m	175 cm	WFP 47	396026
" "	m	177 cm	WFP 52	396030
" "	f	129 cm	WFP 58	396036
" "	f	149 cm	WFP 69	396021
" "	f	163 cm	WFP 57	396035
" "	f	169 cm	WFP 80	396174
" "	f	178 cm	WFP 74	396168
" "	f	178 cm	WFP 54	396032
" "	f	179 cm	WFP 79	396173
Stenella plagiodon	m	179 cm	EOM 844	
Steno bredanensis	m	189 cm	WFP 466	504089
Tursiops truncatus	m	54 cm (fetus)		
" "	f	adult		
" "	f	270 cm	EDM 846	

Literature Cited

Abel, O.

1902a. Les dauphins longirostres du Boldérien. *Memoires de Musee Royal d' Histoire Naturelle de Belgique*, 2:97–199, 8 plates.

1902b. Die Ursache der Asymmetrie des Zahnwalschädels. *Sitzungsberichte der Kaiserliche Akademie der Wissenschaften in Wein, Mathematische—naturwissenshaftliche classe*, 3:510–526, 1 plate.

Ackman, R. G., C. A. Eaton, and C. Litchfield

1971. Composition of Wax Esters, Triglycerides and Diacyl Glyceryl Ethers in the Jaw and Blubber Fats of the Amazon River Dolphin (*Inia geoffrensis*). *Lipids*, 6 (2):69–77.

Allen, G. M.

1923. The Black Finless Porpoise, *Meomeris*. *Bulletin of The Museum of Comparative Zoology*, 65 (7):233–256, 3 plates.

Anderson, H. T. (Ed.)

1969. *The Biology of Marine Mammals*. 511 pages. New York: Academic Press.

Anderson, J.

1878. *Anatomical and Zoological Researches: Comprising an Account of the Zoological Results of the Two Expeditions to Western Yunnan in 1868 and 1875; and a Monograph of the Two Cetacean Genera,* Platanista and Orcella. 985 pages, 85 plates. London: B. Quaritch.

Anthony, R.

1926. Les affinités des cétacés. *Annales de l' Institut Océanographique*, new series, 3 (2):93–133, 1 plate.

Baer, K. E. von

1826. Die Nase der Cetacean erlautert durch Untersuchung der Nase des Braunfisches (*Delphinus phocaena*). *Isis von Oken*, 19:811–847, 2 plates.

Beddard, F. E.

1900. *A Book of Whales*. 320 pages. New York: G. P. Putnam's Sons.

Benham, W.

1901. On the Anatomy of *Cogia breviceps*. *Proceedings of the Zoological Society of London*, 2 (1):107–134, 4 plates, 2 figures.

Boas, J. E. von, and S. Paulli

1908. *The Elephant's Head: Studies in the Comparative Anatomy of the Organs of the Head of the Indian Elephant and Other Mammals*, Part I: *The Facial Muscles and the Proboscis*. 38 pages, 19 plates. Jena: Gustav Fischer.

Borri, C.

1931. L'asimmetria del cranio dei cetacei. *Archivio Zoologico Italiano*, 16:751–759, 4 figures.

Bouvier, E.

1889. *Les cétacés souffleurs*. 218 pages. Thèse présentée au concours d'aggrégation, École Supérieure de Pharmacie de Paris.

Brown, D. H.

1962. Further Observations in the Pilot Whale in Captivity. *Zoologica*, 47 (1):59–64, 2 plates.

Bullock, T. H., A. D. Grinnell, E. Ikenzono, K. Kameda, Y. Katsuki, M. Nomoto, O. Sato, N. Suga, and K. Yanagisawa

1968. Electrophysiological Studies of Central Auditory Mechanisms in Cetaceans. *Zietschrift für Vergleichende Physiologie*, 59(2):117–156, 15 figures.

Burmeister, G.

1867. Descripcion de cuatro especies de Delfinides de la costa Argentina en el Oceano Atlantico. *Annales de Museo Publico de Buenos Aires (Museo Argentino de Ciencias Naturales)*, 1:367–445, 8 plates.

