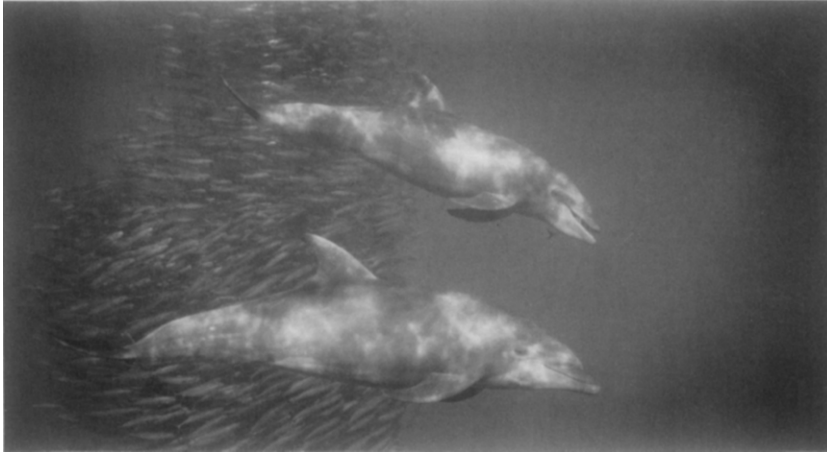




THE BOTTLENOSE DOLPHIN

Edited by
Stephen Leatherwood
Randall R. Reeves

PHOTO: Bottlenose dolphins chasing fish off Socorro Island, Revilla Gigedo Islands, Mexico (Jeff Jacobsen, EARTHVIEWS).



The Bottlenose Dolphin

Edited by

Stephen Leatherwood

Oceans Unlimited

San Diego, California, USA

Randall R. Reeves

Okapi Wildlife Associates

Hudson, Québec, Canada



Academic Press, Inc.

Harcourt Brace Jovanovich, Publishers

San Diego New York Berkeley Boston London Sydney Tokyo Toronto

This book is printed on acid-free paper. (∞)

Copyright © 1990 by Academic Press, Inc.
All Rights Reserved.

No part of this publication may be reproduced or transmitted in any form or by any means, electronic or mechanical, including photocopy, recording, or any information storage and retrieval system, without permission in writing from the publisher.

Academic Press, Inc.
San Diego, California 92101

United Kingdom Edition published by
Academic Press Limited
24-28 Oval Road, London NW1 7DX

Library of Congress Cataloging-in-Publication Data

The Bottlenose dolphin / edited by Stephen
Leatherwood and Randall R. Reeves

p. cm.

Includes index.

ISBN 0-12-440280-1 (alk. paper)

1. Atlantic bottlenose dolphin. I. Leatherwood, Stephen.

II. Reeves, Randall R.

QL737.C432B67 1989

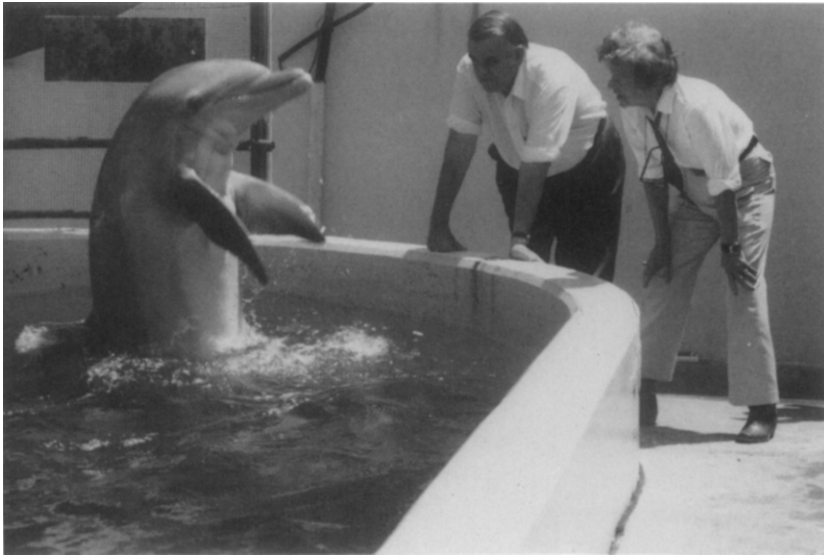
599.5'3--dc19

88-35093

CIP

Printed in the United States of America

90 91 92 93 9 8 7 6 5 4 3 2 1



This volume is dedicated to our friends and colleagues David K. Caldwell and Melba C. Caldwell. By their hard work, integrity, and insight, the Caldwells have inspired many of us in our studies of bottlenose dolphins and other cetaceans.

This page intentionally left blank

Contents

<i>Preface</i>	xi	6. Distinction between Northwest Atlantic Offshore and Coastal Bottlenose Dolphins Based on Hemoglobin Profile and Morphometry	129
Part I		<i>Sandra L. Hersh and Deborah A. Duffield</i>	
Evolution and Fossil Record			
1. The Fossil Record and Evolutionary Relationships of the Genus <i>Tursiops</i>	3		
<i>Lawrence G. Barnes</i>			
Part II		Part IV	
Anatomy and Physiology		Life History and Biology	
2. Osteology of the Bottlenose Dolphin	29	7. Preliminary Observations of Bottlenose Dolphins from the Pacific Coast of South America	143
<i>Sentiel Rommel</i>		<i>Koen Van Waerebeek, Julio C. Reyes, Andrew J. Read, and Jeff S. McKinnon</i>	
3. Axial Muscles and Connective Tissues of the Bottlenose Dolphin	51	8. Bottlenose Dolphin Mortality Patterns in the Indian/Banana River System of Florida	155
<i>D. Ann Pabst</i>		<i>Sandra L. Hersh, Daniel K. Odell, and Edward D. Asper</i>	
4. The Central Nervous System of the Bottlenose Dolphin	69	9. Natural History of Bottlenose Dolphins along the Central Atlantic Coast of the United States	165
<i>Sam H. Ridgway</i>		<i>James G. Mead and Charles W. Potter</i>	
Part III		Part V	
Systematics and Taxonomy		Behavior and Ecology	
5. Comments on Australian Bottlenose Dolphins and the Taxonomic Status of <i>Tursiops aduncus</i> (Ehrenberg, 1832)	101	10. Review of the Signature-Whistle Hypothesis for the Atlantic Bottlenose Dolphin	199
<i>Graham J. B. Ross and Victor G. Cockcroft</i>		<i>Melba C. Caldwell, David K. Caldwell, and Peter L. Tyack</i>	

- | | |
|--|---|
| <p>11. A Long-Term Study of Bottlenose Dolphins on the West Coast of Florida 235
<i>Michael D. Scott, Randall S. Wells, and A. Blair Irvine</i></p> <p>12. Behavior and Ecology of the Bottlenose Dolphin at Sanibel Island, Florida 245
<i>Susan H. Shane</i></p> <p>13. Residence Patterns, Group Organization, and Surfacing Associations of Bottlenose Dolphins in Kino Bay, Gulf of California, Mexico 267
<i>Lisa T. Ballance</i></p> <p>14. Aspects of the Behavioral Ecology of Inshore Dolphins <i>Tursiops truncatus</i> and <i>Sousa chinensis</i> in Moreton Bay, Australia 285
<i>Peter J. Corkeron</i></p> <p>15. Food and Feeding of the Indian Ocean Bottlenose Dolphin off Southern Natal, South Africa 295
<i>V. G. Cockcroft and G. J. B. Ross</i></p> <p>16. Food Habits of Bottlenose Dolphins in the Southeastern United States 309
<i>Nélio B. Barros and Daniel K. Odell</i></p> <p>17. Feeding by Bottlenose Dolphins in Association with Trawling Operations in Moreton Bay, Australia 329
<i>P. J. Corkeron, M. M. Bryden, and K. E. Hedstrom</i></p> <p>18. Review of Incidents Involving Wild, Sociable Dolphins, Worldwide 337
<i>Christina Lockyer</i></p> <p>19. Quantitative Description of a Rare Behavioral Event: A Bottlenose Dolphin's Behavior toward Her Deceased Offspring 355
<i>Richard C. Connor and Rachel A. Smolker</i></p> | <p>20. Site and Association Fidelity in Bottlenose Dolphins off Argentina 361
<i>Bernd Würsig and Graham Harris</i></p> |
|--|---|
-
- | | |
|--|--|
| Part VI | |
| <hr/> | |
| Distribution, Movements, and Abundance | |
| <p>21. Bottlenose Dolphins off the Northeastern United States 369
<i>Robert D. Kenney</i></p> <p>22. Distribution and Herd Structure of Bottlenose Dolphins in the Eastern Tropical Pacific Ocean 387
<i>Michael D. Scott and Susan J. Chivers</i></p> <p>23. California Coastal Bottlenose Dolphins 403
<i>Larry J. Hansen</i></p> <p>24. Northward Extension of the Range of Bottlenose Dolphins along the California Coast 421
<i>Randall S. Wells, Larry J. Hansen, Alan Baldrige, Thomas P. Dohl, Dennis L. Kelly, and R. H. Defran</i></p> | |
-
- | | |
|--|--|
| Part VII | |
| <hr/> | |
| Husbandry and Captive Breeding | |
| <p>25. Breeding Bottlenose Dolphins in Captivity 435
<i>J. Pete Schroeder</i></p> <p>26. Artificial Insemination of Bottlenose Dolphins 447
<i>J. Pete Schroeder and Karl V. Keller</i></p> <p>27. Observations on the Early Development of a Captive Bottlenose Dolphin Calf 461
<i>V. G. Cockcroft and G. J. B. Ross</i></p> | |

28. Hematology and Serum Chemistry Values in Bottlenose Dolphins 479
Edward D. Asper, Lanny H. Cornell, Deborah A. Duffield, Daniel K. Odell, Brian E. Joseph, Bernice I. Stark, and Cathy A. Perry

Part VIII

Research Techniques

29. Tagging and Marking Studies on Small Cetaceans 489
Michael D. Scott, Randall S. Wells, A. Blair Irvine, and Bruce R. Mate
30. Distribution and Movements of Freeze-Branded Bottlenose Dolphins in the Indian and Banana Rivers, Florida 515
Daniel K. Odell and Edward D. Asper
31. Comparison of Bottlenose Dolphin Behavior in Texas and Florida, with a Critique of Methods for Studying Dolphin Behavior 541
Susan H. Shane
32. Ergometry (Exercise Testing) of the Bottlenose Dolphin 559
Harold W. Goforth, Jr.

33. Reading between the Lines: Analysis of Age Estimation in Dolphins 575
Aleta A. Hohn

34. Calibrating Dental Layers in Captive Bottlenose Dolphins from Serial Tetracycline Labels and Tooth Extractions 587
Albert C. Myrick, Jr. and Lanny H. Cornell

35. Use of Chromosome Heteromorphisms and Hemoglobins in Studies of Bottlenose Dolphin Populations and Paternities 609
Deborah A. Duffield and Jan Chamberlin-Lea

Part IX

Management

36. Management-Oriented Research on Bottlenose Dolphins by the Southeast Fisheries Center 623
Gerald P. Scott

- Index* 641

This page intentionally left blank

Preface

Bottlenose dolphins, *Tursiops truncatus*, are among the most familiar cetaceans. Because of their exposure in captivity in marine parks and dolphinaria, movies, and television programs, as well as in the wild along tropical and warm temperate beaches around the world, they are, to most schoolchildren and landlubbers, the quintessential dolphins. They are also well known to field and laboratory scientists. Studies of wild bottlenose dolphins have been encouraged by their relative accessibility. In many lagoons, gulfs, and embayments and along discrete stretches of exposed outer coast, populations of bottlenose dolphins can be observed and studied throughout much of the year. Since they are relatively easy to obtain and thrive in captivity, where they may survive at least as long as in the wild and reproduce successfully, bottlenose dolphins have been used in a great variety of studies. Work with these dolphins in captivity has provided insight about sensory mechanisms, communication systems, energetics, reproduction, anatomy, and many other aspects of cetacean biology generally.

