Annu. Rev. Earth Planet. Sci. 1994. 22:419–55

THE EVOLUTIONARY HISTORY OF WHALES AND DOLPHINS

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KEY WORDS: marine mammal, Cetacea, fossil, systematics

INTRODUCTION

Cetaceans—the whales, dolphins, and porpoises—are the taxonomically most diverse clade of aquatic mammals, with a fossil record going back at least to Middle Eocene time (52 Ma—millions of years before present) (Figure 1). There are 75 to 77 living species in 13 or 14 families and two suborders: Mysticeti (baleen whales) and Odontoceti (toothed whales, dolphins, and porpoises) (Rice 1984, Evans 1987). The extinct Archaeoceti are a third suborder. Extant cetaceans are ecologically diverse; sizes range from under 2 m to over 25 m, and habitats range from shelf and surface water to abyssal settings in tropical to polar oceans; some species live in fresh water. Living species attract marked public and scientific interest, but fossils also have an important role. The excellent fossil record helps us to understand morphological transition series and homologies of structures in living taxa. A resurgence of interest in anatomy has led to pioneering, albeit preliminary, cladistic analyses of fossil and extant Cetacea, with pivotal input from paleontologists. [For a discussion of cladistics, see Padian et al (1993) in this volume.] Although volatile and clearly needing more study, the resulting classifications provide an adequate foundation for broader studies. Cetacean constructional morphology and related aspects of paleobiology are still in their infancy. Fossil taxa are potentially

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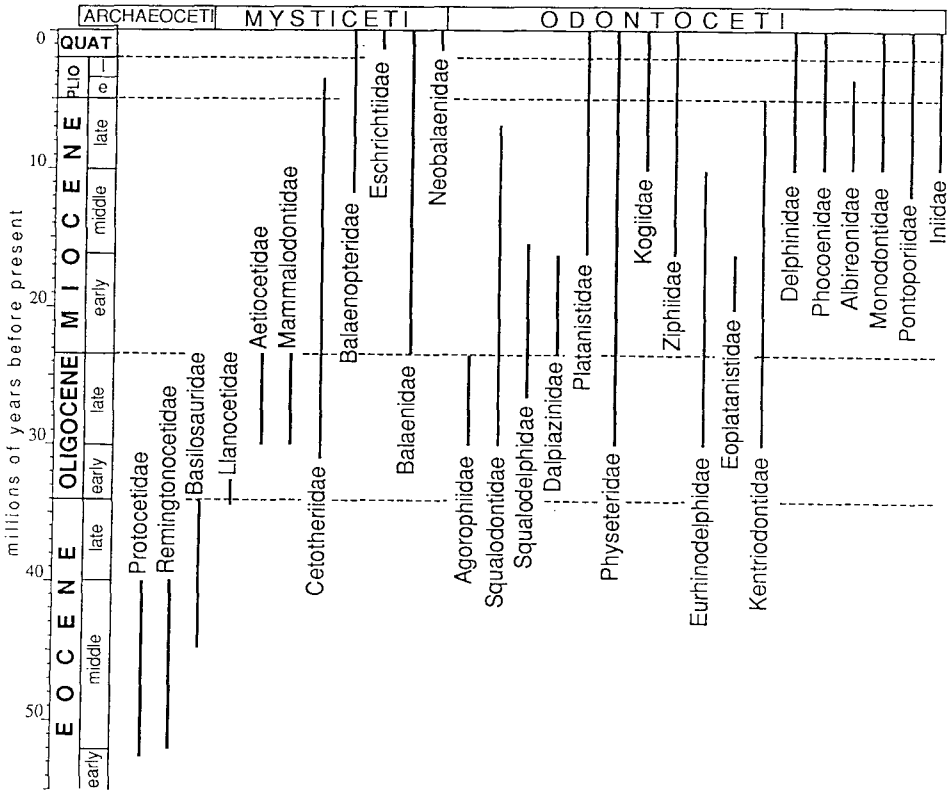

Figure 1 Chronologic ranges of cetacean families worldwide, based on most recently published accurate data and modified slightly based on unpublished data available to the authors. Solid bars show reported or likely maximum ranges. Where ranges fall within a sub-epoch but are not known precisely, range bars are extended to sub-epoch boundaries. Formally named families of uncertain status are not shown.

valuable in stratigraphy. Changes in abundance with changing facies help in the interpretation of ancient depositional settings, while broader changes in diversity through time help us interpret broader changes in currents and climates in the global oceans. We explore these topics below.

Other general reviews of cetacean evolution include Miller (1923), and Kellogg (1928, 1936). Fordyce (1980, 1989b, 1992), Barnes (1984b, 1990, 1992), Barnes & McLeod (1984), and Barnes et al (1985) provided recent synopses. Works on extant Cetacea include those by Evans (1987), Slijper (1979), Rice (1977, 1984), and contributions edited by Ridgway & Harrison

(1985, 1989). Hershkovitz (1966) cataloged extant species; Simpson (1945) listed fossils. We stress references that are accessible, not necessarily the earliest authority.

ANATOMY AND BIOLOGY OF CETACEANS

Fossil Cetacea probably had body forms similar to those of modern species (e.g. Figure 2). Anatomy and biology are documented widely (Rice 1984, Evans 1987). Living Cetacea are streamlined, fusiform, and the smooth body is hairless with few vibrissae (facial hairs). Color patterns vary widely between species; a dark dorsal surface and lighter ventral surface are common. The body is enveloped in blubber which largely obliterates expressions from the facial muscles. Teeth occur in most adult Odontoceti and in embryonic Mysticeti, but toothless adult Mysticeti have baleen plates used in filter-feeding. Relatively small eyes lie laterally. There is no external ear pinna, and the auditory canal is closed. One or two nostrils (blowholes) open dorsally on the head, in contrast to a more anterior position in most mammals. The laterally flattened forelimbs are usually short and rigid, without a flexible elbow. In most species the neck is indistinct and rather inflexible. A dorsal fin supported by connective tissue is normally present. The body is subcylindrical posteriorly to about level with the ventral genital slit and anus, but beyond this the tail peduncle is laterally compressed. Bilateral, rigid tail flukes are supported by connective tissue, with vertebrae only in the midline.

Skeletal and particularly cranial anatomy is a prime basis for cetacean taxonomy. General features of cetacean skulls (Kellogg 1928, Fraser & Purves 1960, Barnes 1990, McLeod et al 1989) include the following, many of which are synapomorphies (see Padian et al 1993) for Cetacea: a distinct and usually long rostrum (upper jaw) formed by elongated prenarial portions of premaxillae and maxillae; paired bony nares displaced back on the skull; discrete origins for muscles associated with the blowholes; bony orbits placed widely apart under long, flat and transversely broad supraorbital processes; postglenoid processes and glenoid fossae (cavities for jaw articulation) shaped for simple hinge movement; large origins for temporalis muscles; robust basioccipital crests with each bulla having a thin outer lip, a sigmoid process with fused malleus, a large tympanic cavity, and a dense involucrum; periotics (earbones) widely separated and loosely attached to the skull, each with distinct anterior and posterior (mastoid) processes, within the ear, a large stapedius muscle fossa, smooth dorsal face on the cochlear portion of the periotic, and small origin for tensor tympani muscle; and reduced foramina for the internal carotid arteries.

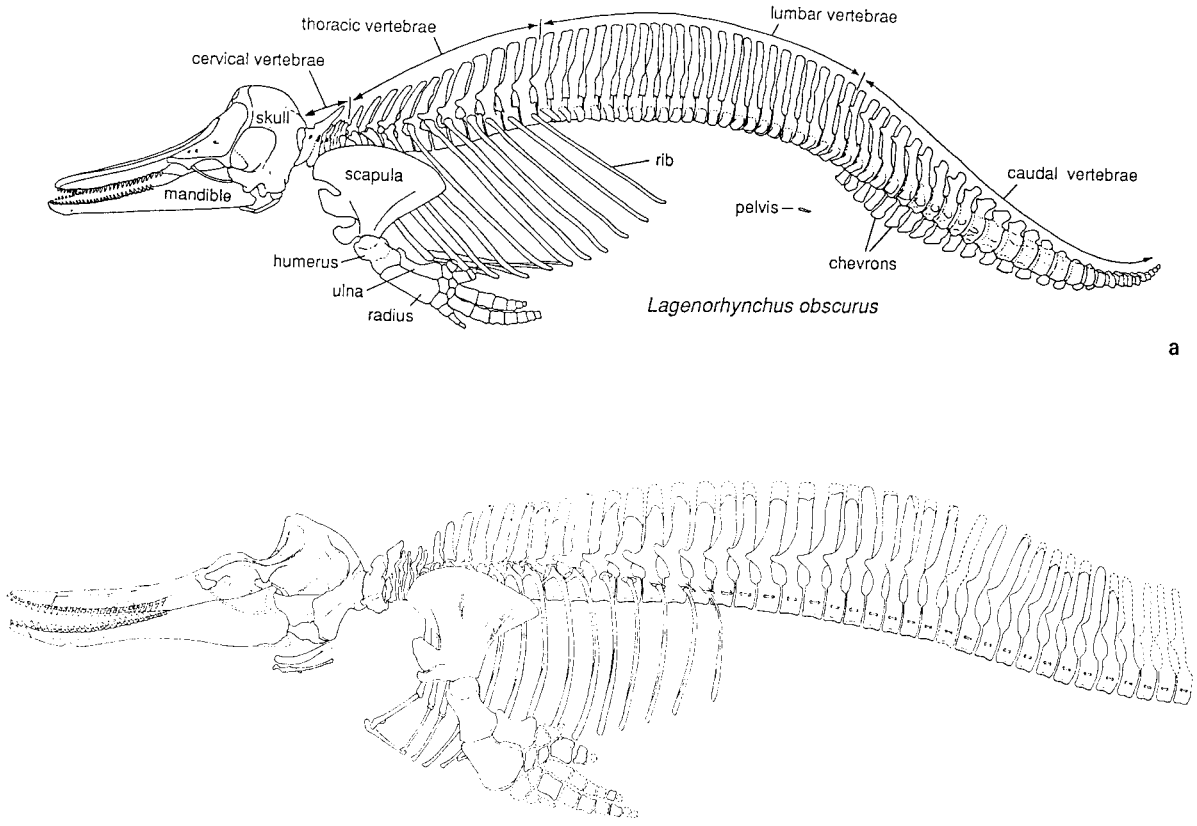

Figure 2 The cetacean skeleton: (*a*) left lateral view, with major parts labeled, of *Lagenorhynchus obscurus*, the living dusky dolphin of the south Atlantic and South Pacific; (*b*) left lateral view of *Albireo whistleri*, an extinct latest Miocene dolphin from the eastern North Pacific, partial skeletal reconstruction based on the holotype fossil skeleton from Isla de Cedros, Baja California, Mexico.