Caldwell, M. C., and D. K. Caldwell

1965. Individualized Whistle Contours in Bottle-nosed Dolphins (*Tursiops truncatus*). *Nature*, 207 (4995): 434–435.

Camper, D., and A. G. Camper

1820. *Observations anatomiques sur la structure intérieure et le squelette de plusieurs espèces de Cétacés*. 218 pages, 2 figures, 53 plates. Paris: Dufour.

Carlsson, A.

1888. Zur Anatomie des *Hyperoodon diodon*. *Kungliga Svenska Vetenskapsakadamiens handlingar*, 13 (4): 3–25, 3 plates.

Carte, A., and A. Macalister

1868. On the Anatomy of *Balaenoptera rostrata*. *Philosophical Transactions of the Royal Society of London*, 158:201–261, 4 plates.

Clarke, M. R.

1970. Function of the Spermaceti Organ of the Sperm Whale. *Nature*, 228:873–874.

Cuvier, F.

1835–1836. Cetacea. Pages 562–594 *in* volume 1 of *Todd's Cyclopedia of Anatomy and Physiology*.

Cuvier, G.

1797. Sur les narines des cétacés. *Bulletin des Sciences, Société Philomathique de Paris*, 2:26–29, 3 figures.

Danois, E.

1910. Recherches sur l'anatomie de la tête de *Kogia breviceps* Blainv. *Archives de Zoologie Expérimentale et Générale*, series 5, 6:149–174, 4 plates.

1911. Description d'un embryon de *Grampus griseus* Gray. *Archives de Zoologie Expérimentale et Générale*, series 5, 8:399–420, 2 plates.

Dohl, T. P., K. S. Norris, and I. Kang

1974. A Porpoise Hybrid: *Tursiops* × *Steno*. *Journal of Mammalogy*, 55 (1):217–221, 1 figure.

Edgeworth, F. H.

1935. *The Cranial Muscles of Vertebrates*. 493 pages, 841 figures. London: University Press.

Edinger, T.
1955. Hearing and Smell in Cetacean History. *Monatsschrift für Psychiatrie und Neurologie*, 129:37–58.

Evans, W. E.
1967. Special Acoustic Problems in Cetacean Research, General Discussion. Pages 395–398 *in* volume 2 *of* Tavolga, editor, *Marine Bio-acoustics*. New York: Pergamon Press.
1973. Echolocation by Marine Delphinids and One Species of Fresh-water Dolphin. *Journal of the Acoustical Society of America*, 54 (1):191–199, 7 figures.

Evans, W. E., and P. F. A. Maderson
1973. Mechanisms of Sound Production in Delphinid Cetaceans: A Review of Some Anatomical Considerations. *American Zoologist*, 13:1205–1213, 8 figures.

Evans, W. E., and J. H. Prescott
1962. Observations of the Sound Capabilities of the Bottlenose Porpoise: a Study of Whistles and Clicks. *Zoologica*, 47 (3):121–126, 6 figures, 4 plates.

Evans, W. E., W. W. Sutherland, and R. G. Beil
1964. The Directional Characteristics of the Delphinid Sounds. Pages 353–372 *in* volume 2 *of* Tavolga, editor, *Marine Bio-acoustics*. New York: Pergamon Press.

Fisher, M. P.
1881. Cétacés du Sud-Ouest de la France. *Actes de la Société Linneene de Bordeaux*, 35:1–219, 8 plates.

Fraser, F. C.
1940. Three Anomalous Dolphins from Blacksod Bay, Ireland. *Proceedings of the Royal Irish Academy*, 45 (17):413–455, 7 plates.
1956. A New Sarawak Dolphin. *Sarawak Museum Journal*, 7:478–503, 5 plates.
1966. Comments on the Delphinoidea. Pages 7–31 *in* Norris, editor, *Whales, Dolphins and Porpoises*. Berkeley: University of California Press.

Fraser, F. C., and P. E. Purves
1960. Hearing in Cetaceans: Evolution of the Accessory Air Sacs and the Structure and Function of the Outer and Middle Ear in Recent Cetaceans. *Bulletin of the British Museum (Natural History), Zoology*, 7 (1):1–140, 53 plates.