This book is intended to serve several purposes. First, we felt it would be useful to publish a series of papers on the most widely studied genus in the family Delphinidae, to demonstrate at once how much and how little is known about these animals. In that sense, we wanted the book to be a benchmark for researchers who, by seeing the variety of topics and approaches presented under one cover, might get a better sense of how to direct their own further work with this and other delphinid species. For example, many of us have begun to ask how important or relevant additional area population inventories of bottlenose dolphins would be. To date, local or regional population studies, using what have become standard procedures for identifying individuals with photographs, have been conducted in at least the United States, Mexico, Argentina, Australia, southern Africa, and Portugal. We know from fish-

ery catches, strandings, and sightings surveys that bottlenose dolphins are present in virtually all tropical and temperate marine waters. Local concentrations of bottlenose dolphins have provided, and will continue to provide, attractive opportunities for students seeking advanced degrees. The increasing creativity shown in approaches to basic population studies encourages newcomers to go beyond what once passed for discovery.

Another reason for initiating this project was that we were aware of some good work that seemed to be taking too long to reach print. By providing an outlet for their contributions, we wanted to stimulate colleagues to write their results for formal presentation and scrutiny. Too much interesting and useful information was languishing in files and contract reports, where access was limited to insiders only.

The first section, "Evolution and Fossil Record," consists of a single chapter. Lawrence G. Barnes outlines and evaluates the fossil record of bottlenose dolphins and offers several new interpretations. The genus is represented by fossils dating to the early Pliocene epoch, about 4 million years ago. Since the earliest fossils referable to *Tursiops* are from North America, the genus probably did not originate in the Mediterranean, as has been postulated. The bottlenose dolphin is a primitive member of the subfamily Delphininae, sharing some anatomical characters with the more primitive stenine delphinids and the extinct Kentriodontidae, the probable Miocene ancestors of the Delphinidae.

In the second section, "Anatomy and Physiology," there are three chapters. Sentiel Rommel has used the excellent collection of skulls and skeletons in the United States National Museum to describe and illustrate the osteology of the bottlenose dolphin. Some skull and skeletal features have been defined ambiguously in the literature. The author has developed more precise definitions and a stan-

standard terminology for the different parts of the dolphin skull and skeleton.

Problems of identifying and describing muscle groups in other mammals are compounded in cetaceans, whose body plans have been uniquely modified for efficient aquatic locomotion. Also using specimens in the United States National Museum, D. Ann Pabst has brought some much-needed order to this branch of cetology. In addition to defining and illustrating the various muscle groups, she has, for the first time, treated the major connective tissues as discrete structures. Her comprehensive treatment of the bottlenose dolphin's axial morphology is intended as a template for similar reviews of other cetaceans. Preliminary comparisons of bottlenose dolphins with other odontocetes suggest that the general axial body plan is very conservative.

As a veterinarian and scientist who has treated and studied bottlenose dolphins for more than 25 years, Sam H. Ridgway is well qualified to review what is known about their central nervous system. Besides critically summarizing the literature on dolphin sensory systems and brain anatomy, he offers comparisons with other mammalian groups, including humans, and suggests ideas and approaches for further research.

Part III, "Systematics and Taxonomy," consists of two chapters. First, Graham J. B. Ross and Victor G. Cockcroft describe bottlenose dolphins in Australian waters by analyzing data mainly from museum specimens and captive live animals, supplemented by new data from populations off southern Africa. An important conclusion is that Ross's previous recognition of *Tursiops aduncus* as a species separate from *T. truncatus* is retracted. *T. aduncus* is a junior synonym of *T. truncatus*. The considerable variability in such features as extent of ventral spotting, body and skull length, and snout length and breadth nevertheless emphasizes the clinal differences between bottlenose dolphin populations living in different habitats, e.g., inshore versus offshore, high versus low latitudes. The approach taken in this study may provide a useful model for understanding the inshore-offshore differences in bottlenose dolphin populations in other parts of the world. Feeding rates for a captive animal suggest that bottlenose dolphins live in conditions close to or below the lower limit of their thermo-neutral zone for most of the year, and conse-

quently increase their blubber mass during colder periods.

Sandra L. Hersh and Deborah A. Duffield report that offshore bottlenose dolphins in the Northwest Atlantic have two electrophoretically distinguishable hemoglobins, whereas coastal bottlenose dolphins from the same regions have only one hemoglobin. The offshore dolphins are larger and have proportionately smaller flippers than the near-shore animals, and the two forms can be distinguished further by certain skull features. The authors suggest that habitat may explain these biochemical and morphological differences. The offshore ecotype lives in cool, deep water; the coastal ecotype, in shallow, warm water.

There are three chapters on "Life History and Biology" (Part IV). Very little is known about the biology of small odontocetes in the eastern South Pacific, despite the fact that large numbers have been taken in fisheries off Peru and Chile. Koen Van Waerebeek and his colleagues began a program in the mid-1980s to document the distribution, natural history, and exploitation of small cetaceans in this region. They point out that bottlenose dolphins occur in coastal waters from at least southern Ecuador to Concepción, Chile, at 37°S. Preliminary evidence indicates the presence of two forms, coastal and offshore, differing in cranial morphology, diet, and parasite fauna. Coastal animals also have significantly wider teeth than offshore animals. It is estimated that hundreds of bottlenose dolphins, in addition to thousands of other dolphins, are killed annually by the artisanal fisheries in central Peru.

Investigators in Florida have been collecting information on stranded cetaceans systematically since the mid-1970s. Using a sample of 170 beached bottlenose dolphins collected from the Indian and Banana River complex, January 1978 through December 1983, Sandra L. Hersh and associates have analyzed mortality patterns in the local dolphin population. They estimate an annual mortality rate of about 7-9%. Mortality is seasonally uniform in most years, with noticeable increases only during exceptionally cold winters. Newborn dolphins have a somewhat higher mortality rate than other age classes. The authors emphasize that this kind of study can be done only in situations where carcass salvage effort is intensive and consistent throughout the year, and when information is

available on the size and age/sex composition of the living population.

Many of us were stunned when in 1987 and 1988 approximately 750 bottlenose dolphins washed ashore on the east coast of the United States, most having died from an insidious cause. This sad series of events was officially said to have been caused by poisoning from red-tide toxins in combination with bacterial and viral infections. Whatever its actual cause, the die-off brought clearly into focus the need for reliable information on the basic biology, diseases, parasites, and feeding habits of the bottlenose dolphins.

Since the early 1970s, James G. Mead and Charles W. Potter of the United States National Museum have been studying the biology of bottlenose dolphins stranded between Massachusetts and South Carolina. They report their basic findings from examination of 248 carcasses, most representing the coastal form. The dolphins had fed mainly on three fish species (croakers, *Micropogon undulatus*, spot, *Leiostomus xanthurus*, and sea trout, *Cynoscion* sp.) and were often infested with the trematode *Braunina cordiformis*. In this area, bottlenose dolphins are born at a mean length of 117 cm, reach an asymptotic length of 250 cm at an age of 12 years, and become sexually mature at 234 cm, 11 years, and a body weight of 150 kg (females); or 160 cm, 11 years, and a single testis weight of about 100 g (males). Skull maturity was found to be expressed at a mean age of 3.46 years in both sexes.

The largest section of the book, Part V, covers topics within the broad subject areas of "Behavior and Ecology." The study of dolphin sound production has been one of the most fruitful and provocative aspects of cetological research. Hearing is, without a doubt, these animals' most important sense. In addition to the well-known echolocation clicks and burst pulsed sounds often described as squawks, yelps, or barks, bottlenose dolphins produce frequency-modulated, narrow-band sounds called whistles. In 1965, David K. and Melba C. Caldwell first noted that captive animals produce individually distinctive, stereotyped whistles. In their chapter, the Caldwells, with co-author Peter Tyack, present and analyze a large sample of whistle recordings made from 126 different dolphins to develop and test their signature-whistle hypothesis. Signature whistles have proven difficult to de-

fine quantitatively, since their stereotypy involves the contour configuration of loops (repetitive elements) as well as more easily measured features. One function of signature whistles presumably is to allow members of a social group to broadcast their identity to their fellows. However, our appreciation of the social function of specific whistle contours produced by particular individuals must await the development and application of techniques for identifying which dolphin in an interacting group produces each whistle. The number of loops in a given signature whistle can vary, depending on such factors as the behavioral context and the dolphin's age.

Detailed local studies have significantly advanced our understanding of the behavior and ecology of coastal bottlenose dolphins. Michael D. Scott and associates present a summary of the methods and findings of their long-term research program in Sarasota Bay on Florida's Gulf Coast, uninterrupted since 1970. Although this chapter offers little that is new, we felt that the study's significance, both for the development of research methods and for the insights obtained about bottlenose dolphin societies, merited the inclusion of this brief review. The Sarasota program has become the prototype for area population studies of bottlenose dolphins. Individual dolphins have been followed over several generations, and changes in behavior and association patterns have been documented as calves mature into adults. The study has illuminated pervasive differences between the reproductive strategies of male and female dolphins.

Susan H. Shane worked in 1985 and 1986 in an area off western Florida south of Sarasota. By instantaneous sampling of focal groups, she was able to identify seven distinct types of feeding, each associated with specific ecological conditions. Diurnal and seasonal activity patterns differed from those in other areas where bottlenose dolphins have been studied. Dolphin behavior was found to be affected by a complex web of interacting environmental features rather than by any one feature.

Lisa T. Ballance studied a community of 155 identifiable bottlenose dolphins in Kino Bay, northeastern Gulf of California, Mexico, during 1984. She presents her findings concerning residence patterns, group stability, and surfacing asso-

ciations. The dolphins exhibited different degrees of site fidelity and three different patterns of group membership. Individuals in some groups remained together over several months; some individuals were seen only once in the presence of a group with frequently seen individuals; and some individuals were often present but not consistently associated with the same individuals. After considering differences and similarities between the dolphins in Kino Bay and those elsewhere, Balance speculates that the degree of site fidelity in this species may be highest in closed habitats, such as bays and lagoons, and lowest in open habitats, such as exposed coasts. Synchrony in surfacing patterns was short-lived and did not always involve long-term associates.

In the next chapter, Peter J. Corkeron compares the behavior of bottlenose dolphins and Indo-Pacific humpbacked dolphins, *Sousa chinensis*, in Moreton Bay, Australia, based on his observation of 334 and 50 photographically identified individuals of the two species, respectively, over nearly three years. The two species occurred in mixed groups, found in association with trawlers and dominated by bottlenose dolphins. Evidence suggests that the size of food patches created by trawling and possibly the threat of predation significantly affect the size of dolphin groups.

Three chapters offer new information on feeding habits of bottlenose dolphins. From examination of stomachs of 127 dolphins which died after entangling in shark nets off southern Natal, South Africa, Victor G. Cockcroft and Graham J. B. Ross document feeding on 72 species of fishes, elasmobranchs, and cephalopods. They found some seasonal variation in proportions of the various species, increases in prey length with predator length, lower feeding rates in calves than in other animals, and differences in feeding by age/sex class. The last finding is important in understanding home range and social structure.

Nélio B. Barros and Daniel K. Odell analyzed the stomach contents of 76 bottlenose dolphins stranded in the southeastern United States. They found otoliths from 43 fish species, including nine prey taxa not previously reported for bottlenose dolphins in this area, and cephalopod beaks representing three families. Observed geographic variation in diet appears consistent with regional differences in relative availability of prey. Inshore

dolphins feed mainly on bottom-dwelling fish; offshore dolphins, on cephalopods. Most fish species consumed are known to be conspicuous sound producers, and the authors suggest that bottlenose dolphins use passive listening to detect prey.

In many areas, bottlenose dolphins feed in association with fishing operations. Peter J. Corkeron and colleagues took advantage of such an association in Moreton Bay, Australia, to evaluate food preferences. They noted how the dolphins following a trawl net selected prey. At the completion of trawls, they offered selected portions of the catch to nearby dolphins. The authors discovered that social factors which vary among groups affect the degree of choice available to any given individual, thereby affecting the composition of its diet. Benefits of feeding around trawlers, e.g., easy access to food, are at least partly offset by increased risk of capture in nets and increased threat of shark predation.

Unsolicited approaches to humans made by wild dolphins are emotionally charged events, recounted enthusiastically in mythology and factual literature. Christina Lockyer reviews the phenomenon of "sociability" in wild dolphins, treating incidents by area, species, and type of interaction. We asked her to prepare this chapter because bottlenose dolphins do affiliate with humans in various parts of their range, and this aspect of their behavior has been widely publicized (and occasionally exaggerated or distorted) in popular books and articles. Lockyer's first-hand experience with what she calls "sociable" wild bottlenose dolphins and her reputation as a scientist make her well qualified to comment on what this extraordinary behavior might mean.