Fossil and Recent cetacean taxa are diagnosed cranially by proportions and size of the skull components including the rostrum, teeth, facial and temporal muscle origins, the basicranial (pterygoid) sinuses that form as outgrowths of the eustachian tubes, and tympano-periotics. In all Odontoceti and Mysticeti, rostral bones and the supraoccipital are "telescoped" (Miller 1923) toward each other, although such telescoping is not demonstrably homologous in these two groups.

The seven cervical (neck) vertebrae are usually compressed anteroposteriorly, and are sometimes fused. There are usually more post-cervical vertebrae than in other mammals. The ribs usually attach loosely to the thoracic vertebrae and sternum, and in extant Cetacea, lumbar vertebrae grade back to caudal (tail) vertebrae without obvious sacral vertebrae. Well-developed vertebral spines and transverse processes on the lumbar vertebrae reflect massive tail muscles. A subspherical "ball" vertebra marks the point of maximum bending at the peduncle-fluke junction (Watson 1991). Caudal vertebrae in the flukes have distinct rectangular profiles. In the forelimb, the scapula has a reduced supraspinatus fossa and subparallel anteriorly directed acromion and coracoid processes, without a clavicle. Cetaceans normally show hyperphalangy (marked increase in number of phalanges). The pelvis in the modern animals is usually present as two separate bilaterally paired simple elements, sometimes with vestigial hind limb bones, although early whales had more complete hind limbs (Gingerich et al 1990).

OPPORTUNITIES AND LIMITS TO THE STUDY OF FOSSIL CETACEA

Fossil Cetacea are conspicuous in outcrop, but rare. The large size and the intrinsic fragility of porous bones make some fossils hard to collect and preserve. Many fossil species are represented by only one published specimen, and stratophenetic approaches, best suited to fossils from successive closely spaced horizons, have dealt poorly with a patchy record that reveals only a few good ancestor-to-descendant sequences. Conversely, information provided by the multiple elements of one skeleton is valuable in cladistic and functional studies. Most skeletal parts have been used at some time as type specimens, with species based on part or whole skulls, teeth, mandibles, vertebrae, or limb bones. Unfortunately, many species based on isolated bones are poorly defined and diagnosed by modern standards, and many cannot be compared directly with one another. Ideally, type specimens should include skulls and associated earbones. Most higher taxa need to be reviewed in light of changing concepts of taxonomy, and many groups are acknowledged to be paraphyletic. For

these reasons, and because some epochs or geographic regions are represented poorly in the fossil record, published lists of taxa must be interpreted carefully.

DISTRIBUTION

Chronologic Distribution

The chronologic record of cetacean families is shown in Figure 1. Such charts are limited by taxonomy (i.e. are the groups real?) and geology (Barnes 1977, Fordyce 1992). Bars mark known limits of stratigraphic ranges, but do not necessarily indicate a continuous record. For most taxa, published information does not allow age resolution below the level of the stage or subepoch. Many age determinations lack lists of age-diagnostic taxa, and few articles cite ages based on the planktic microfossils used in long-distance correlations. Nevertheless, trends are apparent, and are reviewed below. Fossil taxa are indicated by a dagger † prefix.

Geographic Distribution—Regional Studies

Early studies were based in Europe and North America, with few developments occurring elsewhere until early in the twentieth century. Important marine sequences around the Mediterranean (and former Paratethys-Tethys) include the Neogene in Italy and France (Dal Piaz 1977, de Muizon 1988a), Oligocene in Austria (Rothausen 1968, 1971), and Caucasus (Mchedlidze 1984, 1989; Barnes 1985c) and Eocene in Egypt (Gingerich 1992, Kellogg 1936). Eastern North Atlantic faunas are known mainly from the North Sea margins (Abel 1905, Rothausen 1986), but there are a few from Britain (Hooker & Insole 1980). Eocene to Pliocene Cetacea from the western North Atlantic include those documented by Kellogg (listed by Whitmore 1975), Whitmore & Sanders (1977), Hulbert & Petkewich (1991), and Sanders & Barnes (1993). Southwest Atlantic faunas from Argentina include middle Cenozoic taxa (Cabrera 1926, de Muizon 1987) currently under study by M. A. Cozzuol. Eocene presumed Tethyan species from Pakistan and India represent some of the oldest Cetacea (Gingerich et al 1983, Kumar & Sahni 1986, Gingerich & Russell 1990, Thewissen & Hussain 1993), but there are no other significant described faunas from around the Indian Ocean. The Pacific, the largest ocean during cetacean history, deserves more attention. Japanese Neogene fossils are well documented (Oishi 1985, Kimura et al 1992), and studies of Oligocene species are under way (Okazaki 1988, Kimura et al 1992). Eastern North Pacific Neogene assemblages are also well known (Barnes 1977, 1984a), but Oligocene species are mainly undescribed (Whitmore & Sanders 1977).

Peru has yielded Neogene odontocetes (de Muizon 1984, 1988c) and mysticetes (Pilleri 1989). New Zealand assemblages, from the Southern Ocean margin, span from Eocene to Quaternary (Fordyce 1991). A scattered Oligocene to Neogene record from Australia (Fordyce 1984) also hints at the composition of Southern Ocean faunas. Only one Paleogene and one Pliocene site are known from Antarctica (Fordyce 1989b). Extant fluvio-lacustrine odontocetes include species of Platanistidae, Pontoporiidae, Iniidae, and Lipotidae. Fossil odontocetes from fluvio-lacustrine sediments include Miocene †Eurhinodelphidae from Australia (Fordyce 1983), a Miocene ziphiid from Kenya (Mead 1975b), Miocene pontoporiids and iniids from Argentina (Cozzuol 1985), and a possible Miocene lipotid from China (Zhou et al 1984).

Depositional Settings and Taphonomy

Although fossil Cetacea are found mainly in proximal marine sedimentary rocks now exposed on land, distributions are best stated in terms of oceans. Perhaps only early archaeocetes, with amphibious seal-like habits, were linked strongly to land. Most living species occupy coastal waters only occasionally, and strand rarely. Sporadic worn or broken bones from shallow sublittoral inner shelf facies suggest that strandings are at most a minor potential source of fossils. Fossils from more distal shallow, mid- and outer-shelf settings are common, while specimens from bathyal settings are rarely collected. Bone-bearing sediments include muddy conglomerate, quartzose and calcareous sandstones, siltstone and mudstone, limestone, greensand, diatomite, and concretionary mudstone (Barnes 1977, Myrick 1979, de Muizon 1984, Fordyce 1991, Gingerich 1992). Reworked bone-bearing clasts are known from debris flows. Lag accumulations mark unconformities, and remanié elements (Boreske et al 1972) may occur in nodule beds. A few specimens are known from ocean dredgings (Whitmore et al 1986).

Most fossils occur as isolated bones or small clusters of bones, presumably dropped from floating carcasses (Schäfer 1972). Articulated or semi-articulated specimens are found in distal settings, represented by massive mudstones (Squires et al 1991); indeed, cetacean carcasses, oases for obligate bone-dwelling invertebrates, may be an important abyssal energy source both in the past and at the present time (Squires et al 1991, Allison et al 1991). Fossil skeletons are often partly articulated, surrounded by bones scattered by scavenging or currents. A common ventral-up orientation of skeletons reflects the influence on burial position of a gas-filled and thus buoyant abdomen in a decomposing carcass. Semi-articulated fossils are sometimes abundant in bone beds (e.g. Sharktooth Hill, Middle

Miocene, California; Barnes 1977). Fossils in burial position are published widely, but explicit taphonomic studies are few (Myrick 1979, Lancaster 1986).

CLASSIFICATION

Post-Darwinian approaches to cetacean classification have long involved evolutionary systematics, championed by Simpson (1945), and an eclectic approach is still employed (e.g. Mchedlidze 1984, Mitchell 1989). Cladistics is becoming more common (e.g. Barnes 1985b, 1990; de Muizon 1988a, 1991), and has already proliferated names for higher-level taxa (families, superfamilies, and infraorders; Table 1, Figure 3). Only Heyning (1989) has published a computer-aided analysis of cetacean taxonomy (Figure 3). Manual cladistic analyses identify problems, but computer-based analyses make better sense of complex data, thus leading to more stable clades and clade ranks. Phenetic and biochemical techniques are currently unimportant.