Frechkop, S.
1944. Notes sur les mammifères, xxviii: Essai d' interprétation biologique de la structure des cétacés. *Bulletin du Musée Royal d'Historie Naturelle de Belgique*, 20 (13):1–28, 15 figures.

Gallardo, A.
1913. Notas sobre la anatomía del aparto espiracular, laringe y hioides de dos delfines: *Phocaena dioptrica* Lahille y *Lagenorhynchus fitzroyi* (Waterhouse) Flower. *Annales de Museo Nacional de Historia Natural de Buenos Aires (Museo Argentino de Ciencias Naturales)*, 24:235–246, 9 plates.

Gray, J.
1936. Studies in Animal Locomotion, VI: The Propulsive Powers of the Dolphin. *Journal of Experimental Biology*, 13:192–199, 3 figures.

Gruhl, K.
1911. Beitrage zur Anatomie und Physiologie der Cetaceennase. *Jenaische Zeitschrift für Naturwissenschaft*, 47 (3):367–414, 21 figures.

Heel, D. van.
1970. *Dolfijn, hoe doe je het?* 158 pages, 8 plates. Amsterdam: Van Kampen & Zoon.

Hinton, M.
1936. Some Interesting Points in the Anatomy of the Freshwater Dolphin *Lipotes* and Its Allies. *Proceedings of the Linnean Society of London*, 148 (3): 183–185.

Hinton, M., and W. Pycraft
1922. Preliminary Note on the Affinites of the Genus *Lipotes*. *Annals and Magazine of Natural History*, 10:232–234.

Hosakawa, H.
1950. On the Cetacean Larynx, with Special Remarks on the Laryngeal Sacs of the Sei Whale and the Aryteno-epiglottideal Tube of the Sperm Whale. *Scientific Reports of the Whales Research Institute*, 3:23–62, 12 figures.

Houssay, F.
1912. L'asymétrie du crâne chez les cétacés et ses rapports avec la loi de l'action et de la réaction. *Anatomische Anzeiger*, 36:12–17.

Howell, A. B.
1925. Asymmetry in the Skulls of Mammals. *Proceedings of the United States National Museum*, 67 (27):1–18, 8 plates.
1927. Contribution to the Anatomy of the Chinese Finless Porpoise, *Neomeris phocaenoides*. *Proceedings of the United States National Museum*, 70 (13):1–43, 14 figures, 1 plate.
1930. *Aquatic Mammals: Their Adaptations to Life in the Water*. 338 pages, 53 figures. Baltimore: Charles C. Thomas.

Huber, E.
1930. Evolution of Facial Musculature and Cutaneous Field of Trigeminus. *Quarterly Review of Biology*, 5:133–187, 389–437, 46 figures.
1934. Anatomical Notes on Pinnipedia and Cetacea. Pages 105–136 *in* E. L. Packard, R. Kellogg, and E. Huber, *Marine Mammals. Carnegie Institute of Washington, Contributions to Paleontology*, number 447.

Hunter, J.
1787. Observations on the Structure and Oeconomy of Whales. *Philosophical Transactions of the Royal Society of London*, 77:371–450, 8 plates.
1890. Observations on the Structure and Economy of Whales. *Philosophical Transactions of the Royal Society of London*, 15 (1785–1790):306–351, 1 plate. [Abridged by Hutton, Shaw, and Pearson.]

Kellogg, A. R.
1928. The History of Whales: Their Adaptation to Life in the Water. *The Quarterly Review of Biology*, 3(1,2):29–76, 174–208, 10 figures.

1938. Adaptation of Structure to Function in Whales. Pages 649–682 in *Cooperation in Research by Staff Members and Research Associates of the Carnegie Institute of Washington. Carnegie Institute of Washington, Contributions to Paleontology,* number 501.

Kellogg, W. N., R. Kohler, and H. N. Morris
1953. Porpoise Sounds as Sonar Signals. *Science,* 117 (3036):239–243.

Kernan, J. D., Jr., and H. von W. Schulte
1918. Memoranda upon the Anatomy of the Respiratory Tract, Foregut, and Thoracic Viscera of a Foetal *Kogia breviceps. Bulletin of the American Museum of Natural History,* 38 (3):231–267, 16 figures.