With increasing scientific study of wild dolphins, progressively greater care is being taken to replace subjective accounts with quantitative descriptions of behavior. Richard C. Connor and Rachel A. Smolker provide a quantitative description of a female dolphin's behavior toward her deceased calf.

Resightings of recognizable individuals have been at the core of many recent studies of bottlenose dolphins. Among other things, they provide insight into long-term site fidelity and changes in habitat use. In their chapter, Bernd Würsig and Graham Harris report that ten individually identified dolphins in Golfo San José, Ar-

gentina, were associated with the same companions in 1984 and 1986 as they had been in 1974 through 1976. The natural marks permitting identification had persisted for up to 12 years. However, the dolphins had shifted their pattern of movement away from the Gulf and occurred there only sporadically from 1978 to 1986. Eight of the ten recognizable animals were presumed to be females, judging by their proximity to calves born in the previous summer or fall.

Part VI, "Distribution, Movements, and Abundance," contains four chapters. Particularly in view of the recent mass die-off of bottlenose dolphins along the east coast of the United States mentioned above, the extensive surveys of cetaceans on the continental shelf between Cape Hatteras, North Carolina, and the northern Gulf of Maine conducted between 1978 and 1983 by the University of Rhode Island have provided a valuable baseline of information on dolphin populations. Robert D. Kenney summarizes what was learned in this program about the bottlenose dolphin's distribution and population size. He estimates that in the early 1980s the population of bottlenose dolphins off the northeastern United States (Cape Hatteras north) numbered about 10,000–12,000. Only about 3–4% of this total is considered to belong to the migratory nearshore stock which was fished intensively during the 1880s. As Kenney points out, either the nearshore stock is much smaller now than it was in the late nineteenth century, the current population has been significantly underestimated, the surveys did not extend far enough south to census the majority of dolphins in the coastal stock, and/or the nineteenth century fishery also exploited the offshore stock. The offshore stock, centered along the shelf break, has a wider distribution and apparently tolerates a greater range of water temperatures than the inshore stock.

Michael D. Scott and Susan J. Chivers have used the extensive data collected during tuna-fishing and research expeditions to the eastern tropical Pacific to examine hypotheses about how and why bottlenose dolphin herd structure might vary in coastal and pelagic habitats. Small groups (median about 10 animals) are the norm in both kinds of habitat, and herd size does not increase with distance offshore. The greater range of herd sizes (from single individuals to aggregations of several

thousand) distinguishes pelagic from coastal bottlenose dolphins. There is also a tendency for dolphins farther offshore to associate more frequently with other cetaceans, although no more than 30% of the sightings involved such associations even in the areas farthest from shore.

Based on analyses of sightings (1970–1983) and data from photoidentification surveys (1981–1983), Larry J. Hansen estimates that the southern California coastal population of bottlenose dolphins numbers about 240 animals. They normally range from Ensenada, Mexico, to Seal Beach, California, but occur much farther north in some years. About 17% of identified animals exhibited some site fidelity in San Diego County, where they seemed to prefer a particular stretch of coast.

Randall S. Wells and several co-authors report sightings in the Monterey Bay area, central California, of bottlenose dolphins previously photoidentified only in southern California. They discuss similar patterns of association in the two areas as evidence of long-term social bonds and speculate on environmental causes of these long-distance movements.

Part VII contains four chapters on "Husbandry and Captive Breeding." The future of captive dolphin programs may well depend on successful breeding. J. Pete Schroeder presents two chapters, the second co-authored with Karl V. Keller, describing the U.S. Navy's efforts to define reproductive cycles of male and female bottlenose dolphins and then to use that knowledge to enhance captive breeding programs by monitoring hormones, inducing ovulation, and artificially inseminating females in estrus.

In the next chapter, Victor G. Cockcroft and Graham J. B. Ross describe the physical and behavioral development of a bottlenose dolphin from its birth in captivity to two years of age. The calf generally decreased his milk and energy intake with age. He began taking solid food at an age of 321 days but continued sucking facultatively until well past his first year and probably beyond his second year. He apparently received a progressively decreasing energetic contribution from his mother's milk. Energy intake increased substantially immediately after weaning.

Successful maintenance of dolphins in captivity depends on good health care programs. Edward D. Asper and colleagues present normal values and

ranges for 31 hematology and serum chemistry clinical tests of blood from captive and wild bottlenose dolphins. Age-related differences exist in some parameters, sex-related differences in others. However, in general, values for captive dolphins do not differ significantly from those for wild dolphins except insofar as the latter have a greater antigenic challenge and different diets and exercise regimes.

The next section (Part VIII) has seven chapters describing and evaluating recently developed "Research Techniques." Various kinds of tags, including natural marks, freeze-brands, and radiotags, have been useful in studies of dolphins. Michael D. Scott and associates review the history of tagging and marking studies, pointing out strengths and weaknesses of the various approaches. Daniel K. Odell and Edward D. Asper provide details of their study in the Indian and Banana rivers, Florida, in which natural marks and freeze-brands were used to study the distribution, movements, and discreteness of the dolphin population inhabiting this sea-flushed lagoon network. The fact that methods of tagging used required capturing and handling dolphins, some more than once, permitted the authors to conduct biological sampling, and they report some results of that sampling.

Recognizing that the particular research methods employed may be as significant as actual behavior and population characteristics of the dolphins in affecting the outcome of a behavior study, Susan H. Shane compares the approaches used in and results from her own studies in Texas and western Florida. The *ad libitum* sampling used in Texas, and indeed in most studies of bottlenose dolphin behavior, may be biased because it tends to overemphasize the more dramatic social behavior while underemphasizing the less spectacular behavior. The focal group sampling (following Altmann's classic 1974 paper) used in Florida more accurately represents the full range of the animals' behavior. Even allowing for the differences in research methods, however, the dolphins in Texas spent less time feeding than their counterparts in Florida. The Texas dolphins used two of seven identified feeding modes predominantly, while the Florida dolphins used each of the seven modes with approximately equal frequency. The fewer recognizable animals in Texas were identified up to 156 times each, while the larger number of recog-

nizable animals in Florida were seen no more than 19 times each. Flexibility in adapting to different regional conditions is cited as a principal factor in the widespread distribution of bottlenose dolphins in coastal environments, including those with high densities of human activity.

Harold W. Goforth, Jr. describes an experimental method for studying various physiological and metabolic responses to exercise by captive dolphins. A bottlenose dolphin was conditioned to place its rostrum against a load cell (force transducer), swim in place for 3-minute and 8-second periods, and submit to blood sampling and muscle biopsies. The 3-minute trials were used to measure tailbeat force during sustained swimming; the 8-second trials, to measure maximum tailbeat force. The dolphin's maximum thrust on a single tailbeat was 4730 newtons. Its maximum burst effort was 3263 newtons per tailbeat; its maximum sustained swimming level, 1324 newtons per tailbeat. Maximum burst speeds and sustained swimming speeds of wild dolphins, about 21 and 15 knots, respectively, are summarized and discussed. This study demonstrates some of the scientific values of working with trained captive animals in controlled situations.

Increasingly, layering patterns in teeth are being used to estimate ages of dolphins. Such studies depend on knowing the rates at which layers (called Growth Layer Groups, or GLGs) are deposited and what factors influence those rates. Aleta A. Hohn reviews the history of attempts to define GLGs, summarizes her own work on known-age, free-ranging bottlenose dolphins, and points out some pitfalls of reading and interpreting layers in teeth. She also offers counsel on how best to conduct studies and report findings so as to increase their usefulness to future investigators. In the next chapter, Albert C. Myrick, Jr., and Lanny H. Cornell report the results of their age-estimation work with captive dolphins. They establish that one dentinal GLG is deposited per year in the teeth of bottlenose dolphins, and they identify principal factors affecting the rate of dentine deposition.

Deborah A. Duffield and Jan Chamberlin-Lea report that each of 66 bottlenose dolphins they sampled had its own karyotypic signature. They conclude that variability in R-banding of karyotypes and profiles of hemoglobins are useful in studies of populations and paternities.

The final section, Part IX, consists of only one chapter on "Management." The live-capture fishery for bottlenose dolphins in the southeastern United States is managed by the National Marine Fisheries Service under the Marine Mammal Protection Act of 1972. Gerald P. Scott describes the agency's goals and strategies. Annual quotas of 2% or less of the estimated population are set for regional management units, thought to correspond roughly with local stock boundaries. Readers should be advised that this chapter was current only through early 1987. The subsequent die-off of dolphins in the eastern United States has changed the atmosphere in which the management program operates. We expect the current period of re-evaluation, influenced by the sobering recognition that many animals in the coastal bottlenose dolphin population north of central Florida died within a period of less than a year, to result in an even more conservative approach to management of the live-capture fishery.

Inevitably, there are subjects which should have been addressed in a book like this one but were not. We had initially hoped for somewhat broader regional coverage. Although some areas not represented in the book, such as coastal southern Africa, have been treated in previous publications, there are still large parts of the bottlenose dolphin's range for which little has been published. We had hoped to include additional chapters directed at resolving the problems of *Tursiops* systematics. As noted by the Subcommittee on Small Cetaceans of the International Whaling Commission's Scientific Committee in 1974, there appear to be a number of geographical races of this species, defined on the basis of body and tooth size as well as different distributions relative to sea temperature and depth. The names *Tursiops aduncus*, *T. gillii*, *T. nuuanu*, and *T. gephyreus* are still used in certain areas as though they represent valid species, so their status begs to be clarified. We also would like to have included more review chapters, covering such topics as echolocation, sensory systems, language training, pathology and sensitivity to pollutants, exploitation in fisheries and conservation problems, habitat considerations, and world distribution. Some of these are adequately covered elsewhere, but others, such as the last four, are much needed.

In view of widening concern about the often

unforeseen, potentially devastating impacts of pollution and environmental degradation on dolphins and their prey, the conventional approaches to management and conservation of bottlenose dolphins and other species will need to be re-evaluated in the coming years. We trust this book will give that process a boost.

We are particularly grateful to two groups of colleagues for helping to create this book. First and most obviously, the authors have done the research, analyses, and writing. We asked many of them to rethink, reanalyze, and rewrite portions of their chapters after review, and we greatly appreciate the professional manner and positive spirit in which they have done so. The contributions by the reviewers are less obvious but crucial to ensuring a high standard of scholarship. We followed a peer review process similar to that used for scientific journals, sending all manuscripts to at least two anonymous reviewers. We, as editors, took into account the reviewers' comments in deciding to accept or reject a manuscript, and we sent these and our own comments to authors with requests for revision.

The reviewers were invariably generous and constructive in sharing their opinions, insights, and, in some instances, relevant new data. It is with sincere thanks that we list here (in alphabetical order) those who reviewed manuscripts submitted for this book: Frank T. Awbrey, Lawrence G. Barnes, Kurt W. Benirschke, Peter B. Best, Michael A. Bigg, Daryl J. Boness, Jeffrey M. Breiwick, Michael J. Bryden, Robert L. Brownell, Jr., John Calambokidis, Christopher W. Clark, Victor G. Cockcroft, Richard C. Connor, Lanny H. Cornell, James C. Cubbage, Randall W. Davis, Andrew E. Dizon, Robert W. Elsner, John K. B. Ford, R. Ewan Fordyce, David E. Gaskin, Jonathan Gordon, Nicholas Graham, Jack S. Grove, John D. Hall, Philip S. Hammond, Larry J. Hansen, John Harwood, Sandra L. Hersh, Russ Hoelzel, Wayne Hoggard, Aleta Hohn, Jay Hyman, A. Blair Irvine, Ronald J. Jameson, Robert E. Jones, Brian E. Joseph, Steven K. Katona, Dennis Kelly, Margaret Klinowska, Scott D. Kraus, David M. Lavigne, Richard M. Laws, Alfredo A. Lichter, Christina Lockyer, Lloyd F. Lowry, Helene Marsh, William Medway, Albert C. Myrick, Jr., Mary K. Nerini, Daniel K. Odell, Seiji Ohsumi, Thomas J. O'Shea, Josephine E. Pemberton, William F. Perrin, Wayne

Perryman, August Pivorunas, Charles W. Potter, Karen Pryor, Katherine Ralls, Clayton E. Ray, John E. Reynolds, Dale W. Rice, Sam H. Ridgway, Keith Rittmaster, Graham J. B. Ross, David J. Rugh, Victor B. Scheffer, William E. Schevill, Gary D. Schnell, Michael D. Scott, David E. Sergeant, Ingrid K. Shallenberger, Susan H. Shane, Gregory P. Silber, Donald B. Siniff, Tim D. Smith, David J. St. Aubin, Brent S. Stewart, Robert E. A. Stewart, Timothy Strickler, John C. Sweeney, C. Richard Taylor, Peter Tyack, R. V. Walker, William A. Walker, Marc A. Webber, Randall S. Wells, Bradley N. White, Terrie M. Williams, Forrest G. Wood, Bernd Würsig, and Pamela K. Yochem.