Monophyly, Diphyly, and Relationships with Other Eutherian Mammals

Living cetaceans are so well adapted to an obligate aquatic lifestyle that there are few structures that initially reveal close relatives to other Eutheria. Kellogg's (1936) review of relationships was inconclusive, while Simpson (1945) placed the Order Cetacea in an isolated Cohort, Mutica. Such uncertainty arose partly through perceptions that there are few structural intermediates between †Archaeoceti, Odontoceti, and Mysticeti, and thus that Cetacea are diphyletic (Miller 1923, Yablokov 1965). Van Valen's (1968) succinct review led to rapid acceptance of monophyly (McLeod et al 1989), a view further reinforced by an expanding fossil record. Odontoceti and/or Mysticeti have been viewed as originating from †Protocetidae (Van Valen 1968), †Remingtonocetidae (Kumar & Sahni 1986), or, most likely, †Basilosauridae (Barnes & Mitchell 1978). Synapomorphies for Cetacea and for Odontoceti + Mysticeti have been discussed or listed widely (Rice 1984; Barnes 1984b, Barnes 1990; Barnes & McLeod 1984; Heyning 1989; Heyning & Mead 1990; McLeod et al 1989, Milinkovitch et al 1993; Novacek 1993). From the 1950s on, biochemical, karyological, cytological, and other techniques have repeatedly clustered Cetacea close to Artiodactyla (literature cited by Barnes & Mitchell 1978, Heyning 1989, Novacek 1993, Milinkovitch et al 1993). The structure of teeth, skulls and vestigial hind limbs in fossils (Van Valen 1966, Gingerich & Russell 1990, Gingerich et al 1990, Novacek 1993) further supports relationships with

ungulates. Significantlly, Flower (1883) long ago proposed a relationship of cetaceans with ungulates on anatomical grounds.

Osteology vs Molecules in Taxonomy

Milinkovitch et al (1993) suggested, on the basis of DNA analysis, that sperm whales, Physeteridae+Kogiidae, are more closely related to rorquals, Balaenopteridae (Mysticeti) than to other Odontoceti (Figure 3), and that physeterids and balaenopterids had a common ancestor about 10–15 Ma. This would imply that the Odontoceti are paraphyletic, and that the ability to echolocate was probably lost secondarily in rorquals or evolved independently in different odontocete groups. Conversely, osteological and other anatomical studies (Fraser & Purves 1960, Kasuya 1973, Heyning 1989, Heyning & Mead 1990, Barnes 1990, de Muizon 1991) indicate that the traditional Mysticeti and Odontoceti are clades with ancient origins well demonstrated by the fossil record. Many synapomorphies unite physeterids with other odontocetes, including features of the face, basicranium, and tympano-periotic (Barnes 1990, de Muizon 1991). Undisputed Late Oligocene physeterids are known. Balaenopterids have a shorter (Late Miocene to Recent) record. They are universally accepted as Mysticeti, and thus are members of an early Oligocene to Recent clade. Balaenopterids probably originated among the Oligocene to Pliocene †Cetotheriidae. If, as suspected, physeterids are a basal clade of odontocetes, they could be phenetically close to some mysticetes, so that some techniques may not resolve cladistic affinities clearly. Myoglobin DNA, used by some analyses as evidence for relationships, is notoriously unreliable because of numerous cases of convergences. DNA cladistic analyses, like other taxonomic procedures, are probably sensitive to choice and number of data and the interpretation of outgroups. The concept of a sister-group relationship between sperm and baleen whales needs more study; meanwhile, the fossil record provides a valuable check on rates of evolution in cetacean mitochondrial DNA.

REVIEW OF CETACEAN TAXA

†*Archaeoceti*

Archaeocetes are a paraphyletic group of archaic toothed Cetacea that lack cranial features of Odontoceti and Mysticeti (Kellogg 1936). The included grade families †Protocetidae and †Basilosauridae and clade †Remingtonocetidae are Eocene only, while younger supposed archaeocetes are either misidentified or are too incomplete to place conclusively. Mitchell (1989) raised all three families to the rank of superfamily (†Protocetoidea, †Remingtonocetoidea, and †Basilosauroidea) to accommodate

Table 1 Classification of Cetacea[a]

Order Cetacea Brisson 1762.
- Suborder †Archaeoceti Flower 1883.
  - Family †Protocetidae Stromer 1908. Early-Middle Eoc., Tet. Caribbean.
    - Subfamily †Pakicetinae Gingerich and Russell 1990.
  - Family †Remingtonocetidae Kumar and Sahni 1986. Middle Eoc., Tet.
  - Family †Basilosauridae Cope 1868. Middle-Late Eoc. Tet., N. Atl., SW. Pac.
    - Subfamily †Dorudontinae (Miller 1923) Slijper 1936.
    - Subfamily †Basilosaurinae (Cope 1868) Barnes & Mitchell 1978.
- Suborder Mysticeti Flower 1864.
  - Family †Llanocetidae Mitchell 1989. Late Eoc. or Early Olig., SE. Pac. SW. Atl.
  - Family †Aetiocetidae Emlong 1966. Late Olig., N. Pac.
  - Family †Mammalodontidae Mitchell 1989. Late Olig., SW. Pac.
  - Family †Kekenodontidae (Mitchell 1989). Fordyce 1992.
    - Late Olig., SW. Pac.
  - Family †Cetotheriidae (Brandt 1872) Miller 1923.
    - Early?, Late Olig.-Early or Late? Plio. Pac., Atl., Med. Par.
  - Family Balaenopteridae Gray 1964. Middle?, Late.-Rec.
    - Fossil: Pac., Atl., Med. Rec.: cos.
    - Subfamily Megapterinae (Gray 1866) Gray 1868.
    - Subfamily Balaenopterinae (Gray 1864) Brandt 1872.
  - Family Eschrichtiidae Ellerman and Morrison-Scott 1951.
    - Quat. Rec. Fossil: N. Pac., Rec.: N. Pac.;
    - recently extinct, N. Atl.
  - Family Neobalaenidae Gray 1873. Rec.: SOc.
  - Family Balaenidae Gray 1825. Early Mio. Rec.
    - Fossil: Atl., Pac., SOc. Rec: temperate polar oceans.
- Suborder Odontoceti Flower 1864.
- Superfamily unresolved.
  - Family †Agorophiidae Abel 1913. Late Olig., N. Atl.
- Superfamily Physeteroidea (Gray 1821) Gill 1872.
  - Family Physeteridae Gray 1821. Sperm whales.
    - Late Olig.–Rec. Fossil: Atl., Med. Par., Pac., SOc., Rec.: cos.
    - Subfamily †Hoplocetinae Cabrera 1926.
    - Subfamily Physeterinae (Gray 1821) Flower 1867.
  - Family Kogiidae (Gill 1871) Miller 1923. Pygmy sperm whales.
    - Late Mio.–Rec. Fossil: E. Pac., SW. Pac., NW. Atl. Rec., temperate–tropical oceans.
- Superfamily Ziphioidea (Gray 1865) Gray 1868.
  - Family Ziphiidae Gray 1865. Beaked whales: Middle Mio. Rec.
    - Fossil: cos., FW. Africa. Rec.: cos.
    - Subfamily Ziphiinae (Gray 1865) Fraser & Purves 1960.
    - Subfamily Hyperoodontinae (Gray 1846) Muizon 1991.

[a] Infraorders, discussed in the text, are not cited. Only common synonyms are cited. For emended names, original authors are cited in parentheses, followed by revisers. Taxonomic references are not cited in the bibliography unless the articles are also cited in the text.

Abbreviations: N—north; S—south; SW—southwest; SE—southeast; E—east, Eoc—Eocene; Olig—Oligocene; Mio—Miocene; Plio—Pliocene; Quat—Quaternary; Rec—Recent; e—early; m—middle; l—late; FW—fresh water; Pac—Pacific; Tet—Tethys; Med—Mediterranean; Atl—Atlantic; cos—cosmopolitan; Par—Paratethys; SOc—Southern Ocean.

Table 1—(*continued*)

Superfamily Platanistoidea (Gray 1863) Simpson 1945.
Family †Squalodontidae Brandt 1872. Late Olig. Middle Mio.,
Atl., Med.–Par., Pac.
Subfamily †Patriocetinae (Abel 1913) Rothausen 1968.
Subfamily †Squalodontinae (Brandt 1872) Rothausen 1968.
Family †Squalodelphidae Dal Piaz 1916. Early Mio.,
Med., SW. Atl., SW. Pac.
Family †Dalpiazinidae de Muizon 1988a. Early Mio.,
Med., Sw. Atl., SW. Pac.
Family Platanistidae (Gray 1863).
Middle Mio.–Rec., Fossil: NE. Atl. Rec.: FW. India.
Superfamily †Eurhinodelphoidea (Abel 1901) de Muizon 1988.
Family †Eoplatanistidae de Muizon 1988a. Early Mio. Med.
Family †Eurhinodelphidae Abel 1901. (=Rhabdosteidae Gill 1871).
Late Olig.?, Early- Middle Mio. Atl., Med., ?Par., Pac., FW. Australia.
Superfamily Delphinoidea (Gray 1821) Flower 1864.
(including Monodontoidea Fraser & Purves 1960)
Family †Kentriodontidae (Slijper 1936) Barnes 1978.
Late Olig.–Late Mio. Atl., Med. Par., Pac., SOc.
Subfamily †Kampholophinae Barnes 1978.
Subfamily †Kentriodontinae (Slijper 1936).
Subfamily †Lophocetinae Barnes 1978.
Family †Albireonidae Barnes 1984a. Late Mio.–Early Plio. NE. Pac.
Family Monodontidae Gray 1821.
Fossil: NE. Pac., N. Atl. Rec.: Arctic N. Pac. N. Atl.
?Subfamily Orcaellinae (Nishiwaki 1963) Kasuya 1973.
Subfamily Delphinapterinae Gill 1871.
Subfamily Monodontinae (Gray 1821) Miller & Kellogg 1955.
Family Delphinidae Gray 1821.
(including Holodontidae Brandt 1873, Hemisyntrachelidae Slijper 1936).
Late Mio.-Rec. Fossil: Atl., Med. Par., Pac., SOc. Rec.: cos.
Subfamily Steninae (Fraser & Purves 1960) Mead 1975.
Subfamily Delphininae (Gray 1821) Flower 1867.
Subfamily Globicephalinae (Gray 1866) Gill 1872.
Family Phocoenidae (Gray 1825) Bravard 1885. Late Mio.-Rec.
Fossil: Pacific, Rec.: Cos.
Subfamily Phocoenoidinae Barnes 1985a.
Subfamily Phocoeninae (Gray 1825) Barnes 1985a.
Superfamily unresolved.
Family Iniidae Flower 1867. Late Mio. Rec. Fossils:
FW. Argentina. Rec.: Brazil Venezuela.
Family Pontoporiidae (Gill 1871) Kasuya 1973. Late Mio. Rec.
Fossils: SW. Atl., N. Pac. Rec.: SW. Atl., FW. China.
Subfamily Lipotinae (Zhou et al 1979) Barnes 1985b.
Subfamily †Parapontoporiinae Barnes 1985b.
Subfamily Pontoporiinae Gill 1871.