Khomenko, B. H.
1970. Pro gistotructuru ta innervatsiyu zbukovo aparatu (nasalnikh mishkiv) dilfiniv (The Histostructure and Innervation of the Sound Apparatus-Nasal Sacs- in Dolphins). *Dopovidi Akademiyi Nauk Ukrayinskoyi RSR,* 32 (1):83–87, 4 figures.

Kleinenberg, S. E., and A. V. Yablokov
1958. O morfologii verkhnikh dykhatelnykn putei kitoobraznykh (Morphology of Upper Respiratory Passages in the Cetaceans). *Zoologicheskii Zhurnal,* 37 (7):1091–1099, 10 figures.

Kleinenberg, S. E., A. V. Yablokov, B. M. Belkovich, and M. N. Tarasevich
1969. *Beluga* (Delphinapterus leucas): *Investigation of the Species.* 376 pages, 118 figures. Israel Program for Scientific Translations. [Translated from Russian.]

Kooyman, G. L., and H. T. Andersen
1969. Deep Diving. Pages 65–94 *in* Anderson, editor, *The Biology of Marine Mammals.* New York: Academic Press.

Kritzler, H.
1952. Observations on the Pilot Whale in Captivity. *Journal of Mammalogy,* 33:321–334.

Kükenthal, W.
1893. Vergleichend-anatomische und entiwickelungsgeschichtliche Untersuchungen an Walthieren. *Denkschriften der Medicinisch-Naturwissenschaftlichen Gesellschaft zu Jena,* 3 (2):1–448, 25 plates.
1908. Ueber die Ursache der Asymmetrie des Walschädels. *Anatomische Anzeiger,* 33:609–618.

Lahille, F.
1908. Notas sobre un ballenato de 2.10 metros de largo (*Balaenoptera acuto-rostrata* Lac.). *Annales de Museo Publico de Buenos Aires* (*Museo Argentino de Ciencias Naturales*), 16:375–401, 8 figures, 1 plate.

Lawrence, B., and W. E. Schevill
1956. The Functional Anatomy of the Delphinid Nose. *Bulletin of the Museum of Comparative Zoology,* 114 (4):103–151, 30 figures.

Lillie, D. G.
1910. Observations on the Anatomy and General Biology of Some Members of the Larger Cetacea. *Proceedings of the Zoological Society of London,* 1910:769–792, 10 figures, 1 plate.

Lilly, J. C.
1961. *Man and Dolphin.* 312 pages. Garden City: Doubleday & Co., Inc.
1962. Vocal Behavior of the Bottlenose Dolphin. *Proceedings of the American Philosophical Society,* 106 (6):520–529, 11 figures.

Lilly, J. C., and A. M. Miller
1961. Sounds Emitted by the Bottlenose Dolphin. *Science,* 5:1689–1693, 4 figures.

Litchfield, C., and A. Greenberg
1974. Comparative Lipid Patterns in the Melon Fats of Dolphins, Porpoises, and Toothed Whales. *Comparative Biochemistry and Physiology,* 47B:401–407, 1 figure.

Litchfield, C., R. Karol, and A. Greenberg
1973. Compositional Topography of Dolphin Melon Lipids: Implications for Echolocation. *Marine Biology,* 23:165–169.

Macalister, A.
1867. On Some Points in the Anatomy of *Globicephalus svinval* (Gray). *Proceedings of the Zoological Society of London,* 1867:477–482.

Maderson, P. F. A.
1968. The Histology of the Nasal Epithelia of *Tursiops truncatus* (Cetacea) with Preliminary Observations on a Series of Glandular Structures. *American Zoologist,* 8:810 (abstract).

Miller, G. S., Jr.
1923. The Telescoping of the Cetacean Skull. *Smithsonian Miscellaneous Collections,* 76 (5):1–70, 8 plates.

Miller, M. E., G. C. Christensen, and H. E. Evans
1964. *Anatomy of the Dog.* 941 pages. New York: Saunders.

Mitchell, E. D.
1970. Pigmentation Pattern Evolution in Delphinid Cetaceans: An Essay in Adaptive Coloration. *Canadian Journal of Zoology,* 48 (4):717–740, 15 plates.