In addition to the authors and reviewers, we owe a special debt of gratitude to several other

individuals. Lanny H. Cornell, Sea World of California, provided funding to initiate the project and marshaled the Sea World staff to complete their contributions. Kerry Pinchbeck, our production editor at Academic Press, cheerfully and professionally shepherded the unwieldy manuscript through the production process. Copy editor Connie Parks improved the book markedly by her thorough attention to fine detail. Kathy Kangas was a valuable assistant throughout the project. She watched over the files and kept our voluminous correspondence with authors, reviewers, and each other from getting bogged down. Randi Olsen kept the Reeves family together while we worked on the book, and we appreciate her dedication to that unheralded but much-valued endeavor.

San Diego, California
6 April 1989

PHOTO: Lateral and dorsal views of skull of *Tursiops cortesii* (from Sacco, 1893: plate 2, Figures 10 and 11; see Barnes, Chapter 1, this volume, for full citation) (courtesy Kellogg Library, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution).



Part I

Evolution and Fossil Record

This page intentionally left blank

The Fossil Record and Evolutionary Relationships of the Genus *Tursiops*

1

Lawrence G. Barnes

Section of Vertebrate Paleontology
Natural History Museum of Los Angeles County
Los Angeles, California 90007

INTRODUCTION

Species in the genus *Tursiops* are generalized delphinids, judging by their morphology, evolution, and behavior. They share anatomical features with certain primitive fossil dolphins. Unlike the fossil records of most of the Recent (=extant) genera in the family Delphinidae, that of the genus *Tursiops* is moderately good and extends back several million years in geologic time. Much of the research on fossils of *Tursiops* dates from the 1800s, so this chapter provides an opportunity for a much-needed review and summary. All of the named fossil species of *Tursiops* are listed and reviewed in this chapter. Various other fossils attributed to the genus are summarized as well.

Referral of fossils to any extant delphinid genus must be evaluated with caution because modern names often have been misapplied to fossil specimens (e.g., the many reputed fossil species of the

genus *Delphinus*). The fossil record of *Tursiops* is nonetheless good enough to help elucidate parts of the evolutionary history of the family Delphinidae, the subfamily Delphininae, and the genus *Tursiops* itself.

The currently accepted hypothesis is that the ancestors of all Cetacea were terrestrial mammals that adapted to a totally aquatic existence. This is consistent with the fact that modern cetaceans have features, even if they are only vestiges, of the anatomical and physiological qualities of terrestrial mammals. Studies of fossil cetaceans can document changes and adaptations in skeletal anatomy that provide clues to ancestry and the course of evolution of the various lineages.

Comparative osteology is presently the only widely available method of comparing fossil and extant species. By analogy with the living animals, we can make inferences about the soft anatomy, physiology, and behavior of the fossil species from

their bones. The important features in paleontological analyses include overall body size, stage of maturity, shapes of individual bones (with emphasis on the skull), positions of foramina that mark the courses of nerves and blood vessels through bones (especially those of the cranium), distribution of air sinuses extending from the middle ear into other parts of the skull, shape and number of teeth, numbers of fused neck vertebrae, numbers of vertebrae and ribs, length and numbers of digits in the pectoral limb, and shape, size, and location of muscle scars and articular surfaces on bones. Characters are judged to be primitive or derived according to when they appear in the fossil record, their degree of complexity, and their occurrence in other organisms ("outgroups") not belonging to the group in question. Sound comparative osteological work is a prerequisite for the vertebrate paleontological studies that can relate the history of *Tursiops* to the geologic time scale, to the evolutionary history of Cetacea, and to the principles of classification and biogeography.

Some evolutionary patterns are discernible from the fossil record of *Tursiops*, and inferences can be made regarding the genus's area of origin, the effects of climate on the evolution and distribution of its species through time, and the morphological characters useful in analyzing relationships among different taxa. The fossil record is not yet sufficient to answer all questions about the origin, evolution, and classification of bottlenose dolphins, but a review at this time can at least indicate areas for future research. The purpose of this chapter, therefore, is to review the fossil record of bottlenose dolphins, to put these animals into evolutionary and taxonomic perspective, and to determine needs for future work.

PHYLOGENETIC POSITION OF *TURSIOPS*

Overview of Cetacean Evolution

Cetaceans were perhaps the earliest mammals to adapt to a marine existence, and the order is the most diverse of aquatic mammals. Whales appear in the fossil record about 50 million years ago (mya), in Early or Middle Eocene time. The earliest

appearance in the fossil record of any species referable to the genus *Tursiops* is relatively recent, at about 5 mya. To place *Tursiops* in evolutionary perspective and to indicate the reasons why certain osteological features are used in determining relationships and stages of evolution, I summarize briefly the evolutionary history of cetaceans. This summary concentrates on those groups that are either directly on or close to the lineage leading to *Tursiops*. The taxa mentioned are outlined in the section on classification (see p. 9, 11).

Information derived from modern mammals about blood composition, chromosomes, uterine morphology, insulin, fetal blood sugar, and tooth-enamel microstructure points to closest relationships between cetaceans and ungulates, especially the Artiodactyla. Flower (1883) was one of the first to propose this relationship, based on comparative gross morphology. Van Valen (1966) and Szalay (1969a,b) argued on paleontological grounds that archaeocetes evolved from terrestrial ungulates known as mesonychid condylarths. The condylarths, in the broad sense, are also regarded as the ultimate ancestors of all later ungulates. This leads to the inference that cetaceans and artiodactyls share a common ancestor, as yet unknown or unrecognized in the fossil record, among the condylarths. This inference is supported by the morphological and physiological similarities that have been noted for many years. Of course, this does not imply that cetaceans evolved from the artiodactyls. Barnes and Mitchell (1978), Evans (1987), Gaskin (1982), Gingerich *et al.* (1983), and Rice (1984) have discussed origins of cetaceans (see also references cited therein).

All living whales, dolphins, and porpoises share certain basic anatomical and physiological characteristics with other mammals. Living cetaceans have remnant vestigial features (e.g., facial hairs, olfactory nerves, and hind-limb bones) that are clearly inherited from their terrestrial ancestors. Living cetaceans have become obligate aquatic animals, with a fusiform body shape, blubber, pectoral flippers, a short neck, horizontal caudal flukes supported by fibro-cartilage, and a dorsal fin (a derived character which is secondarily lost in some groups). All of these characters, except the dorsal fin, are convergent with such different groups of mammals as the sirenians and pinnipeds, and if considered individually they are

not necessarily diagnostic of cetaceans. All cetaceans, fossil and living, share the following unique suite of derived osteological characters (also called apomorphies):

1. Anterior palatine foramina lost
2. Falcate processes of the basioccipital large
3. Peribullary and pterygoid air sinuses present as diverticula from the middle-ear air sinus
4. Tympanic bulla involuted and inflated
5. Supraorbital process of the frontal large and tabular
6. Hypoglossal foramen in the basioccipital located either at the apex of or inside the jugular notch
7. Mandibular foramen large
8. Scapula with reduced suprascapular fossa and acromion and coracoid processes that are parallel and directed anteriorly

Skeletal evolution in the Cetacea is also characterized by telescoping of the cranial bones, isolation of the ear bones from the other cranial bones by air sacs or fat bodies, shortening and/or fusion of cervical vertebrae, addition of thoracic, lumbar, and caudal vertebrae, and hyperphalangy. The highest point on the skull is usually behind the nares, and this is called the cranial vertex.

Telescoping of the cetacean skull (see Miller, 1923) is a process that involves posterior movement of the nasal openings, linked with the posterior extension of the bones comprising the rostrum (the elongate maxillae, premaxillae and vomer, and the mesethmoid cartilage, which lies in a mesorostral gutter), ultimately reaching the top of the braincase around the cranial vertex. In most groups of cetaceans, the occipital shield also projects forward a certain amount. A major step in the evolution of both the odontocetes and the mysticetes was the progressive movement of the maxillae over and/or under the front of the supraorbital processes of the frontals as the nares moved posteriorly on the rostrum. The orientation and location of the mammalian infraorbital foramen were thereby changed from its primitive position on the cheek in front of the zygomatic arch, and became expressed as multiple maxillary foramina on the dorsal surface of the face and on the posterior part of the rostrum and, in the Odontoceti, as premaxillary foramina as well.

For general reviews of cetacean evolution, the

reader may wish to consult Winge (1921), Miller (1923), Kellogg (1928, 1938), Slijper (1936, 1979), Rice (1967, 1984), Fordyce (1980), Gaskin (1982), Barnes (1984b, in press a,b), Barnes *et al.* (1985), and Evans (1987).

In most traditional classifications (e.g., Simpson, 1945; Hall and Kelson, 1959; Romer, 1966; Gaskin, 1982; Evans, 1987) the order Cetacea is divided into suborders: The primitive Eocene and Oligocene Archaeoceti, the Oligocene (~36 mya) to Recent Odontoceti (toothed whales), and the Oligocene to Recent Mysticeti (baleen whales). Archaeocetes are early whales that retained many primitive structures. Mysticetes and odontocetes evolved special structures, many of which are correlated with the method of feeding.

The Protocetidae are the oldest and most primitive of the archaeocetes, known from Middle Eocene fossils from Pakistan, India, Egypt, Nigeria, and the southeastern United States (see Barnes and Mitchell, 1978; Gingerich *et al.*, 1983). Van Valen (1968) suggested that the later odontocete and/or mysticete suborders were derived directly from the early protocetids rather than from any of the later archaeocetes, as was suggested by Barnes and Mitchell (1978) and Fordyce (1980). The protocetids were relatively small-bodied animals (for whales), less than about 3 m long, having primitive characters such as nontelescoped skulls, nostrils on the anterior part of the snout, and the normal mammalian dental formula, with two roots on P1-2/ and three roots on P3/-M3/. At least one species of protocetid is known which retained facets on its sacral vertebrae for articulation with large innominate bones, suggesting that it probably had external, if not functional, hind limbs. It might even have been amphibious! In all of the later cetaceans, the bones of the pelvic girdle are reduced and the facets on the sacral vertebrae are lost (derived characters).

The more highly evolved family Basilosauridae includes medium-sized, generalized archaeocetes in the subfamily Dorudontinae and the giant archaeocetes of the subfamily Basilosaurinae. Apparently, the later Eocene basilosaurids dispersed throughout most of the world's oceans, because their fossils have been found in Africa, Great Britain, Australia, Antarctica, and the southeastern United States. Compared with the more primitive Protocetidae, the skulls were somewhat

more telescoped, and the molars and premolars had achieved a more derived state, with only two roots and with accessory denticles on the anterior and posterior edges of the crowns. They had also lost the M3/ (derived character). *Basilosaurus cetoides*, a huge Late Eocene (~37 mya) archaeocete, retained an innominate bone and a femur, but these were reduced in size. Generalized dorudontines have been suggested as the possible ancestors of all mysticetes and odontocetes (see Barnes and Mitchell, 1978; Fordyce, 1980). This conflicts with Van Valen's (1968) idea that later cetaceans instead evolved from the Protocetidae, but it is important to note the widely supported theory that all of the later cetaceans must have evolved from some group of archaeocetes (see Fordyce, 1980; Barnes, 1984b).