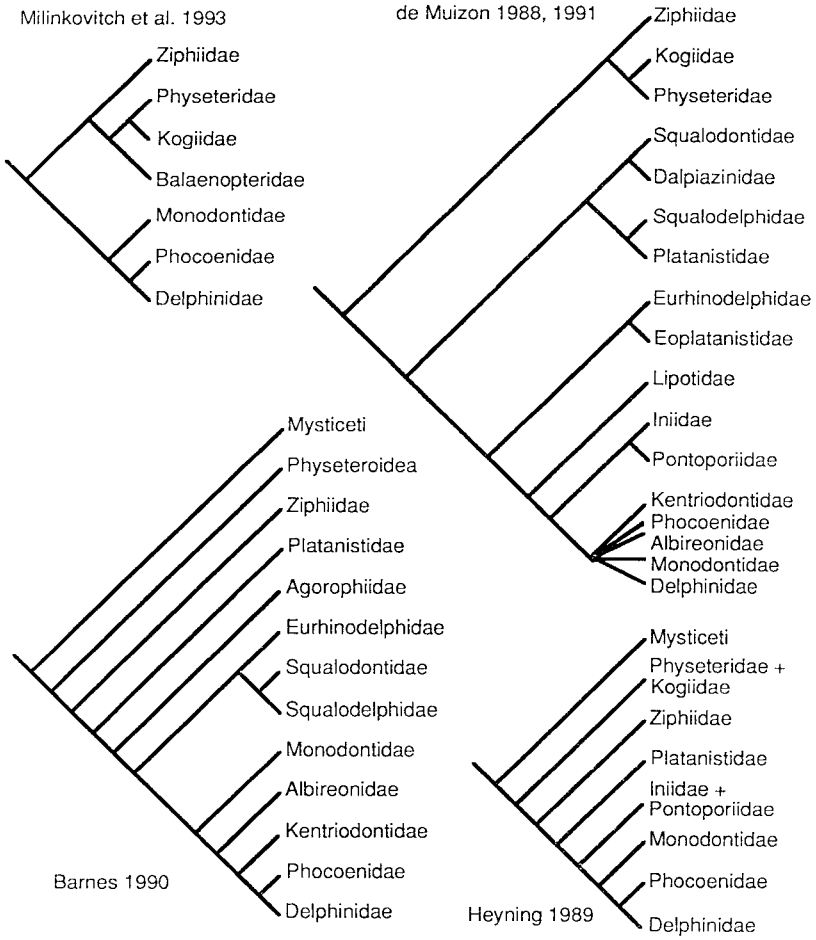

Figure 3 Alternative classifications of the Odontoceti.

"a wide diversity of species greatly different in morphology," but this move needs to be supported by careful cladistic analysis.

†PROTOCETIDAE The ancient grade †Protocetidae, which Kellogg (1936) regarded as "an unnatural assemblage," derives its identity from the small long-beaked †*Protocetus atavus* (Middle Eocene, Egypt-Tethys) which has sacral vertebrae that might have articulated with pelvic bones. The reputed oldest and perhaps amphibious cetacean, †*Pakicetus inachus* (Early or

Middle Eocene, Pakistan), has ears adapted for underwater hearing (Gingerich et al 1983, Gingerich & Russell 1990, Thewissen & Hussain 1993). The great variety of protocetid teeth suggests diverse feeding modes not yet substantiated by described skulls or skeletons. Protocetids include Middle Eocene taxa reported only from the Tethys–equatorial Atlantic–Caribbean (Kellogg 1936, Barnes & Mitchell 1978, Kumar & Sahni 1986, Hulbert & Petkewich 1991). These records support the idea of a Tethyan, presumed warm-water origin for cetaceans.

†REMINGTONOCETIDAE Species of †*Remingtonocetus* and †*Andrewsiphius* formed the bizarre remingtonocetids (Middle Eocene, India), a short-lived archaeocete clade characterized by a long, narrow skull and jaws, with cheek-teeth placed relatively far forward of the eyes. Kumar & Sahni (1986) suggested that remingtonocetids have pterygoid sinuses in the orbits, like those of odontocetes, and thus that the group is ancestral to odontocetes. Illustrations of the skull base of remingtonocetids suggest that the sinuses are not expanded, and relationships with odontocetes are unproven.

†BASILOSAURIDAE The paraphyletic Middle to Late Eocene †Basilosauridae are highly evolved taxa because they have cheek-teeth with multiple accessory denticles (small cusps) and expanded pterygoid sinus fossae in the skull base. More sophisticated feeding and hearing capabilities are indicated. These features suggest a sister group relationship with Odontoceti + Mysticeti. Barnes & Mitchell (1978), Gingerich (1992), and Gingerich et al (1990) suggested revisions to the taxonomy proposed by Kellogg (1936). The subfamily †Basilosaurinae appears to form a clade of large species with elongate vertebral bodies, of which †*Basilosaurus cetoides* (latest Eocene, North American Gulf Coast) is the largest (to >15 m). Large size and elongate vertebral bodies are perhaps synapomorphies which preclude basilosaurines from being the ancestors of Odontoceti or Mysticeti. The diverse paraphyletic †Dorudontinae includes species without elongate vertebral bodies, perhaps even the immediate ancestors of odontocetes and mysticetes (Barnes & Mitchell 1978). At least some, and probably all basilosaurids had hind legs (Gingerich et al 1990). Genera and species are diagnosed mainly on proportions of the skull and teeth.

Mysticeti

All living Mysticeti are large filter-feeders (Slijper 1979, Rice 1984), and filter-feeding can be inferred for most, perhaps all, fossil Mysticeti. Major evolutionary trends within the group include the loss of teeth, development of large body size and large heads, shortening of the intertemporal region as rostral bones and the supraoccipital approach each other, and shortening of the neck. Mysticetes have a uniquely "telescoped" skull in which

the maxilla uniquely extends posteriorly under the orbit to form a plate-like infraorbital process (Miller 1923). In living Mysticeti the expanded maxilla forms the origin for the epithelially-derived baleen plates used in filter-feeding—a unique and characteristic behavior of the group (Pivorunas 1979), although archaic toothed mysticetes perhaps lacked baleen. Other skull features, many related functionally to filter-feeding, help diagnose Mysticeti (e.g. Barnes 1990, Barnes & McLeod 1984). The evolution of filter-feeding was a key factor in the origin of mysticetes (Fordyce 1980, 1989b).

HIGHER CLASSIFICATION Family-level subdivisions of the Mysticeti (see Table 1) are currently not as contentious as those of odontocetes. This generally reflects a lack of recent detailed work; the mysticetes await cladistic reappraisal. Mitchell (1989) proposed a non-cladistic subdivision of Mysticeti into two infraorders. A grade Infraorder †Crenaticeti, which was not strictly diagnosed, includes only †*Llanocetus denticrenatus*. †Aetiocetidae and †Mammalodontidae are of uncertain infraordinal position. Infraorder Chaeomysticeti, interpreted here as a clade, encompasses all baleen-bearing taxa, including superfamilies Eschrichtioidea, Balaenopteroidea and Balaenoidea. Mitchell's proposed subdivisions and ranks are not used in Table 1; they await justification by careful cladistic study.

TOOTHED ARCHAIC MYSTICETES: †AETIOCETIDAE, †LLANOCETIDAE, †MAMMALODONTIDAE, AND †KEKENODONTIDAE †*Aetiocetus cotylalveus* Emlong 1966 (Late Oligocene, northeast Pacific) gives its name to the †Aetiocetidae, the first toothed mysticete family established. Emlong identified †*A. cotylalveus* as an archaeocete because it has teeth, but Van Valen (1968) placed it more appropriately in the Mysticeti. The mix of archaeocete-like and mysticete skull features seen in †*Aetiocetus* influenced cetologists into accepting that mysticetes arose from archaeocetes (Barnes 1987, 1989; Kimura et al 1992). Barnes (1987) referred the enigmatic late Oligocene †*Chonecetus sookensis* (also northeast Pacific; Russell 1968) to the †Aetiocetidae. Mchedlidze (1976) identified †*Mirocetus* and †*Ferecetotherium* (late Oligocene, Paratethys) as aetiocetids, but †*Mirocetus* is not clearly so and †*Ferecetotherium* is probably a physeterid (Barnes 1984b).