Moris, F.
1969. Étude anatomique de la région cephalique du marsouin, Phocaena phocaena L. (cétacé odontocète). *Mammalia,* 33 (4):666–726, 27 figures, 4 plates.

Moss, M. L., and L. Salentijn
1969. The Primary Role of Functional Matrices in Facial Growth. *American Journal of Orthodontics,* 55 (6): 566–577, 5 figures.

Murie, J.
1870. On Risso's Grampus, *G. rissoanus* (Desm.). *Journal* of *Anatomy and Physiology,* 5:118–138, 2 figures, 1 plate.
1871. Notes on the White-beaked Bottlenose, *Lagenorhynchus albirostris* Gray. *Journal of the Linnean Society, Zoology,* 11:141–153, 1 plate.
1873. On the Organization of the Caaing Whale, *Globiocephalas melas. Transactions of the Zoological Society of London* 8 (4):235–301, 9 plates.

Negus, V. E.

1949. *The Comparative Anatomy and Physiology of the Larynx.* 230 pages. London: Heinemann.

Ness, A. R.

1967. A Measure of Asymmetry of the Skulls of Odontocete Whales. *Journal of Zoology,* 153:209–221, 4 figures.

Nishiwaki, M.

1963. Taxonomical Consideration on Genera of Delphinidae. *Scientific Reports of the Whales Research Institute,* 17:93–103.

Norman, J. R., and F. C. Fraser

1937. *Giant Fishes, Whales, and Dolphins.* 376 pages, 8 plates. London: Putnam.

Norris, K. S.

1964. Some Problems of Echolocation in Cetaceans. Pages 317–355 *in* volume 1 *of* Tavolga, editor, *Marine Bio-Acoustics.* New York: Pergamon Press.

1968. The Evolution of Acoustic Mechanisms in Odontocete Cetaceans. Pages 297–324 *in* Drake, editor, *Evolution and Environment.* New Haven: Yale University Press.

1969. The Echolocation of Marine Mammals. Pages 391–423 *in* Andersen, editor, *The Biology of Marine Mammals.* New York: Academic Press.

Norris, K. S., and W. E. Evans

1967. Directionality of Echolocation Clicks in the Roughtooth Porpoise, *Steno bredanensis* (Lesson). Pages 305–316 *in* volume 2 *of* Tavolga, editor, *Marine Bio-Acoustics.* New York: Pergamon Press.

Norris, K. S., J. H. Prescott, P. V. Asa-Dorian, and P. Perkins

1961. An Experimental Demonstration of Echolocation Behavior in the Porpoise, *Tursiops truncatus* (Montagu). *Biological Bulletin, Woods Hole,* 120(2):163–176, 4 figures.

Norris, K. S., K. J. Dormer, J. Pegg, and G. J. Liese

1971. The Mechanism of Sound Production and Air Recycling in Porpoises: A Preliminary Report. *Proceedings of the Eighth Annual Conference on Biological Sonar and Diving Mammals, Stanford Research Institute,* pages 113–129, 4 figures.

Norris, K. S., and G. W. Harvey

1974. Sound Transmission in the Porpoise Head. *Journal of the Acoustical Society of America,* 56(2):659–664, 4 figures.

Osburn, R. C.

1903. Adaptation to Aquatic, Arboreal, Fossorial, and Cursorial Habits in Mammals, I: Aquatic Adaptations. *American Naturalist,* 37(442):651–665.

Palmer, E., and G. Weddell

1964. The Relationship between Structure, Innervation, and Function of the Skin of the Bottlenose Dolphin (*Tursiops truncatus*). *Proceedings of the Zoological Society of London,* 143(4):553–567, 7 plates.

Parry, D. A.

1949. The Anatomical Basis of Swimming in Whales. *Proceedings of the Zoological Society of London,* 119:49–60, 5 figures.

Pouchet, M. G.

1886. *De l'Asymétrie de la face chez les Cétodontes.* 16 pages. Paris: Libraire de l'Academie de Médicine.