The two derived suborders, Odontoceti and Mysticeti, are considered a monophyletic unit (an evolutionary clade) because they share the following derived characters not found in archaeocetes:

1. Multiple maxillary foramina derived from the infraorbital foramen
2. Advanced stages of cranial telescoping
3. Vomer extended backward and exposed on the basicranium to cover the basisphenoid/basioccipital suture
4. Zygomatic process of the squamosal contacting the postorbital process of the frontal or connected to it by a ligament
5. Monophyodonty
6. Elbow joint nonrotational with anteroposterior position of radius and ulna
7. Olecranon fossa of the humerus lost
8. Hyperphalangy

Some published diagnoses of the two living cetacean suborders were based solely on the characters of living animals, and, unfortunately, these excluded the numerous fossil representatives. For example, the suborder Odontoceti has been diagnosed as those cetaceans having asymmetrical skulls, and the mysticetes as those having baleen instead of teeth (e.g., Rice, 1967), but this would place in limbo those (numerous) fossil odontocetes which had symmetrical skulls as well as the early fossil mysticetes which still had teeth. Comprehensive diagnoses for these groups must include both the modern and fossil taxa and be based on osteology.

Odontocetes always have teeth present, the rostrum has thick lateral edges, the maxillae do not project beneath the orbits as infraorbital plates, and dorsally do not interlock with the frontals, but spread outward over the expanded supraorbital processes. The facial region is occupied by a fatty organ, the melon, and the internal nares are two bony openings (derived feature) while the external nares form a single opening (the blowhole). The posterior mandibular foramen is greatly enlarged and filled with adipose tissue, and its lateral wall (the pan-bone) is thin. All hyoid bones are separate.

Mysticetes have baleen and vestigial teeth that are lost before birth (except in the primitive Aetiocetidae, which had functional teeth); the rostrum has thin lateral edges. The maxillae have infraorbital plates and laterally projecting antorbital processes; they interlock with the frontals and do not spread over the supraorbital process. There is no melon, and the internal naris is a single bony opening (primitive) while the external nares are a pair of openings. The posterior end of the mandible is not greatly excavated (primitive), and there is no articulated or ankylosed mandibular symphysis but instead a ligamental attachment marked by a lingual groove (derived characters). Mysticetes never developed the echolocation capabilities of odontocetes and do not have cranial asymmetry.

Mysticetes and odontocetes were widespread and diverse in the Oligocene and afterward. Some primitive members of each of these groups are both chronologic and morphologic intermediates between archaeocetes and more highly evolved cetaceans. By the the start of the Miocene (~25 mya), all the major modern adaptive types of cetaceans had appeared, but the earliest known fossil records of the family Delphinidae (which includes *Tursiops*) and some of the other extant families are considerably more recent, dating from the Late Miocene (~11 mya) (see Barnes, 1976, 1984b; Barnes *et al.*, 1985).

Evolutionary Position of *Tursiops* among Toothed Whales

In this section I place *Tursiops* in context within the suborder Odontoceti. First, some functional and morphological attributes of odontocetes are dis-

cussed, then the genealogy of *Tursiops* is traced, as deduced from the fossil record, from primitive odontocetes of the Oligocene to the first *Tursiops*-like animals in the Late Miocene.

Odontocetes have retained the apparently primitive feeding mode employed by archaeocetes (and many other marine predators) of selecting and capturing individual prey. This contrasts with the bulk-feeding methods used by mysticetes. Teeth are obviously useful to odontocetes for holding slippery animals. From the primitive heterodont mammalian tooth formula of the archaeocetes, the trend in the derived odontocetes has been toward simplification of the teeth by development of single roots and conical crowns (homodonty) and increase in their numbers (polydonty). Some highly derived odontocetes have secondarily lost or reduced parts of their dentition or have developed specialized teeth with enamel rugosities or large teeth in the form of tusks. Some modern odontocetes that have secondarily lost teeth have acquired cornified structures on the palate in their stead. The species of *Tursiops* have tooth counts in the middle range for odontocetes, and upper and lower teeth are fully functional.

In general, progressive evolutionary trends in the odontocetes are toward further homodonty, polydonty (sometimes secondary reduction), cranial asymmetry, expansion of the middle-ear air-sinus system into various parts of the skull (Fraser and Purves, 1960), telescoping with an emphasis on movement of rostral bones over the face toward the occiput, shortening and/or fusion of cervical vertebrae, and increase in number of vertebrae. These characters evolved to varying degrees at different times in separate lineages.

Odontocetes have evolved sound-making abilities, which aid them in catching prey, communicating, and echolocating in dark waters. Sound, in the form of clicks, is produced during the movement of recycled air within complex diverticula, sacs, and valves of the nasal passages (see Lawrence and Schevill, 1956; Schenkken, 1973) and by friction/stiction of the nasal plugs (Evans and Maderson, 1973). The current working hypothesis is that this sound is projected into the water after passing through a fatty melon on the face which acts as an acoustic lens. Most of the sacs and associated structures are in the flesh of the facial region and, therefore, cannot be

detected by examining only a skull. However, the positions of two of the largest of these, the paired premaxillary sacs, can be detected on a fossil or modern odontocete skull by the presence of a distinctive flat surface (premaxillary sac fossa) next to the naris at the back end of each premaxilla. The former existence of the premaxillary sacs can be inferred in even the earliest odontocetes of the Oligocene (~30 mya), indicating that either these animals actively echolocated or they were at least preadapted to do so. These premaxillary sacs are primitively symmetrical in most fossil odontocetes but asymmetrical in most living odontocetes. *Tursiops* has the typical delphinid, derived condition of asymmetrical sacs and premaxillae.

The external acoustic meatus, the primary path of sound conduction to the inner ear in land mammals, is closed in cetaceans, and hearing is by a different method. Sound waves in the water (whether from another source or produced by the odontocete and reflected back off another object) are received by the head of the animal and transmitted to the ear region by a thin bony area in the posterior part of the lower jaw. The ear bones are acoustically isolated from bone and muscle by fat bodies and air sacs, and this allows directional hearing (see Norris, 1968, for a summary).

The field of sound emitted by some living odontocetes has been shown to be asymmetrical. Norris *et al.* (1971) have also demonstrated asymmetrical movements of soft tissues in and around the nasal passages of dolphins during sound production, and Mead (1975) linked these with the specialized sounds made during echolocation. Mead also postulated that in the course of odontocete evolution the development of asymmetrical soft tissues preceded asymmetry of the bones. The majority of early fossil odontocetes did not have cranial asymmetry, and the majority of later fossil and living ones do. Even in the franciscana, *Pontoporia blainvillei*, one of the few living odontocetes with cranial symmetry, the nasal sacs are asymmetrical (Schenkken, 1973). In most odontocetes with asymmetry, the bones of the top of the skull around the nares are always offset to the left side. In one group of delphinoids, the pithanodelphine kentriodontids, however, the cranial vertex is displaced to the right side (Barnes, 1985b). At least six odontocete lineages, and possibly as many as ten (see Barnes *et al.*, 1985, their Fig. 1), must have acquired cranial asymmetry independently, either

because they appear to have evolved from different ancestors which had symmetrical skulls or because the bones on the top of the skull have been modified in different ways.

The evolutionary lineage leading from the primitive odontocetes to the Delphinidae, including *Tursiops*, is moderately well understood from the fossil record. The suborder Odontoceti includes five major evolutionary groupings, usually recognized as the superfamilies Squalodontoidea (fossils only, totally extinct), Platanistoidea (river dolphins, etc.), Delphinoidea (belugas, true dolphins, porpoises, etc.), Ziphioida (beaked whales), and Physeteroidea (sperm whales, etc.) (see Barnes *et al.*, 1985).

The extinct squalodontoid family Agorophiidae is the most primitive recognized family in the suborder Odontoceti and includes animals that are in many ways morphologically (and also chronologically) intermediate between archaeocetes and the family Squalodontidae. All known agorophiids are Oligocene in age (Whitmore and Sanders, 1976), not Late Eocene as sometimes reported in the literature. These animals are not known by many postcranial bones, and the few known skulls demonstrate that they had only a moderate degree of telescoping (the nares were still well anterior to the orbits) and that the cheek teeth had multiple roots and accessory denticles on the crowns.

The extinct family Squalodontidae is believed to have evolved directly from agorophiids. Simpson (1945) was one of the first to imply this relationship when he classified Agorophiidae and Squalodontidae in the same superfamily, Squalodontoidea. Rothausen (1968) further developed this idea of relationships and showed a phylogeny of squalodontoids with various grades of evolution. Squalodontids are probably the group from which most later odontocetes, principally "dolphins" in the broad sense, have their ultimate ancestry. Many species of squalodontids have been named, and skulls and skeletons are frequently represented in museum collections and in the literature. Most squalodontids were relatively large animals with bodies 3 m or more in length. Their crania were almost fully telescoped, with the nares located on top of the head, between the orbits, and with the intertemporal constriction much reduced. The dentition was polydont, but still heterodont with long, pointed (caniniform)

anterior teeth and wide, multiple-rooted cheek teeth with many denticles.

The superfamily Delphinoidea represents a major evolutionary radiation of "dolphins" that started in the Late Oligocene and includes the majority of living cetacean species. This group apparently evolved directly from squalodontids. The currently recognized families in the Delphinoidea are the extinct Miocene Kentriodontidae and Albireonidae, and the extant Delphinidae (true dolphins), Phocoenidae (porpoises), and Monodontidae (belugas and narwhals) (Barnes *et al.*, 1985). All three of the living delphinoid families have fossil records that may be traced back to Late Miocene time (~11–12 mya), and they are characterized by having asymmetrical cranial vertices. In each group this asymmetry affects the bones of the vertex in different ways and was possibly acquired independently in each family.

Most kentriodontids were small dolphins approximately 2 m or less in length. They had skulls with short- to medium-length rostra, and most had symmetrical cranial vertices, the primitive odontocete condition. Their teeth were polydont and homodont, although some primitive species had small denticles on the posterior teeth. The family was relatively diverse in the Middle and Late Miocene, represented by fossil species in both the Atlantic and Pacific oceans, but there are no published records of any species that survived more recently than about 10 mya (Barnes, 1978).

The family Delphinidae might have evolved directly from Middle Miocene kentriodontids. In fact, such primitive living delphinids as species of *Steno*, *Sotalia*, and *Sousa* share numerous osteological similarities with kentriodontids. The crania of the latter differ mostly by not being asymmetrical. Delphinidae is the most diverse living cetacean family and includes what are commonly known as dolphins, killer whales, pilot whales, etc. Several extinct species have been named, primarily in extant genera, and most are *Tursiops* from Pliocene deposits in Europe. The fossil record of the family extends back in time no more than approximately 11–12 mya. Supposed earlier records of the family (see Kellogg, 1928; Simpson, 1945; Mchedlidze, 1976) are either erroneous or based on fossils that are simply indeterminable or do not have the diagnostic characters of the family (Barnes, 1978, 1985a). Especially in the first part of this century, many small fossil odontocetes (most notable ex-

ceptions being sperm whales and beaked whales) were assigned to the Delphinidae (Simpson, 1945, p. 216). Delphinids (*sensu stricto*) are, rather surprisingly, not very abundant in the fossil record; however, since they are for the most part pelagic, fossil collecting in Pliocene formations of deep-water origin may yield more fossils.

Living delphinids have varying diets. Some are stenophagous, feeding exclusively on either fish or cephalopods, while others are generalists, feeding on a variety of animals, including crustaceans. The more primitive of the living delphinids (e.g., Steninae, some Delphininae) are generalists and have rostra of intermediate length and width. This latter group includes *Tursiops*. Rostra of generalized delphinids are most like those of the fossil kentriodontids, and this is one line of evidence suggesting relatively close relationships. The diverse living delphinids have a variety of skull, dental, and body adaptations that reflect their varying diets as well as their methods of locomotion. Broad-headed delphinids such as pilot whales (*Globicephala*) and Risso's dolphins (*Grampus*) eat cephalopods; narrow-headed ones such as common dolphins (*Delphinus*) and spinner dolphins (some *Stenella*) usually eat fish; and animals with intermediate-width skulls such as bottlenose dolphins, striped dolphins (some *Stenella*), and white-sided dolphins (*Lagenorhynchus*) usually are more generalized feeders. Among the delphinids, some rather extreme anatomical adaptations have evolved. Killer whales (*Orcinus*) have a relatively robust body with a high dorsal fin, while the fast-swimming right whale dolphins (*Lissodelphis* spp.) have long, slender bodies with no dorsal fin. False killer whales (*Pseudorca*) have only a few large teeth, common dolphins have many small teeth, but Risso's dolphins have totally lost the upper teeth (a feature independently evolved in some other families). In comparison with the various living delphinoids and the fossil kentriodontids, the bottlenose dolphins are generalized in their morphology and diet.