The oldest described mysticete is the toothed †*Llanocetus denticrenatus*, the only species in the family †Llanocetidae. It was based on a fragment of large inflated mandible (Mitchell 1989) of Late Eocene or probable Early Oligocene age (Seymour Island, Antarctica; southeast Pacific–southwest Atlantic). The relatively complete but undescribed holotype skull (Fordyce 1989b) is still under preparation. The †Llanocetidae has yet to be strictly diagnosed, and its cladistic relationships are uncertain.

The small †*Mammalodon colliveri* (Late Oligocene or Early Miocene, southwest Pacific), for which Mitchell (1989) proposed the monotypic family †Mammalodontidae, has a relatively very short rostrum, flat palate, and heterodont (differentiated) teeth. Only the holotype is described formally (Pritchard 1939, Fordyce 1984), but other Late Oligocene specimens occur in the southwest Pacific (Fordyce 1992). Mitchell (1989) offered a synoptic description of the †Mammalodontidae, but did not diagnose it on synapomorphies. Its possible relationships with the trans-Pacific †Aetiocetidae are uncertain.

†*Kekenodon onamata* is an enigmatic and long-debated cetacean (Late Oligocene, southwest Pacific) known only from large teeth, earbones, and a few other fragments. Mitchell (1989) provided a synoptic description for a new subfamily †Kekenodontinae, which he placed in the †Archaeoceti. Fordyce (1992, Figure 18.2) placed †*K. onamata* in Mysticeti: †Kekenodontidae. Cladistic relationships are uncertain. Other enigmatic probable mysticetes are known mainly from teeth (Fordyce 1992). Such fossils include two unnamed Early Oligocene species (Fordyce 1989a), several named Oligocene species wrongly placed in the odontocete genus †*Squalodon*, and probably †*Phococetus vasconum* (early Oligocene?, northeast Atlantic) which Kellogg (1936) and Mitchell (1989) regarded as an archaeocete.

In summary, primitive toothed mysticetes are more widespread and diverse than formerly understood. Their teeth may have been used, in the mysticete fashion, for bulk feeding rather than for selecting individual prey, but functional studies are needed to confirm this. Fossils include Early Oligocene basal Mysticeti which may prove critical in interpreting their archaeocete ancestry and the later Cenozoic diversification of mysticetes. Most of the fossils described so far are too fragmentary to be placed cladistically.

†CETOTHERIDAE Cetotheres are a paraphyletic group of archaic, baleen-bearing, toothless mysticetes whose name derives from the Late Miocene †*Cetotherium rathkii* (Paratethys; Kellogg 1928). Cetotheres have flat rostra with prominent ventral nutrient foramina for baleen, and a frontal that slopes gently (Miller 1923). The earliest cetotheres, †*Mauicetus* and †*Cetotheriopsis*, appeared by Late Oligocene time (Rothausen 1971, Fordyce 1992, Sanders & Barnes 1993). More than 30 genera and about 60 named Late Oligocene to Late Pliocene species are known (Kellogg 1931, Barnes & McLeod 1984, Fordyce 1992). Studies are plagued by taxa based on noncomparable and, often undiagnostic elements (Kellogg (1968). Cabrera (1926) and others identified some potential but as yet unformalized subfamilial groups. Cetotheres include taxa apparently close to

the ancestry of balaenopterids, but not putative ancestors for balaenids or eschrichtiids (McLeod et al 1993).

BALAENOPTERIDAE Rorquals include six extant species placed in two subfamilies, Balaenopterinae and Megapterinae (Rice 1984, Ridgway & Harrison 1985). Balaenopterids differ from cetotheres in their more complex interdigitation of rostral and cranial bones, and particularly in the supraorbital process, which is depressed abruptly from the cranial vertex to form a deeper origin for the temporalis muscle. There are firm Late Miocene records (Barnes 1977), and Bearlin (1988) reported an apparent Middle Miocene species from the western South Pacific. Some of the many named fossil genera and species have been placed occasionally with cetotheres, whence rorquals probably arose.

ESCHRICHTIIDAE Gray whales are represented by only one extant species, *Eschrichtius robustus*, which has only a fossil Quaternary record in the North Pacific and a prehistoric record in the North Atlantic (Barnes & McLeod 1984). It is not clear whether relationships are closer to balaenopterids or balaenids (McLeod et al 1993). Barnes & McLeod (1984) discounted other fossil records of *Eschrichtius*, noting that these represent balaenopterids or undiagnosable taxa. There is no close relationship between *Eschrichtius* and cetotheres.

NEOBALAENIDAE The small living pygmy right whale, *Caperea marginata*, found only in the Southern Hemisphere, is variously placed with the balaenids or in its own family (Miller 1923, Kellogg 1928, Barnes & McLeod 1984). The one reported fossil record of a neobalaenid, the Chilean †*Balaena simpsoni*, is dubious. They seem to be a primitive sister taxon of the Balaenidae (McLeod et al 1993).

BALAENIDAE Living right whales and bowheads are large slow swimming mysticetes with a narrow, highly arched rostrum and long baleen (Rice 1984). These are adaptations to "skimming" filter-feeding (Pivorunas 1979). There are many later Neogene records, mostly fragmentary specimens from around the North Atlantic and North Pacific (Barnes & McLeod 1984, McLeod et al 1993). The early Miocene †*Morenocetus parvus* (southwest Atlantic; Cabrera 1926) is the oldest known balaenid; it reveals no obvious clues to the origins of the right whales.

Odontoceti

All species in the clade Odontoceti (toothed whales, dolphins, and porpoises) have skulls in which the maxilla uniquely "telescopes" or extends posteriorly over the orbit to form an expanded bony supraorbital process (Miller 1923). In living odontocetes this supraorbital process forms an

origin for facial (maxillonasolabialis) muscle (Mead 1975a), which inserts around the single blowhole and associated complex nasal diverticula. The facial muscle complex and nasal apparatus probably generate the high-frequency sounds used by living odontocetes (Wood & Evans 1980) to echolocate in navigation and hunting. Fordyce (1980) suggested that the evolution of echolocation was critical in the origin of odontocetes. Other cranial features help diagnose Odontoceti (e.g. Barnes 1990), but teeth, long used in odontocete taxonomy, seem unreliable (Barnes 1977). The oldest certain odontocetes that are accurately dated and described are from the Late Oligocene. Supposed Early Oligocene species (Fordyce 1992) are recorrelated as Late Oligocene, while other reported Early Oligocene odontocetes (Squires et al 1991) have yet to be described. A diverse Late Oligocene record (Fordyce 1992) indicates a significant earlier Oligocene radiation.

Evolutionary trends within Odontoceti include expansion and increase in size of the face, shortening of the intertemporal region, elevation of the cranial vertex posterior to the nasals, increased facial asymmetry, enlargement of basicranial pterygoid sinus fossae, and isolation of the earbones from the skull. The jaws may become extremely long, narrow, and polydont, or short and blunt, or toothless.

HIGHER CLASSIFICATION The higher classification of odontocetes (Table 1) is currently volatile, with little chance of a consensus view that would allow a detailed correlation between evolution and geological processes. Volatility has arisen through advances in alpha taxonomy of fossils and neontological anatomy. Traditional subdivisions of the Odontoceti have been questioned mostly by paleontologists, creating disagreement about a basic framework for the extant species. Alternative cladograms are shown in Figure 3. Broader issues in odontocete classification include the ranks of taxa, the role and definition of paraphyletic taxa, the typological status of some fossil families, and the value of traditional superfamily subdivisions. Contentious issues include the placement of Physeteridae, Ziphiidae, †Eurhinodelphidae, and species of river dolphins (traditionally joined in the Platanistoidea), and the definition and diagnosis of the †Agorophiidae and †Squalodontidae. Some of these issues were covered by Barnes (1984a, 1985b, 1990), Heyning (1989), de Muizon (1987, 1988a, 1988b, 1991), Milinkovitch et al (1993), and Novacek (1993).

†AGOROPHIIDAE Traditionally, the grade †Agorophiidae Abel 1914 encompases heterodont odontocetes which primitively retain parietals exposed across the intertemporal region. Rothausen (1968) viewed †Agorophiidae as a structural and temporal grade between †Archaeoceti and the odontocete family †Squalodontidae, whence most later odontocetes

arose. Supposed agorophiids include †*Xenorophus*, †*Archaeodelphis*, †*Microzeuglodon*, †*Atropatenocetus*, and †*Mirocetus*, and undescribed fossils from the Atlantic and Pacific margins of North America (Whitmore & Sanders 1977); all are apparently Late Oligocene. Fordyce (1981) rejected the notion of a grade Agorophiidae, suggesting that the only certain member of the family is †*Agorophius pygmaeus* (Late Oligocene, northwest Atlantic) of uncertain cladistic relationships. Supposed "agorophiids" probably represent a plethora of low-diversity and perhaps high rank archaic taxa, such as would be expected during early phases of evolutionary radiations.

PHYSETEROIDEA, PHYSETERIDAE, AND KOGIIDAE Sperm whales—Physeteridae— have an ancient and diverse record, although only one species, *Physeter catodon*, survives. Primitive sperm whales had both upper and lower functional teeth; more highly evolved sperm whales, like the living species, have reduced or vestigial upper teeth. The Early Miocene †*Diaphorocetus poucheti* (western South Atlantic; Kellogg 1925b), one of the oldest described physeterids, has a skull with a distinctive supracranial basin which presumably held a large fatty melon and spermaceti organ. The older †*Ferecetotherium* (Late Oligocene, Paratethys; Mchedlidze 1984) is probably also a physeterid (Barnes 1984b, 1985c). It is likely that †*Diaphorocetus*, †*Idiorophus*, and other early physeterids were, like *Physeter*, deep diving squid-eaters. Sperm whales are widespread in Pliocene and Miocene sediments (Kellogg 1925b), whence come many dubious genera and species based on isolated teeth.