Pouchet, M. G., and H. Beauregard

1885. Sur "l'organe des Spermacéti." *Comptes Rendus de Société Biologique,* 11:343–344.

1892. Recherches sur le cachalot. *Nouvelle Archives du Musée d' Histoire Naturelle,* series 3, 4:1–90, 12 plates.

Purves, P. E.

1966. Anatomy and Physiology of the Outer and Middle Ear in Cetaceans. Pages 320–380 *in* Norris, editor, *Whales, Dolphins and Porpoises.* Berkeley: University of California Press.

1967. Anatomical and Experimental Observations on the Cetacean Sonar System. Pages 197–270 *in* volume 1 *of* Busnel, editor, *Animal Sonar Systems, Biology and Bionics.* GAP (Hautes-Alpes): Imprimerie Louis-Jean.

Purves, P. E., and G. Pilleri

1973. Observations on the Ear, Nose, Throat, and Eye of *Platanista indi.* Pages 13–57 *in* volume 5 *of* Pilleri, editor, *Investigations on Cetacea.*

Raven, H. C.

1942. Some Morphological Adaptations of Cetaceans (Whales and Porpoises) for Life in the Water. *Transactions of the New York Academy of Sciences,* second series 5(2):23–29.

Raven, H. C., and W. K. Gregory

1933. The Spermacetic Organ and Nasal Passages of the Sperm Whale (*Physeter catodon*) and Other Odontocetes. *Novitates, American Museum of Natural History,* 677:1–18, 9 figures.

Rawitz, B.

1900. Die Anatomie des Kehlkopfes und der Nase von *Phocaena communis* Cuv. *Internationale Monatsschrift für Anatomie und Physiologie,* 17:245–354.

Ray, J.

1671. An Account of the Dissection of a Porpess. *Philosophical Transactions of the Royal Society of London,* 6(76):2274–2279.

Reysenbach de Haan, F. W.

1957. Hearing in Whales. *Acta Oto-laryngologica,* supplement 134, 114 pages, 41 figures.

Richard, C.

1930. Di una peculiare asimmetria dei fiseteridi (asimmetrie emapofisaria) e delle sue relazioni con l'asimmetria cranica. *Accademia Nazionale dei Lincei, Rome, classe di Science Fisiche, Rendiconti,* series 6, 12:165–172, 2 figures.

Richard, J.

1936. Documents sur le Cétacés et Pinnipèdes des Croisières du Prince Albert ler de Monaco. Fascicule XCIV in *Resultats des Campagnes Scientifiques Accomplies sur son Yacht par Albert ler, Prince Souverain de Monaco.* 72 pages, 8 plates.

Ridgway, S. H.

1966. Dall Porpoise, *Phocoenoides dalli* (True): Observations in Captivity and at Sea. *Norsk Hvalfangst-Tidende* (*Norwegian Whaling Gazette*), 1966(5):97–110, 11 figures.

1971. Buoyancy Regulation in Deep Diving Whales. *Nature*, 232(5306):133–134.

Scammon, C. M.

1874. *The Marine Mammals of the North-western Coast of North America, Described and Illustrated: Together with an Account of the American Whale-Fishery*. 319 pages, 27 plates. San Francisco: John H. Carmany & Co.

Schenkkan, E. J.

1971. The Occurrence and Position of the "Connecting Sac" in the Nasal Tract Complex of Small Odontocetes (Mammalia, Cetacea). *Beaufortia*, 19(246): 37–43, 3 figures.

1972. On the Nasal Tract Complex of *Pontoporia blainvillei* Gervais and d'Orbigny 1844 (Cetacea, Platanistidae). Pages 83–90 *in* volume 4 *of* Pilleri, editor, *Investigations on Cetacea*.

1973. On the Comparative Anatomy and Function of the Nasal Tract in Odontocetes (Mammalia, Cetacea). *Bijdragen tot de Dierkunde*, 43(2):127–159, 16 figures.

Schenkkan, E. J., and P. E. Purves

1973. The Comparative Anatomy of the Nasal Tract and the Function of the Spermaceti Organ in the Physeteridae (Mammalia, Odontoceti). *Bijdragen tot de Dierkunde*, 43(1):93–112, 12 figures.