Classification

The following abridged classification is intended only to provide a systematic context for *Tursiops* within the Cetacea. Thus, several groups of ce-

taceans peripheral to the lineage leading to *Tursiops* have been omitted, but the major groups mentioned in the text are represented, including all of those that are probably involved in the direct ancestry of *Tursiops*. The classification is derived from that of Barnes *et al.* (1985) and indicates some synonyms that are occasionally encountered in the literature. For those groups which are not used here at the same rank as they were originally proposed, the name of the author who proposed the revised rank follows that of the original author, which is in parentheses. All taxa marked with a + are wholly extinct and therefore known only as fossils.

Order Cetacea Brisson, 1762

- +Suborder Archaeoceti Flower, 1883 (archaeocetes)
 - +Family Protocetidae Stromer, 1908
 - +Family Basilosauridae Cope, 1868
 - +Subfamily Dorudontinae (Miller, 1923) Slijper, 1936
 - +Subfamily Basilosaurinae (Cope, 1868) Barnes and Mitchell, 1978
- Suborder Mysticeti Flower, 1864 (baleen whales)
- Suborder Odontoceti Flower, 1867 (toothed whales)
 - +Superfamily Squalodontoidea (Brandt, 1872) Simpson, 1945
 - Superfamily Delphinoidea (Gray, 1821) Flower, 1864 (incl. Monodontoidea Fraser and Purves, 1960)
 - +Family Albireonidae Barnes, 1984a
 - +Family Kentriodontidae (Slijper, 1936) Barnes, 1978
 - Family Monodontidae Gray, 1821
 - Family Delphinidae Gray, 1821 (incl. Holodontidae Brandt, 1873; + Hemisyntrachelidae Slijper, 1936; Grampidae Nishiwaki, 1964)
 - Subfamily Steninae (Fraser and Purves, 1960) Mead, 1975 (incl. Sotaliinae Kasuya, 1973)
 - Subfamily Delphininae (Gray, 1821) Flower, 1867
 - Tursiops* Gervais, 1855 (incl. *Hemisyntrachelus* Brandt, 1873)
 - Grampus* Gray, 1828
 - Peponocephala* Nishiwaki and Norris, 1966
 - Lagenorhynchus* Gray, 1846
 - Lagenodelphis* Fraser, 1956
 - Stenella* Gray, 1866
 - Delphinus* Linnaeus, 1758
 - Subfamily Lissodelphinae Fraser and Purves, 1960
 - Subfamily Cephalorhynchinae Fraser and Purves, 1960
 - Subfamily Globicephalinae (Gray, 1866) Gill, 1872 [incl. Orcininae (Brandt, 1873) Slijper, 1936; Globidelphinidae Nishiwaki, 1963]

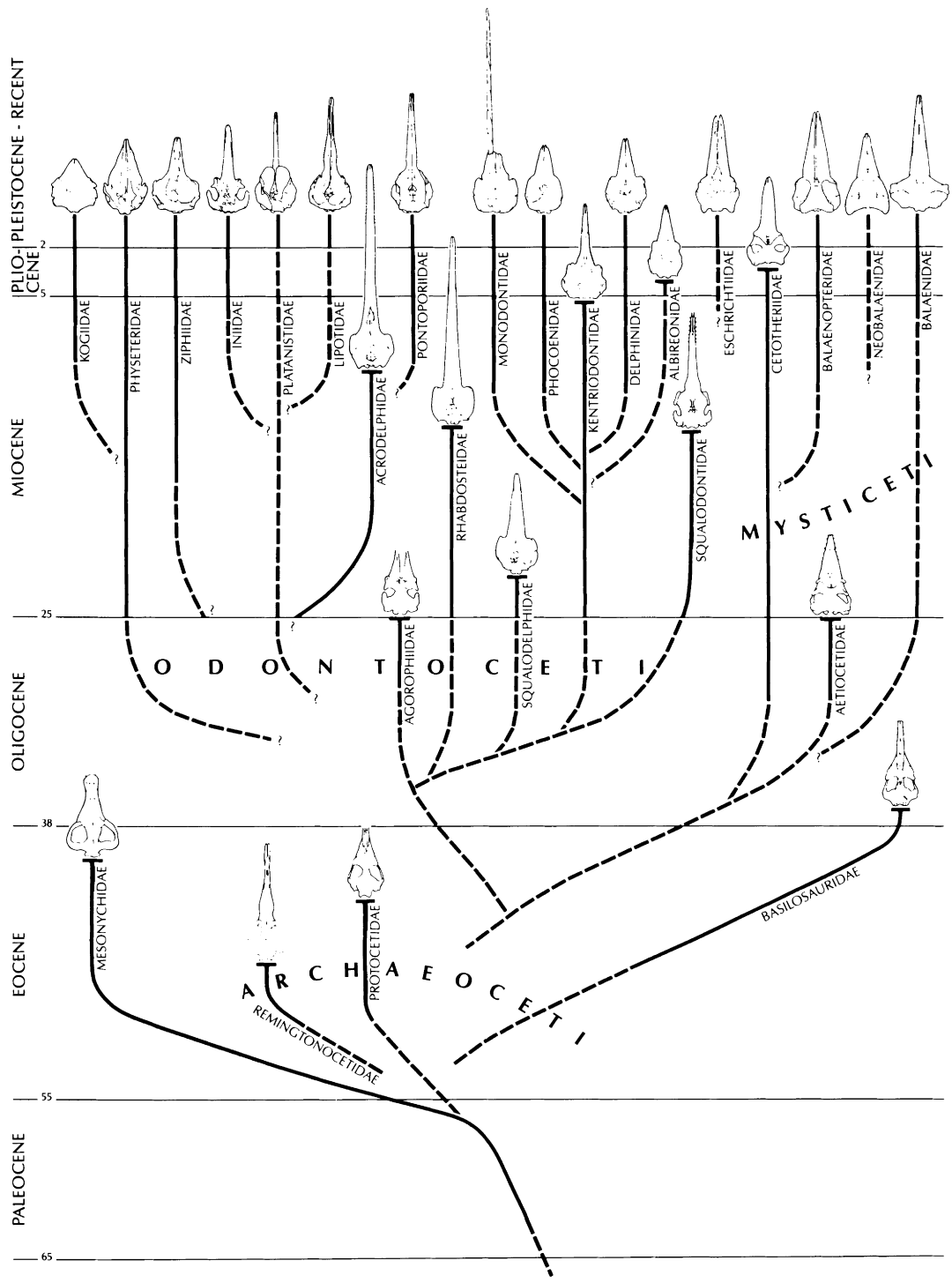


Figure 1 Phylogeny of Cetacea including all currently recognized fossil and living families. Solid lines indicate the known fossil record. Except for Delphinidae, Rhabdosteidae, Squalodelphidae, and Mesonychidae, the skulls used as examples belong to the type genus of the family. All skulls are in dorsal view and are not to scale. (Modified from Barnes *et al.*, 1985, their Fig. 1.)

Family Phocoenidae (Gray, 1825) Bravard, 1885
 Superfamily Platanistoidea (Gray, 1863) Simpson, 1945
 Superfamily Ziphioidea (Gray, 1865) Fraser and Purves, 1960
 Superfamily Physeteroidea (Gray, 1821) Gill, 1872

EVOLUTIONARY HISTORY OF *TURSIOPS*

Synonymy of the Genus *Tursiops*

Genus *Tursiops* Gervais, 1855

Delphinus (part) Fabricius, 1780

Tursio Gray, 1843:xxiii, 105 (type species, *Delphinus truncatus* Montagu, 1821:75, plate 3, preoccupied by *Tursio* Fleming, 1822:211 = *Physeter* Linnaeus, 1758; non *Tursio* Wagler, 1830:30)

Tursiops Gervais, 1855:323 (new name for *Tursio* Gray, 1843); Trouessart, 1898:1029; Miller and Kellogg, 1955:658; Hall and Kelson, 1959:821; Hershkovitz, 1966:47

Tursio (part) Gray, 1866

Gudamu Gray, 1868:6 [subgenus of *Clymenia*, type species, *Clymenia gudamu* [sic] = *Delphinus (Steno) gudamu* Owen, 1866 = *Tursiops truncatus aduncus* Ehrenberg, 1832, by monotypy]

Hemisyntrachelus Brandt, 1873:vi, 240 (subgenus of *Delphinapterus*, type species, *Delphinus cortesii* = *Tursiops cortesii* Fischer, 1829; to include *Delphinus brochii*); Slijper, 1936:553 (genus of the family Hemisyntrachelidae)

Type species: *Tursiops tursio* of authors, by tautonymy (= *Delphinus truncatus* Montagu, 1821)

The *Hemisyntrachelus* Controversy

Brandt (1873, p. 240) proposed the subgenus *Hemisyntrachelus*, having *Delphinus cortesii* as its type species and also including the species *Delphinus brochii*. At the time, neither species had yet been allied with the extant genus *Tursiops*, so Brandt's proposal was a relatively radical shift from previous authors, most of whom had assigned these two species to the genus *Delphinus*. Even more unusual was Brandt's assignment of *Hemisyntrachelus* to *Delphinapterus*, the genus of modern belugas or white whales (*D. leucas*).

Brandt's classification of these two species was

not accepted by subsequent authors such as Van Beneden and Gervais (1880), Capellini (1882), Sacco (1891, 1893), del Prato (1898), Trouessart (1898), and Simonelli (1911), who put one or both of these fossil species in *Tursiops*. *Hemisyntrachelus* was resurrected, however, by Slijper (1936), who elevated it to full generic status and disassociated it from both the Delphinidae and the Monodontidae (which includes *Delphinapterus*) by naming a new family, the Hemisyntrachelidae. Slijper, however, did not assign to the Hemisyntrachelidae the fossil species *Tursiops osennae*, which has a high tooth count and cranial morphology close to the living *T. truncatus*. He did transfer *Tursiops capellini* to *Hemisyntrachelus* and added the fossil Miocene odontocete *Lophocetus calvertensis* (Harlan) to the family.

Simpson (1945, pp. 102–103) listed the Hemisyntrachelidae with the included genera *Hemisyntrachelus* and *Lophocetus*, but the family name fell out of usage with subsequent authors. Barnes (1978) transferred *Lophocetus* to another extinct delphinoid family, the Kentriodontidae. This served to reduce the Hemisyntrachelidae to monotypy, and Barnes (1978, p. 4), noting that the species of *Hemisyntrachelus* have always been considered as having affinities with the Delphinidae, pointed out the need for a restudy of the group. Neither Hemisyntrachelidae nor *Hemisyntrachelus* was recognized by Pilleri (1979, 1980, 1985; Pilleri and Pilleri, 1982). Barnes *et al.* (1985) synonymized Hemisyntrachelidae with the Delphinidae.

Review of Nominal Fossil Species of *Tursiops*

Following are discussions of all of the nominal species (and subspecies) of fossil *Tursiops*. These are simply listed in alphabetical order, regardless of chronology or taxonomic priority. My new observations and conclusions are based on the published record because I was unable to examine the original specimens personally prior to this writing.

Tursiops cortesii var. *astensis* Sacco, 1891

Tursiops Cortesii (Desm.) var. *astensis* Sacco, 1891:703, 704, 710; Sacco, 1893

Tursiops cortesii var. *astensis* Sacco. Pilleri, 1985

Tursiops astensis Sacco. Trouessart, 1898:1029 (synonym of *T. cortesii*)

Tursiops cortesii (var. *astensis* Sacco, 1891). Pilleri, 1980:41

The subspecies (variety) *Tursiops cortesii* var. *astensis* was described by Sacco (1891) based on a partial cranium found near Valdondona (not at Cortandone as listed in Pilleri, 1985, his Table 2), in the Astigiana in the Piedmont region, Italy. Sacco (1891) concluded that it came from the yellow sand of Valldunga, which represents the lower beds of the Astian. These beds are early Late Pliocene in age (~3–3.5 mya).

Although Sacco (1891) proposed the variety *astensis* (today we would probably use the term subspecies), he speculated that it could be perhaps a distinct species (Sacco, 1891, p. 704). The holotype cranium of *T. cortesii astensis* was differentiated by Sacco from the holotype of *T. cortesii* based on several principal characters, mostly relating to different degrees of development of the cranial crests and fossae. All of these, as Sacco admitted, could reflect merely age, sex, or individual variability. Three of the characters, however, seem to be taxonomically significant. These are differently shaped occipital condyles and nasal bones and the presence of two fossae (possibly for air sinuses) on the ventral surface of the sphenoid. These latter characters indicate that Sacco's taxon probably should be retained as valid, and I recognize it at the species level. It has 14 teeth on each side of each jaw.