The extant pygmy sperm whales (see Caldwell & Caldwell 1989)—Kogiidae—are closely related to Physeteridae. As in physeterids, there is a supracranial basin, but kogiids differ markedly in their small size, short rostrum, and skull details. The oldest clearly identified kogiids are †*Praekogia* (Barnes 1973, Early Pliocene) and †*Scaphokogia* (de Muizon 1988c, Late Miocene), both from the subtropical eastern Pacific. Isolated fossil teeth, reportedly those of kogiids, do not clearly belong to the family.

ZIPHIIDAE Extant beaked whales are medium to large, semi-solitary pelagic cetaceans which are mostly near-toothless squid-eaters. *Mesoplodon* is one of the most diverse extant genera of odontocetes (Mead 1989). Ziphiids range back to the Middle Miocene (Mead 1975b), with many specimens represented by robust, dense rostra that are sometimes recovered from the sea floor (Whitmore et al 1986). †*Squaloziphius emlongi* de Muizon 1991 (Early Miocene) was placed in a new subfamily †Squaloziphiinae, although its skull lacks convincing ziphiid features and appears more reminiscent of †Eurhinodelphidae. Ziphiids have been classified

either with sperm whales in a superfamily Physeteroidea, or as a sister group to extant odontocetes other than physeterids (Figure 3).

PLATANISTOIDEA The extant Asiatic river dolphins, *Platanista* spp., are the basis for the family Platanistidae and superfamily Platanistoidea--taxa with a long and confusing history of use (Kellogg 1928; Simpson 1945; Fraser & Purves 1960; Barnes 1984b, 1985b; Zhou et al 1979; Heyning 1989). de Muizon (1987, 1988a, 1991) suggested that †Squalodontidae, †Squalodelphidae, ‡Dalpiazinidae, and Platanistidae form a clade unified by features of the scapula. Key features cannot be seen in some squalodontids and squalodelphid-like species, and more study is needed to justify this concept of Platanistoidea. Platanistoids sensu de Muizon have a longer fossil record than suspected previously, with moderate species diversity from the late Oligocene to about Middle Miocene, but they declined as delphinoids radiated dramatically late in the Miocene. Among platanistoids, only the extant *Platanista* spp. inhabit fresh waters.

†SQUALODONTIDAE The taxonomic limits of the Late Oligocene to Late Miocene family †Squalodontidae are not clear. In key reviews, Kellogg (1923) and Rothausen (1968) used the †Squalodontidae as a grade. Rothausen identified a need for cladistic review, but despite recent study (de Muizon 1991), clear synapomorphies have not been published. Squalodontids are still identified mainly by their close topographic match with well-documented skulls of †*Squalodon*. Probably only the long-beaked †*Eosqualodon*, †*Squalodon*, †*Kelloggia*, and †*Phoberodon* (and possibly †*Patriocetus*) are actually members of the †Squalodontidae, while many nominal squalodontids, including some named species of †*Squalodon*, probably belong in other families. The robust-snouted †*Prosqualodon australis* (Early Miocene, Southern Ocean) is enigmatic; Cozzuol & Humbert-Lan (1989) suggested affinities with dolphins (Delphinida), but relationships need more (cladistic) study.

†SQUALODELPHIDAE Three Early Miocene taxa are known: †*Notocetus* (southwest Atlantic), †*Medocinia* (northeast Atlantic), and †*Squalodelphis* (Mediterranean) (de Muizon 1988a). These have small slightly asymmetrical skulls with moderately long rostra, near-homodont teeth, and pterygoid lateral laminae (de Muizon 1987). Late Oligocene to Early Miocene species of †*Microcetus* and †*Prosqualodon* (southwest Pacific) and †*Sulakocetus* (Late Oligocene, Paratethys; Mchedlidze 1984) formerly referred to the †Squalodontidae probably belong within or close to the †Squalodelphidae.

†DALPIAZINIDAE de Muizon (1988a) established a new family, †Dalpiazinidae, and new genus, †*Dalpiazina*, for "†*Acrodelphis*" *ombonii* (Early

Miocene, Mediterranean). †Dalpiazina ombonii has a small symmetrical skull, reduced median dorsal exposure of frontals, and a long rostrum with many near-homodont teeth. Fordyce & Samson (1992) reported an undescribed earliest Miocene species from the southwest Pacific. †*Dalpiazina* is not firmly placed within the Platanistoidea (de Muizon 1991, Figure 15), and more study is needed.

PLATANISTIDAE The blind endangered Ganges and Indus River dolphins, *Platanista* spp., have no fossil record, and the time of invasion of fresh waters is unknown. Middle to Late Miocene marine species of †*Zarhachis* and †*Pomatodelphis* (both eastern North Atlantic) are closely related to *Platanista*, although they differ in rostral profiles and cranial symmetry, and in their development of pneumatized bony facial crests. These taxa have sometimes been placed in the †Acrodelphidae, a family that de Muizon (1988a) regarded as too poorly defined to use.

†EURHINODELPHOIDEA, †EURHINODELPHIDAE, AND †EOPLATANISTIDAE Dramatically long-beaked polydont dolphins in the extinct family †Eurhinodelphidae were widespread and moderately diverse during the Early to Middle Miocene (Kellogg 1925a, Barnes 1977, Myrick 1979). Late Oligocene provisional records (Fordyce 1992) include †*Iniopsis* (Paratethys), and an apparently Miocene species occurs in lacustrine sediments in central Australia (Fordyce 1983). Eurhinodelphid relationships are contentious (Figure 3; Barnes 1984b, 1990; de Muizon 1988a, 1991). The †Eoplatanistidae (Early Miocene, Mediterranean), which is unrelated to Platanistidae (Barnes 1984), includes only two species of †*Eoplatanista* Dal Piaz (1917; de Muizon 1988a). Like eurhinodelphids, these have small and virtually symmetrical skulls and long, polydont upper and lower jaws.

DOLPHINS—DELPHINIDA AND DELPHINOIDEA Dolphins are taxonomically diverse Odontoceti, mostly species of small to medium size. Formal names (Table 1) derive from the living common dolphin, *Delphinus delphis*. Most of the fossils are Late Miocene or younger, although the delphinoidean record extends back to the Late Oligocene. Simpson (1945) used a superfamily Delphinoidea to include Delphinidae, Monodontidae, and Phocoenidae, to which Barnes (1978, 1984a) added †Kentriodontidae and †Albireonidae. de Muizon (1988b) placed Pontoporiidae and Iniidae in a new superfamily Inioidea, the Lipotidae in the new Lipotoidea, and joined these superfamilies together with Delphinoidea in a new infraorder Delphinida. Diagnostic features of the skull include pterygoid sinus fossae and earbones (de Muizon 1988b, Barnes 1990).

†KENTRIODONTIDAE Most early dolphins, including many previously supposed Delphinidae, are placed in the grade family †Kentriodontidae. Ken-

triodontids are archaic dolphins with polydont teeth, elaborate basicranial sinuses, and symmetrical cranial vertices (Barnes 1978); most were probably 2–4 m long (see Figure 4). The oldest records, of Late Oligocene age [†*Oligodelphis* (Barnes 1985c), †*Kentriodon*? (Fordyce 1992)], provide few clues as to their sister group; an origin among †Squalodontidae (Barnes et al 1985) seems unlikely. Early to Late Miocene taxa, such as †*Kentriodon* and †*Pithanodelphis*, are generically diverse and widespread (Barnes & Mitchell 1984, Barnes 1985d). Kentriodontids seem related to the living Delphinidae, and perhaps were similarly pelagic.

†ALBIREONIDAE This Late Miocene–Pliocene family is known from the superficially porpoise-like †*Albireo whistleri* and an undescribed species from the temperate eastern North Pacific (Barnes 1984a). Barnes discounted close relationships with Phocoenidae because of differences in skull sutures, basicranial sinuses, and periotics, and noted that †*Albireo* is too specialized to have given rise to any extant phocoenid, delphinid, or monodontid. Barnes suggested that †*Albireo* was derived from kentriodontids, and de Muizon (1988b) placed †*Albireo* as a sister group to phocoenids.

MONODONTIDAE The living narwhal (*Monodon*) and beluga (*Delphinapterus*) live in Arctic waters (Rice 1984), and are known from Atlantic Subarctic Quaternary records, but Late Miocene to Late Pliocene monodontids, including †*Denebola*, occur in temperate to subtropical settings in the East Pacific (Barnes 1977, 1984a; de Muizon 1988c). Recent habitat shifts are indicated. Kasuya (1973), Barnes (1984b), and others regarded the Australian-Indonesian *Orcaella* as a monodontid, with intriguing paleozoogeographic and evolutionary implications, but de Muizon (1988b) and Heyning (1989) placed *Orcaella* firmly as a delphinid.

DELPHINIDAE Living delphinids are ecologically diverse. Their habits may be neritic (the small *Cephalorhynchus*) or oceanic (*Lissodelphis*, *Stenella*); some dolphins are near-cosmopolitan (the large *Orcinus*). A key diagnostic feature is cranial asymmetry, particularly involving the premaxillae (Barnes 1977, 1978). The oldest firm records of delphinids thus defined are from the later Middle or early Late Miocene (Barnes 1977). Abundant published older records (Kellogg 1928, Simpson 1945), often based on isolated elements, are mostly misidentifications or are based on undiagnostic specimens (see Barnes 1978). Barnes (1990) provided a general overview of delphinids as part of a review of *Tursiops*.