Schevill, W. E.

1964. General Discussion. Pages 395–398 *in* volume 1 *of* Tavolga, editor, *Marine Bio-Acoustics*. New York· Pergamon Press.

Schevill, W. E., and B. Lawrence

1956. Food-finding by a Captive Porpoise (*Tursiops truncatus*). *Breviora of the Museum of Comparative Zoology*, 53:1–15.

Schevill, W. E., and W. A. Watkins

1966. Sound Structure and Directionality in *Orcinus* (killer whale). *Zoologica*, 519(6):71–76, 6 plates.

Schulte, H. von W.

1916. Anatomy of a Foetus of *Balaenoptera borealis*. *Memoirs of the American Museum of Natural History*, new series, 1(6):389–502, 15 plates.

Scoresby, W.

1823. *Journal of a Voyage to the Northern Whalefishery: Including Researches and Discoveries on the Eastern Coast of Greenland, Made in the Summer of 1822, in the Ship Baffin of Liverpool*. 472 pages, 8 plates, London: Hurse, Robinson and Co.

Sibson, F.

1848. On the Blow-hole of the Porpoise. *Philosophical Transactions of the Royal Society of London*, 1848: 117–123, 1 plate.

Simpson, G.

1945. The Principles of Classification and a Classification of Mammals. *Bulletin of the American Museum of Natural History*, 85:1–350.

Sleptsov, M. M.

1939. K voprosy ob asimmetrii cherepa u odontoceti (On the Question of the Asymmetry of the Skull in Odontoceti). *Zoologicheskii Zhurnal*, 18:367–386, 6 figures. [English summary.]

Slijper, E. J.

1936. Die Cetaceen, Vergleichend-anatomisch und systematisch. *Capita Zoologica*, 7:1–590, 251 figures.

1958. Organ Weights and Symmetry Problems in Porpoises and Seals. *Archives Neerlandaises de Zoologie, supplement*, 8(1):97–113, 5 figures.

1961. Locomotion and Locomotory Organs in Whales and Dolphins (Cetacea). *Symposia of the Zoological Society of London*, 5:77–94, 10 figures.

Stannius, H.

1849. Beschreibung der Muskeln des Tummlers (*Delphinus phocaena*). *Archiv für Anatomie, Physiologie und wissenschaftliche Medicin*, 1849:1–41.

Steinmann, G.

1912. Ueber die Ursache der Asymmetrie der Wale. *Anatomische Anzeiger*, 42:45–54, 5 figures.

Sterling, S.

1910. O asymetryi czaszki wielorybow (On the Asymmetry of the Skulls of Whales). *Towarzystwo naukowe warszawskie, Warsaw, sprawozdinia z posiedzen* (*Comptes Rendus des Seances de la Societe scientifique de Varsovie*), 3(5):231–235, 2 figures.

Tomilin, A. G.

1967. *Cetacea, Mammals of the U.S.S.R. and Adjacent Countries*, IX. 717 pages, 146 figures. Israel Program for Scientific Translations. [Translated from Russian.]

True, F. W.

1889. Contributions to the Natural History of the Cetaceans, a Review of the Family Delphinidae. *Bulletin of the United States National Museum*, 36:1–191, 47 plates.

Turner, W.

1867. A Contribution to the Anatomy of the Pilot Whale (*Globiocephalus svineval*, Lacepede). *Journal of Anatomy and Physiology*, 2:66–79.

Watson, M., and A. H. Young

1879. The Anatomy of the Northern Beluga (*Beluga catodon* Gray; *Delphinapterus leucas* Pallas) Compared with That of Other Whales. *Transactions of the Royal Society of Edinburgh*, 29(1):393–435, 2 plates.

Weber, M.

1886. *Studien über Säugethiere: Ein Beitrag zur Frage nach dem Ursprung der Cetaceen*. 252 pages, 4 plates. Jena: Gustav Fischer.

Wedmid, G., C. Litchfield, R. G. Ackman, and J. C. Sipos

1972. Heterogeneity of Lipid Composition within the Cephalic Melon Tissue of the Pilot Whale. *Journal of the American Oil Chemists Society*, 48:332 A [abstract].