Trouessart (1898, p. 1029) listed *T. astensis* as a synonym of *T. cortesii*. The species was mentioned by both Slijper (1936) and Pilleri (1985) and, as listed by the latter, is known only from the original specimen, stored at the Institute of Geology of the University of Turin. Pilleri (1985, his Fig. 4) phylogenetically showed the taxon as derived from typical *T. cortesii* and ancestral to *T. cortesii capellinii*, but he presented no morphological evidence to support these proposed relationships.

***Tursiops brocchii* (Balsamo-Crivelli, 1842)**

Delphinus Brocchii Balsamo-Crivelli, 1842:132; 1843:629.

Capellini, 1863a:264, 269; 1863b:86; Barnes, 1978:4

D. (elphinus) Brocchi. Capellini, 1863a:267

Delphinapterus (Hemisyntrachelus) Brocchii [sic] Crivelli. Brandt, 1873:241

non *Tursiops Brocchii* (part). Van Beneden and Gervais, 1880:588–589, plate LIX, Fig. 5 (holotype of *T. cortesii*)

Tursiops Cortesii (Desm.) . . . variety *Brocchii* Bals. Sacco, 1891:710

Tursiops Brocchii Crivelli. Trouessart, 1898:1029

Tursiops Brocchii. Sacco, 1893; del Prato, 1898

Delphinapterus Brocchii Bals. del Prato, 1898:2

T. (ursiops) Brocchii (Bals. Criv.). Simonelli, 1911:251

Tursiops brocchii [sic] Crivelli. Slijper, 1936:552

Hemisyntrachelus brocchii [sic] Crivelli. Slijper, 1936:553
Delphinus brocchii [sic] Balsamo-Crivelli, 1842. Barnes, 1978:4

Tursiops brocchii (Balsamo-Crivelli, 1842). Pilleri and Pilleri, 1982:298–299, plate VIII; Pilleri, 1985:15

Tursiops cortesii brocchii. Pilleri, 1985:15 (Table 2)

Balsamo-Crivelli (1842) proposed the new species, *Delphinus Brocchii*, for a mandible and teeth found by Cortesi at Montezago in 1804 (see also Capellini, 1882, p. 571). This was the holotype specimen and is apparently omitted in Pilleri's (1985) Table 2. It was, however, mentioned by Pilleri and Pilleri (1982, p. 299) as having been destroyed when the Milan Museum was bombed during World War II.

The illustration presented by Pilleri and Pilleri (1982, their Fig. 4) shows the outlines of two skulls. The caption explains that one is *Tursiops brocchii*(?) and the other *T. cortesii* (holotype). Aside from the fact that the authors do not explain which outline is which specimen, neither can in fact be *T. brocchii* because a skull has never been identified in print as belonging to that taxon. On comparison, I have concluded that the skull represented by the heavy lines in their illustration is the same skull from San Lorenzo in Collina referred to *T. cortesii* by Simonelli (1911), while the lighter outlines represent the holotype of *T. cortesii*.

A second specimen in the Giovanni Capellini Museum, Bologna University Geological Institute, from San Lorenzo in Collina, Orciano Pisano, Tuscany, Italy, was referred to *T. brocchii* by Capellini (1863a,b). This fossil consists of a partial rostrum, mandible, teeth, tympanic bulla, cervical and other vertebrae, and rib fragments. Slijper (1936, p. 552) gave the age of this specimen as Early Pliocene, and Pilleri and Pilleri (1982, their Figs. 3, 4, plate 8) reillustrated it and gave some measurements.

Capellini contrasted his referred specimen with *T. cortesii* by its having 16 teeth in each dentary in contrast to 14 in *T. cortesii*. The dentary has a very short symphysis (see Capellini, 1863a, his plate 2, Fig. 2), and a higher coronoid crest than that of *Tursiops cortesii*. Judging by the variability in the tooth counts of individuals of Recent *T. truncatus* (range 19–26; see Hall and Kelson, 1959, p. 821; Nishiwaki, 1963, p. 102; Leatherwood *et al.*, 1982, pp. 176–177; Baker, 1983, p. 107), *T. cortesii* and *T. brocchii* are, in this feature, within the expected range of variation for one species. Unless other characters can be shown to separate these two fossil species, the two might be considered as one species. Pilleri (1985) discussed *Tursiops brocchii*, but listed it in his Table 2 as a subspecies (=variety) of *T. cortesii*. Pilleri (1985, p. 15) also stated, “. . . *T. brocchii* is difficult to distinguish from *T. cortesii*. . . .” Certainly, since subspecies are virtually impossible to recognize in the fossil record, even with large samples, Pilleri's recognition of *T. cortesii*

brocchii is at this time not acceptable. I do agree with Pilleri and Pilleri (1982) that the taxonomic distinction of *T. brocchii* is questionable, especially now that the holotype has been destroyed. The solution, however, is not to recognize it at the subspecies level.

***Tursiops capellini* del Prato, 1898**

Il delfino pliocenico di Camerano Casasco (Astigiana). Sacco, 1893

Tursiops Capellini Sacco. del Prato, 1898:1, 5, plate 1

T. Capellini. del Prato, 1898:12, 14

Tursiops Capellini. Simonelli, 1911:251

T. Capellini Sacco. Simonelli, 1911:251

Tursiops capellini Sacco. Slijper, 1936:552; Barnes, 1978:4

Hemisyntrachelus capellini Sacco. Slijper, 1936:553

Tursiops cortesii ("var. *capellini* Sacco, 1893"). Pilleri and Pilleri, 1982:plate 6

Tursiops cortesii capellini (Sacco, 1893). Pilleri, 1985:16, his Table 2 (p. 15)

Surprisingly, *Tursiops capellini*, attributed by virtually all subsequent authors to Sacco (1893), was not actually named by Sacco. At no place in his text, or even in his illustration captions, did he use the binomial, *Tursiops capellini*, or refer to the species as *capellini*. Only on p. 14, the last page of the paper, did he write, "... mi permetto di imporgli il nome dell' illustre Prof. Capellini, a cui la Cetologia italiana già deve tante scoperte e da cui essa attende una Monografia generale." The first author actually to apply the Latin binomial to the fossil described by Sacco apparently was del Prato (1898), and it is because of this that he should be credited with authorship of the taxon.

This species was named subsequent to Brandt's (1873) assignment of various earlier-named fossil species to *Hemisyntrachelus*. By the time of Sacco's (1893) writing, the genus *Tursiops* had become firmly accepted for both fossil and living taxa (cf. Van Beneden and Gervais, 1880), and Sacco (1891) had already described the fossil *Tursiops cortesii* var. *astensis*. Slijper (1936) complicated the taxonomy, however, by assigning *T. capellini* to Brandt's genus *Hemisyntrachelus* and to the new family Hemisyntrachelidae. Except for Pilleri's work (Pilleri and Pilleri, 1982; Pilleri, 1985), authors have recognized the taxon at the species level. Pilleri (1985, p. 16) wrote in conjunction with his use of the trinomial, *T. cortesii capellini*, that the "subspecies level remains uncertain."

The holotype cranium and mandible are from Valle dello Stramonte, tributary of the Chiavenna River, Casa Ghia, Piacenza region, Italy, and are stated to be middle Pliocene in age. This would make it about 3.5 million years old. Pilleri (1985, his Table 2) indicated that the (holotype?) specimen should be at the Geological Institute of the University of Parma but is apparently lost. The specimen, as illustrated by Sacco (1893), is excellent,

and clearly shows many important features including sutures, the number of alveoli, and the morphology of the narial region. The tooth count is 16 on each side of the palate and 15 in each dentary, 2 and 1 more, respectively, than in *T. cortesii*.

Another specimen was described by del Prato (1898) from the Camerano Cascasco area of Riero, Val Camerano, Piedmont region, Italy. He did not illustrate it fully, but it included the cranium, vertebrae, ribs, sternbrae, and limb bones.

***Tursiops cortesii* (Fischer, 1829)**

Not named. "*Delphinus Phocaena*." Cortesi, 1819:48

Dauphin de (M.) Cortesi. Cuvier, 1824:312; Desmoulins, 1824:360

D. (elphinus) Cortesii Fischer, 1829:512–513

Delphinus Cortesi oder *platyrhynchus*. Keferstein, 1834:203

Delphinus Cortesi Cuvier. Balsamo-Crivelli, 1842:129, 1843:629

Phocaena Cortesii. Laurillard, 1844:634

D. (elphinus) Cortesii. Capellini, 1863a:264

D. (elphinus) Cortesi. Capellini, 1863a:266–267

Delphinapterus (Hemisyntrachelus) Cortesii. Brandt, 1873:240

Tursiops Brocchii (part). Van Beneden and Gervais, 1880:588–589, plate LIX, Fig. 5 (holotype of *T. cortesii*)

Tursiops Cortesii (Desm.). Sacco, 1891

Tursiops Cortesii. Sacco, 1893

Tursiops Cortesii Desmoulins, 1824. Capellini, 1882; Sacco, 1891, 1893; del Prato, 1898; Trouessart, 1898; Simonelli, 1911; Slijper, 1936:552 (as *Tursiops cortesii* Desm.)

Hemisyntrachelus cortesii Desm. Slijper, 1936:553

Tursiops cortesi Keferstein, 1834. Pilleri, 1979, 1980

Tursiops cortesii Keferstein, 1834. Pilleri and Pilleri, 1982:294–296, Fig. 1, plates 1–6

Tursiops cortesii (Fischer, 1829). Kellogg, 1928:69; Barnes, 1978:4; Pilleri, 1985

Tursiops cortesii is the first fossil representative of the genus *Tursiops* to have been recognized. Capellini (1882) provided a history of the taxon (see also Pilleri, 1979), and some of the synonymy above is extracted from his paper. The holotype skeleton was found in 1793 (not 1783 as stated by Pilleri, 1979, p. 71) by Giuseppe Cortesi, who later described the fossil in 1806 and 1819. It was not named, however, until Fischer later (1829) called it "*D. cortesii*." The holotype skeleton was from Colle della Torrazza, near the town of Chiavenna, Piacenza, Italy, and was, unfortunately, destroyed at the Museo Civico of Milan by a bomb in World War II (Pilleri, 1979, 1985, p. 14). Luckily, plaster-cast replicas were long ago distributed to various other European institutions (Sacco, 1891). Pilleri reported that one cast of the holo-

type cranium had been located in the Paleontological Institute of the University of Parma and that casts of the skull and atlas vertebra are at the University of Turin Paleontological Institute. Pilleri and Pilleri (1982, p. 296) reported casts of the left dentary and cervical vertebrae in the Giovanni Capellini Museum of Paleontology in the Bologna University Geological Institute.

The age of the holotype is commonly cited as being Early Pliocene and from the Plaisancian Stage (Cuvier, 1824; Kellogg, 1928, p. 69; Slijper, 1936, p. 552). However, the Plaisancian is correlative with the Astian Stage (Berggren and Van Couvering, 1974, p. 53), which would make the specimen Late Pliocene in age (between approximately 1.75 and 3.5 mya).

The holotype skull (see Cortesi, 1819; Cuvier, 1824, plate 23, Figs. 1–2; Kellogg, 1928, p. 69; Pilleri, 1979, Figs. 3–6, plates 1–3) had 14 teeth on each side of the rostrum and in each dentary, and the atlas and axis vertebrae were fused. The illustration that Pilleri (1979, his Fig. 2) indicates to be Cuvier's (1824) representation of *Tursiops cortesii* actually includes specimens of various other fossil and Recent odontocetes. Only Figs. 1–2 of Cuvier's plate portray *T. cortesii*.

This is the most commonly reported fossil species of *Tursiops* from Italy, with more than ten specimens recorded in the literature (Capellini, 1882; Pilleri and Pilleri, 1982; Pilleri, 1985, his Table 2). Earlier referrals of the species to the genus *Delphinus* reflect the then-broader definition of that genus, not a radically different interpretation of the relationships of the fossil.