PHOCOENIDAE Porpoises, like Delphinidae, have a record that extends back to the Late Miocene, although with only six small extant species, the porpoises are less diverse than living delphinids (Barnes 1985a). †*Pisco-*

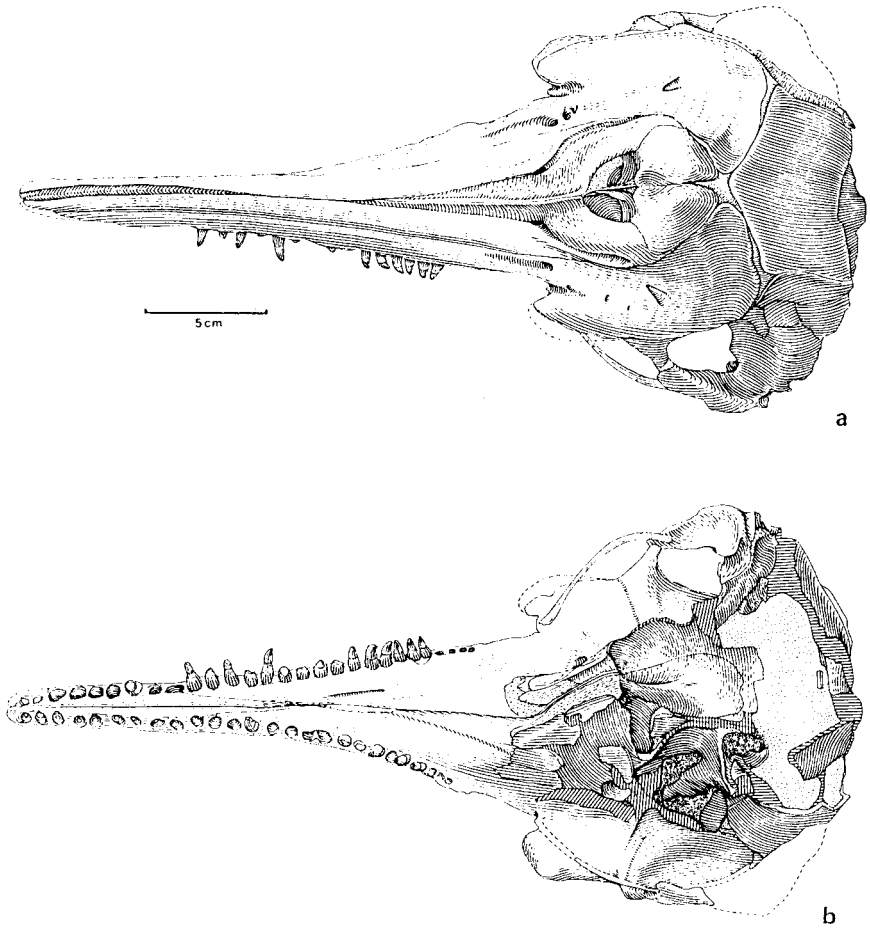

Figure 4 Skull of the small Late Miocene kentriodontid dolphin, *Atocetus nasalis* (originally named as *Pithanodelphis nasalis*), an extinct delphinoid from the eastern North Pacific Ocean. Such relatively complete fossil specimens are responsible for recent advances in the interpretation of cetacean morphology, phylogeny, and systematics. Views of the holotype cranium from Orange County, California: (*a*) dorsal view; (*b*) ventral view; modified from Barnes 1985d.

lithax tedfordi Barnes 1984a seems to be the most primitive fossil phocoenid and is much like generalized delphinids (Barnes 1993a, 1993b). The oldest members are East Pacific taxa such as †*Salumiphocaena* Barnes 1985a and †*Australithax* de Muizon 1988c; these have rather symmetrical skulls,

premaxillary eminences, and basicranial sinus fossae like extant phocoenids. Earlier records of supposed phocoenids are misidentifications (Barnes 1978, Fordyce 1981).

PONTOPORIIDAE, INIIDAE, AND LIPOTIDAE The genus- and species-level status of living "non-platanistoid river dolphins" is fairly clear. The small, long-beaked species *Pontoporia blainvillei* (Pontoporiidae), which lives nearshore in the western South Atlantic, is the only extant pontoporiid. *Inia geoffrensis* (Iniidae) is a fresh-water species found in Amazon drainages, and *Lipotes vexillifer* (Lipotidae of Zhou et al 1979; Lipotinae of Barnes 1985b) lives in the Yangtze River, China. Relationships above the genus level are complicated; different arrangements affect the placement of fossils and interpretations of evolution and paleozoogeography.

Fossil *Pontoporia*-like taxa include species of †*Pliopontos* and †*Parapontoporia* from temperate to subtropical marine settings in the east Pacific (Barnes 1977, 1984a; de Muizon 1983, 1988c). Late Miocene or Pliocene †*Pontistes* and *Pontoporia* species come from marine sediments in Argentina (Cozzuol 1985). All pontoporiidas except for †*Parapontoporia* have virtually symmetrical cranial vertices, and most have long rostra and many tiny teeth. Barnes (1984a, 1985b) recognized †*Parapontoporia* as morphologically intermediate between *Pontoporia* and *Lipotes*, and thus subdivided Pontoporiidae into Pontoporiinae, †Parapontoporiinae, and Lipotinae. Conversely, de Muizon (1988b) placed †*Parapontoporia* with *Lipotes* in his Lipotoidea, uniting Pontoporiidae and Iniidae on features including markedly triangular transverse processes of the lumbar vertebrae. The only fossil placed close to *Lipotes* is †*Prolipotes*, based on an unrevealing fragment of mandible from freshwater Neogene sediments in China (Zhou et al 1984).

Inia geoffrensis (Amazon and Orinoco rivers) is the only extant iniid. Despite the lack of a significant fossil record, Grabert (1983) linked the evolution of *I. geoffrensis* to tectonic changes associated with Andean uplift. Like the Delphinidae, the Iniidae has been a repository for many fossils (Simpson 1945, Barnes 1978, Pilleri & Gihr 1979), but few species are placed there now. Cozzuol (1985) reviewed the Late Miocene or Pliocene fluvial †*Ischyrorhynchus* and †*Saurodelphis*, listing most other named iniid genera and species as synonyms.

INTERPRETING THE RECORD

Broader Patterns

The 10 or 11 species of early Middle Eocene Cetacea indicate a modest early radiation (Fordyce 1992), but cetacean family-level diversity was low

during the Eocene. Major times of change occurred at the family level (Figure 1) during the Oligocene, when Odontoceti and Mysticeti appeared and radiated rather explosively, and during the Middle to Late Miocene, when extant delphinoid and mysticete groups appeared. There are no certain large-scale extinctions in cetacean fossil history. Important turnover at the genus level, for example, later in the Pliocene, is not revealed by family ranges. Clades below the suborder but above the family level are defined too poorly to be indicators of sure trends.

Clade durations vary (Figure 1), with 25 million years for Odontoceti and Mysticeti and, for families, about 10 million years (for example, Delphinidae, Phocoenidae, and Monodontidae) to over 20 million years (Physeteridae, Balaenidae). Short geologic histories for families such as Eschrichtiidae, †Mammalodontidae, and †Albireonidae, are probably artificial; a longer but unrecorded time span is more likely (Fordyce 1992), while others may ultimately be reduced to subfamily rank. Genera need care because some, such as †*Cetotherium* and †*Squalodon*, have been used as "scrap basket" grades. The extant *Balaenoptera* and *Megaptera* range to the late Middle Miocene (Barnes 1977), about 11 million years, and the extant dolphin *Tursiops* has middle Pliocene records (Barnes 1990). The reported Early to Late Miocene range (Rothausen 1968) for †*Squalodon* seems anomalously long and the family probably died out in Middle Miocene time. At the species level, Fordyce (1992) noted that no Eocene or Oligocene cetacean clearly ranges through more than one stage. Fossil records for living species of *Eschrichtius* and *Tursiops* are Pleistocene (Barnes & McLeod 1984, Barnes 1990). Overall, species durations of 1–2 million years seem likely, so that geographically separate occurrences of the same species may have stratigraphic value.

Diversity Trends

Discussion of cetacean diversity usually assumes that global diversity reflects broad oceanic heterogeneity, with local diversity patterns reflecting restricted ecological opportunities. Geographic diversity patterns for extant Cetacea include: the tropics—about 48 species; temperate regions—about 55 species; poles—about 28 species; and the eastern North Pacific—about 30 species (Barnes 1977). Faunal diversity for fossil assemblages along the northeast Pacific margin may exceed 20 species, comparable to the Recent, and with comparable ecological partitioning in terms of inferred habit (Barnes 1977).

Changes in diversity at genus and species level potentially reveal links between cetacean evolution and geological events. The record is too poor and too poorly calibrated to reveal global taxonomic-diversity over short intervals (on the order of 1–2 million years), which would best indicate

ecological and habitat opportunities, but more crude assessments are possible. For the Paleogene, Orr & Faulhaber (1975) plotted diversity changes at the genus level to show a marked drop in diversity from Late Eocene (ten genera) to Early Oligocene (two genera), followed by three genera in the Late Oligocene; diversity increased in the Miocene. Changes were attributed to changing paleotemperatures and plankton diversity (Barnes 1977). Previous characterizations of Oligocene time as having low cetacean diversity have now been dispelled. Fordyce (1992; Figure 1) emphasized species level rather than generic diversity. He reported an increase in species diversity for most of the Eocene, a drop in the latest Eocene, and a marked increase from Early to Late Oligocene. The latter was attributed to increasing oceanic heterogeneity, particularly circulation changes associated with the breakup of Gondwana and the creation of the Southern Ocean. A high diversity for Late Oligocene time (35–50+ species) is not fully comparable with the Recent, since the former reflects an over 5 my long sample. Data have not been published for Neogene species.