Williston, S. W.
1902. On Certain Homoplastic Characters in Aquatic, Air-breathing Vertebrates. *Kansas University Science Bulletin,* 1:259–266.

Wood, F. G.
1964. General Discussion. Pages 395–398 *in* volume 1 *of* Tavolga, editor, *Marine Bio-Acoustics.* New York: Pergamon Press.

☆ U.S. GOVERNMENT PRINTING OFFICE: 1975—586–382/39

Publication in *Smithsonian Contributions to Zoology*

Manuscripts for serial publications are accepted by the Smithsonian Institution Press, subject to substantive review, only through departments of the various Smithsonian museums. Non-Smithsonian authors should address inquiries to the appropriate department. If submission is invited, the following format requirements of the Press will govern the preparation of copy.

Copy must be typewritten, double-spaced, on one side of standard white bond paper, with 1½" top and left margins, submitted in ribbon copy with a carbon or duplicate, and accompanied by the original artwork. Duplicate copies of all material, including illustrations, should be retained by the author. There may be several paragraphs to a page, but each page should begin with a new paragraph. Number consecutively all pages, including title page, abstract, text, literature cited, legends, and tables. The minimum length is 30 pages, including typescript and illustrations.

The *title* should be complete and clear for easy indexing by abstracting services. Taxonomic titles will carry a final line indicating the higher categories to which the taxon is referable: "(Hymenoptera: Sphecidae)." Include an *abstract* as an introductory part of the text. Identify the *author* on the first page of text with an unnumbered footnote that includes his professional mailing address. A *table of contents* is optional. An *index,* if required, may be supplied by the author when he returns page proof.

Two *headings* are used: (1) text heads (boldface in print) for major sections and chapters and (2) paragraph sideheads (caps and small caps in print) for subdivisions. Further headings may be worked out with the editor.

In *taxonomic keys,* number only the first item of each couplet; if there is only one couplet, omit the number. For easy reference, number also the taxa and their corresponding headings throughout the text; do not incorporate page references in the key.

In *synonymy,* use the short form (taxon, author, date:page) with a full reference at the end of the paper under "Literature Cited." Begin each taxon at the left margin with subsequent lines indented about three spaces. Within an entry, use a period-dash (.—) to separate each reference. Enclose with square brackets any annotation in, or at the end of, the entry. For *references within the text,* use the author-date system: "(Jones, 1910)" and "Jones (1910)." If the reference is expanded, abbreviate the data: "Jones (1910:122, pl. 20: fig. 1)."

Simple *tabulations* in the text (e.g., columns of data) may carry headings or not, but they should not contain rules. Formal *tables* must be submitted as pages separate from the text, and each table, no matter how large, should be pasted up as a single sheet of copy.

Use the *metric system* instead of, or in addition to, the English system.

Illustrations (line drawings, maps, photographs, shaded drawings) can be intermixed throughout the printed text. They will be termed *Figures* and should be numbered consecutively; however, if a group of figures is treated as a single figure, the components should be indicated by lowercase italic letters on the illustration, in the legend, and in text references: "Figure 9*b*." If illustrations (usually tone photographs) are printed separately from the text as full pages on a different stock of paper, they will be termed *Plates,* and individual components should be lettered (Plate 9*b*) but may be numbered (Plate 9: figure 2). Never combine the numbering system of text illustrations with that of plate illustrations. Submit all legends on pages separate from the text and not attached to the artwork. An instruction booklet for the preparation of illustrations is available from the Press on request.

In the *bibliography* (usually called "Literature Cited"), spell out book, journal, and article titles, using initial caps with all words except minor terms such as "and, of, the." For capitalization of titles in foreign languages, follow the national practice of each language. Underscore (for italics) book and journal titles. Use the colon-parentheses system for volume, number, and page citations: "10(2):5-9." Spell out such words as "figures," "plates," "pages."

For *free copies* of his own paper, a Smithsonian author should indicate his requirements on "Form 36" (submitted to the Press with the manuscript). A non-Smithsonian author will receive 50 free copies; order forms for quantities above this amount with instructions for payment will be supplied when page proof is forwarded.