Capellini (1882, not 1881 as given by Pilleri and Pilleri, 1982, p. 296) referred to *Tursiops cortesii* a second specimen, consisting of the facial part of the cranium, rostrum, and mandible. This specimen (listed as number 2 in Pilleri and Pilleri, 1982, p. 296) was found at Mombercelli, Astigiano, Piedmont region and, although supposedly in the Museum at Turin, was not located by Pilleri and Pilleri. Capellini's identification seems to have been correct because the cranial, dental, and mandibular features in his (1882) plate (reproduced by Pilleri and Pilleri, 1982, Fig. 1) are similar to those of the holotype of *T. cortesii*.

Unfortunately, as noted by Pilleri and Pilleri (1982, p. 296), most of the remaining specimens attributed to, or attributable to, *T. cortesii* are either incomplete, lack cranial parts that are directly comparable with the two published skulls, or have imprecise collection data. For example, their identification of the limb bones, their items 4 and 5, as *T. cortesii* is based on Sacco's illustrations of similar bones of *T. capellini*. Also, unfortunately, both published skulls have been destroyed and/or are lost, and no neotype has been designated.

***Tursiops miocaenus* Portis, 1885**

Tursiops n. sp. (miocaenus) Portis, 1885:344, Fig. 106
Tursiops miocaenus Portis, 1885:344

Tursiops miocaenus Portis, 1886. Trouessart, 1898:1029
Tursiops miocaenus. Dal Piaz, 1977:49; Pilleri, 1985:19,
Fig. 4, 5a,b

Although Portis (1885, p. 344) referred to *Tursiops miocaenus* as “. . . a species which still remains to be found,” he did propose the name, and he described and illustrated specimens. These specimens, therefore, are the type material (=syntypes), namely, six isolated teeth on which Pilleri (1985, p. 19) commented. Pilleri also repeated Portis' description and reillustrated two teeth from Portis' work. The type material is stated to be Middle Miocene in age (which would be ~12–15 mya) and from Rosignano in the Piedmont region of Italy.

Although Portis favorably compared them “without hesitation” to those of *Tursiops cortesii*, such teeth are usually considered nondiagnostic in the fossil record, and the taxon is realistically a *nomen dubium*. Unfortunately, Pilleri (1985) uncritically accepted the previously proposed relationships, showed the taxon in a phylogeny, and even proposed that *T. miocaenus* was an ancestor of later species of *Tursiops*.

***Tursiops osennae* Simonelli, 1911**

Tursiops osennae Simonelli, 1911:259
Tursiops osennae Simonelli, 1911; Kellogg, 1928:69; Slijper, 1936:553; Pilleri and Pilleri, 1982:296–298, plates 7–8; Pilleri, 1985

Tursiops osennae was described by Simonelli (1911) on the basis of a partial cranium, mandible, teeth, tympanic bulla, periotic, and fused atlas and axis vertebrae found in glauconitic clay at Il Palazzo Estate, San Quirico d'Orcia, in the Province of Siena, Tuscany, Italy. This species has met with little taxonomic controversy. Simonelli's specimen, the holotype, is in the Giovanni Capellini Museum, Bologna University Geological Institute, and was reillustrated by Pilleri and Pilleri (1982, their Figs. 2, 3, plates 7–8), who also provided some measurements. Either the measurements (Pilleri and Pilleri, 1982, their Table 2) or the scale lines on their illustrations are incorrect, because they are not compatible. The specimen does, however, appear to be larger than living *T. truncatus*.

The specimen is stated to be from the Sicilian Marine Stage, which was once considered to be Late Pliocene in age but is now considered to be middle or early Late Pleistocene (~0.5–0.8 mya; Berggren and Van Couvering, 1974). Kellogg (1928, p. 69; also cited by Slijper, 1936, p. 553) considered *T. osennae* to be a “true” *Tursiops*. It has not been referred to the genus *Hemisyntrachelus*, in contrast to most other nominal fossil species of *Tursiops*.

Tursiops osennae has 21 teeth on each side of the rostrum, which is within the range of 19–29 for the tooth count of Recent *Tursiops truncatus* (Hall and Kelson, 1959, p. 821; Nishiwaki, 1963, p. 102; Leatherwood et al., 1982,

pp. 176–177; Baker, 1983, p. 107). It has a much higher tooth count than the other Italian fossil species of *Tursiops*. The holotype of *T. osennae* resembles Recent *T. truncatus* because of a similar transverse expansion of the premaxillae anterior to the nares, similarities in the shape of the lateral edges of the facial region, the shape of the rostrum (see Pilleri and Pilleri, 1982, their Fig. 2), the short mandibular symphysis, and the shape and degree of fusion of the atlas and axis vertebrae. It differs by having deeper and narrower antorbital notches, a periotic with a shorter, blunter anterior process and a smaller, more laterally deflected posterior process, more slender teeth, and shorter transverse processes on the atlas vertebrae. Interestingly, in each of these characters, *T. osennae* is more derived than Recent *T. truncatus*. Unfortunately, the holotype cranium lacks the basi-cranium and the facial bones around the nares, rendering some critical morphology unobservable in the species.

Pilleri (1985) referred to the species a newly discovered specimen found along the Marecchia River, which is now in the Verona Natural History Museum. In reference to the age, he wrote, "Chronostratigraphically speaking, we are at the beginning of the lower Pliocene-middle Pliocene." He asserted but, aside from a speculation that the tooth count of the new fossil would have been similar to that of the holotype, did not demonstrate that the two specimens belong to the same species. This is unfortunate, because Pilleri's new specimen is apparently significantly older geologically than the holotype, and this should have dictated caution in making such an identification.

The morphology of the new specimen described by Pilleri from Marecchia River is unclear because of the incompleteness both of the fossil itself and of the preparation, and because the illustrations and descriptions do not elucidate its anatomy. It does appear to represent a *Tursiops*-like delphinid, and it has teeth like other fossil and Recent *Tursiops*. Like the holotype of *T. osennae*, it apparently is a larger individual than other species of *Tursiops*. For example, Pilleri's (1985, plates 1–2) illustrations indicate the bones to be approximately 50% larger than those of a Recent *T. truncatus*. The humerus and ulna of the fossil both appear to have longer, more slender shafts than do the corresponding bones of *T. truncatus*.

Following the earlier suggestion by Simonelli (1911), Pilleri (1985) considered *T. osennae* to be ancestral to Recent *T. truncatus* (including *T. aduncus*), and showed *T. osennae* on a phylogeny (his Fig. 4) in a position intermediate between the extant taxa and fossil *T. cortesii*. Unfortunately, except for the unconvincing references to tooth counts, Pilleri offered no other morphological evidence to support either his phylogeny or a postulated worldwide biogeographical history (his Fig. 6) of the genus. As noted above, my comparisons with

the holotype of *T. osennae* indicate that it may be more derived than *T. truncatus*; this would rule out any possibility of an ancestral–descendant relationship between the two.

Tursiops cortesii pedemontana Sacco, 1891

Tursiops Cortesii (Desm.) . . . variety *pedemontana* Sacc.
Sacco, 1891:708–710

The taxon *Tursiops cortesii pedemontana* has not been cited subsequently, but it was proposed by Sacco (1891) for specimens from Cortandone identified as *Tursiops cortesii* by Portis (1885, p. 96, 97 of reprints, plate ix, Figs. 103–105). Sacco used the phrases (as translated): "var. *pedemontana* of *T. cortesii*" and "*Tursiops cortesii* (Desm.) presents until now three varieties, namely: *Brochii* Bals., *astensis* Sacc., and *pedemontana* Sacc." Whether or not he was justified in recognizing such a taxon, it is one which must at least be acknowledged. In the classification I synonymize it with *Tursiops cortesii*.

Other Fossil Records of *Tursiops*

There are pre-Pleistocene fossils of *Tursiops* which have been reported yet are not named. Barnes (1976, p. 334, his Table 6) reported the occurrence of a dolphin species having affinities with *Tursiops* from California. The fossil is of Late Pliocene age, correlative with the Blancan North American Land Mammal Age, approximately 2–4 mya, and was recovered from rocks stratigraphically high in the Capistrano Formation in Orange County.

A slightly older occurrence of a species of *Tursiops* is known from the North Atlantic realm. Whitmore (in press) reports relatively complete cranial material from Lee Creek Mine near Aurora, North Carolina. The fossils are derived from the Yorktown Formation, which is removed as overburden in the mine, and is of latest Miocene age, about 4–7 mya, and correlative with the Hemphillian North American Land Mammal Age.

Fossil Records of *Tursiops truncatus*

There have been several discoveries of fossil *Tursiops* of Pleistocene age (<1.75 mya) throughout the world. These reflect the "Ice Age" distribution of the modern species. Bones attributed to *Tursiops truncatus*, apparently of Pleistocene age, have been recovered from the bottom of the North Sea (Kortenaar van der Sluijs, 1983). Other specimens from the Atlantic realm, and thus within the

present range of the species, have been found on Edisto Island, South Carolina (Roth and Laerm, 1980). These are definitely Pleistocene in age, and were found with fossils of other Late Pleistocene vertebrates (~10,000–50,000 years old).

A partial skeleton of a dolphin, identified as "*Tursiops* sp., near *T. truncatus* (Montagu), but probably not identical with that species," was reported by Blake (1939) from Maryland. The specimen consisted of associated ribs and vertebrae, and undoubtedly represents the remnants of what was formerly a complete skeleton. The fossil was found in a well-studied Pleistocene marine bed that contains abundant mollusk fossils, at Wailes Bluff, St. Marys County. The bed was called Bed 1 by Mansfield (1928), who concluded that the associated fauna of littoral marine mollusks included some brackish-water species and was indicative of quiet, shallow water protected from the sea, with a muddy bottom, and water temperatures the same as at the locality today or slightly warmer. This postulated environment is similar to that which inshore populations of *Tursiops truncatus* are known to frequent today, in coastal bays along the Atlantic coastal plain.

From the Pacific realm there is an excellently preserved skull of *Tursiops* described by Tsao (1978) from Kiangsu Province. The specimen was apparently derived from an uplifted coastal Pleistocene deposit. Tsao identified the specimen as *Tursiops* sp., and discussed both *Tursiops truncatus* and *T. catalonia* as modern species. Since the latter is a junior synonym, that comparison is a moot point. The fossil skull is morphologically within the range of *Tursiops truncatus*, and I reidentify it more precisely as *Tursiops* sp., cf. *T. truncatus*.

DISCUSSION AND CONCLUSIONS

Problems with Interpreting the Fossil Record

Research on fossil organisms can include the study of paleobiogeography, but, unfortunately, some of the taxonomic conclusions of past paleontological researchers have been biased by the land mass on which the fossils were found. This is no less true with fossil cetacean research, and systematic

works have in some cases been written without full consideration of the ancient ocean basin and paleoenvironment in which the animals once lived. Many living cetacean species are widely distributed, and some are even cosmopolitan. It is reasonable, therefore, to expect fossil species to have had similar distributions, and the practice of naming separate fossil taxa simply because they are separated geographically should be questioned.

Similarly, time differences should not necessarily bias taxonomic decisions. A species of fossil cetacean, as with those in other groups of mammals, might be expected to have existed for hundreds of thousands or even a million years but, usually, not for several millions of years. A species may evolve into another, or may become extinct, and it is this random turnover of species that provides the record of a sequence of fossil animals through the rocks, the data used in biostratigraphy. For this reason, the identification by Pilleri (1985) of an Early to middle Pliocene fossil dolphin as *Tursiops oseanae*, a species previously known only from the Pleistocene holotype, may be questionable. Specimens of *T. cortesii* have been reported from rocks of both Early and Late Pliocene age, and even this time range is more than might be expected for one species. Larger samples and detailed studies would be necessary to confirm the identifications.

Comparisons among many of the named fossil species of *Tursiops* can be hindered by the lack of directly comparable skeletal parts. If different parts of fossil skeletons are designated as holotypes, then problems might arise in the systematic treatment of the group. Sample sizes of the named fossil species of *Tursiops* are simply not statistically significant, and in fact some species are known by only a single occurrence. An ideal fossil record would consist of stratigraphically superimposed samples of several successive species from rocks at different locations throughout the world, but the fossil record of *Tursiops* does not approach this ideal. Instead, it is limited mainly to Italy, and is spotty geographically, stratigraphically, and chronologically.

Pilleri (1985) reviewed the fossil occurrences of *Tursiops* in Italy, the source of all named fossil species. His review is of limited use, however, because new taxonomic combinations are pro-