Structure and Function

Cetacean structures can be viewed as constrained by interacting components of constructional morphology (Fordyce 1989b). Historical factors include the plesiomorphies of cladists. These conservative features, many of which have long been fixed for functional reasons, reveal distant ancestry (for example, with artiodactyls; above), but little about the immediate adaptations of a species. Functional factors are reflected in profound adaptations for aquatic life, such as locomotory, feeding, and acoustic complexes. Fossils may reveal the minimum age of such complexes, in which innovations may reflect adaptation to new physical environments and geological change (Fordyce 1980, 1989b, 1992). Ecological interaction may be indicated; mirror-image changes in diversity, for example, the decline of platanistoids concomitant with the radiation of delphinoids (especially delphinids), could reflect ecological displacement through functional superiority. Structural or fabricational changes include those constrained by geometry, such as surface area: volume ratios, and area of the feeding apparatus relative to body mass.

Locomotion

Modern (e.g. post Oligocene) cetaceans are typically streamlined, have no external hind limbs, and have nonrotational elbow joints, paddle-like forelimbs for steering, elongate tail stocks, and horizontal propulsive tail flukes that are somewhat stiff and rigid. Terminal caudal vertebrae within the tail fluke are nearly square and the vertebra at the point of up-and-down rotation at the front of the fluke has a rounded intervertebral face.

These features exist in fossil skeletons, including those of archaeocetes, which indicates the presence of typical horizontal tail flukes early in cetacean evolution. Dorsal fins vary in size, shape, and presence among living species, and animals with missing or damaged fins can still navigate. Dorsal fins are not indicated by any skeletal structure, and are therefore not determinable from the fossil record.

The pectoral flipper in modern Cetacea, composed of the mammalian forelimb elements, has a rigid elbow joint and the flipper is used as a rudder in locomotion. In Archaeoceti, the more primitive elbow joint is flexible (rotatable), the humerus long, and the flipper not as streamlined as in extant Cetacea. Some (possibly all) archaeocetes also had external hind limbs [the pelvic facets on sacral vertebrae of †*Protocetus* suggest a well developed pelvis; hind limbs have been discovered on †*Prozeuglodon*; an undescribed protocetid from the Eocene of Georgia also has a pelvis (Hulbert & Petkewich 1991)]. Early archaeocetes might have been able to haul out on beaches as do pinnipeds. Requirements of amphibious land-breeding inferred from this probably compromised adaptation for long distance locomotion; if amphibiousness persisted in later archaeocetes, it was doubtless lost in early odontoceti and mysticeti whose key adaptations (echolocation, filter-feeding) allowed exploitation of food farther offshore (Fordyce 1980). The small functional hind limbs of †*Prozeuglodon isis* (Middle Eocene, Egypt) perhaps aided copulation (Gingerich et al 1990) or locomotion in shallow waters. Dense pachyostotic ribs in †*Basilosaurus cetoides* and other extinct cetacea possibly helped buoyancy control (de Buffrénil et al 1990) as in sirenians.

Hearing and Echolocation

All cetaceans have a modified ear structure that allows them to hear directionally in water. Cetaceans can also hear out of water. The auditory structure in archaeocetes and mysticetes is more primitive and less modified from the structures in terrestrial mammals than the anatomy of odontocetes, which is highly modified. No fossil or living mysticete shows bone features that might be construed as echolocation adaptations, undermining the idea (Milinkovitch et al 1993) of secondary loss of echolocation in mysticetes. Underwater acoustic communication is important in Odontoceti and Mysticeti (Wood & Evans 1980, Evans 1987) and, given the development of the tympanic bulla and auditory ossicles, was probably also important in the Archaeoceti.

All modern cetaceans lack an external ear, and only a tiny hole remains. Therefore, sound is received principally through other parts of the head. Underwater sound travels into the head and reaches the ears differentially, thus allowing directional hearing. The ear bones are isolated, to varying

degrees among different groups, within a fat capsule, and this isolates the ear for hearing by impedence mismatching.

Active echolocation—the ability to detect the distance and size of objects underwater using reflected sound produced by the animal—has been evolved in the odontocetes. It involves the highly evolved hearing apparatus coupled with a unique sound making system (Norris 1968). An odontocete produces high-frequency sound ("clicks") by moving recycled air in a network of sacs and valves of the nasal passages, focuses it and projects it into the environment through the fatty melon (which acts as an acoustic lens) on the face (Norris 1968, Norris & Evans 1967). Asymmetrical structures of the face may be involved in the sophisticated production of both high- and low-frequency sounds.

Elaborate air sinuses have invaded the basicranium and orbit in several odontocete lineages (Fraser & Purves 1960), and may prevent sound generated in the nasal passages from directly impacting the ears and brain. Sound that reflects off objects in the environment and returns to the animal is transmitted through the side of the lower jaw via a thin area called the "pan bone," to the ear (Norris 1968).

This development may be a key feature of the successful Later Neogene oceanic delphinoid radiation (Fraser & Purves 1960). Perhaps the better echolocation of delphinoids, through more elaborate pterygoid sinuses and better-isolated earbones, allowed them to replace the more primitive groups of the Miocene. Most fossil odontocetes do have the same basic skull structure as modern odontocetes, and they undoubtedly could echolocate. However, most of the primitive Oligocene and Miocene odontocetes do not have asymmetrical crania, and this suggests that they had not acquired a sophisiticated level of echolocation. Squalodontids have a symmetrical facial region, and its depression indicates the presence of moderately developed facial muscles that could have been used to control the melon and nasal sacs. Periotics of Late Oligocene odontocetes show adaptations for receiving high-frequency sound (Fleischer 1976).

Body Size

Cetaceans include the largest living animals; even the smallest Cetacea are rather large for mammals. Minimum body size, which governs surface area to volume ratio, is constrained by rates of heat loss in water, and there is a predictable lower limit to body size for aquatic endotherms (Downhower & Blumer 1988). Large size, such as seen in Physeter and the migratory Mysticeti, could minimize heat loss in cold waters, could be an anti-predator strategy, and could minimize drag per unit mass during swimming or deep diving. The upper limit to size is probably constrained by the need to lose heat in proportion to mass, by the feeding apparatus

(which must be scaled in proportion to body volume unless feeding method or type of food changes), and by the surface area of flukes (which must provide propulsion capable of moving the body mass).

Some theories of vertebrate evolutionary strategies view large species as K-selected indicators of highly stable environments, with small generalized species more characteristic of the early phases of radiations. This appears to be true of Cetacea. Among Paleogene Cetacea (Fordyce 1992), early protocetids at the base of the cetacean radiation were small, although probably larger than the smallest extant odontocetes. Contrary to published suggestions (reviewed by Fordyce 1992), Early Oligocene Cetacea include large species, discounting the notion that an episode of Late Eocene gigantism (†Basilosaurinae) was followed by times of smaller Oligocene species. Known Oligocene Odontoceti are small but some contemporaneous Mysticeti were large. There is little published evidence of large species early in the Miocene, but one late Miocene balaenopterid (Barnes et al 1987) is comparable in size with the living blue whale, *Balaenoptera musculus*.

In most odontocetes the males are larger than the famales; exceptions include only about six species among the beaked whales (Ziphiidae), porpoises (Phocoenidae), and Platanistidae, Pontoporiidae, and Iniidae. In all living mysticetes the females are larger than the males (Ralls 1976). While the reasons for this patterns are not known, it might be related to the unusually large size of cetacean newborn and the need to provide huge amounts of milk for rapid growth. Some cetacean species mature in less than five years.

Paedomorphism

Various species of living cetaceans in different families are paedomorphic. Paedomorphosis is the persistence of fetal or juvenile characters in reproductive age adults, and it appears evolutionarily as a derived character among cetaceans; it is less prevalent or nonexistent in earlier fossil members of the order. Paedomorphism appears in skulls of various derived mysticetes and odontocetes, and is extreme in the living species of phocoenids (Barnes 1985a), in which it is universally present and pronounced.

Primitive Cetacea lack paedomorphism, and most Miocene and earlier cetaceans have heavily built skulls with relatively small braincases, large zygomatic arches, large occipital and lambdoidal crests, prominent tuberosities, long rostra, large deeply socketed teeth, and an absence of cranial vacuities. Most of these structures are enhanced during maturation. Kentriodontids, the Late Oligocene to Late Miocene family of probable basal delphinoid dolphins, show little evidence of paedomorphism. Adults of

Recent phocoenids have relatively short rostra, large braincases, small zygomatic arches, and small occipital and lambdoidal crests. These cranial characters and proportions of adult phocoenid skulls are characteristic of newborn skulls of some other odontoceti, and their appearance in some groups is evidence of paedomorphism.

Feeding

Protocetids (Early Middle Eocene) have simple heterodont teeth with prominent anterior diastemata. †*Pakicetus* could probably shear and grind as well as snap (Gingerich & Russell 1990), in contrast to later Cetacea. †*Protocetus* has a long narrow rostrum and simple jaw articulation, presumably for forceps-like quick grasping of single prey, as also seen in many later Cetacea. Longer jaws in remingtonocetids perhaps indicate pursuit of fast prey. Basilosaurids include small to large species with complex denticulate diphyodont teeth, but are not polydont. Their cheek teeth commonly show apical wear, but shearing and crushing were probably minor aspects of their feeding. Basilosaurids show a greater range of tooth and jaw form, and body size, as expected for a geographically more widespread group living in increasingly heterogeneous, cooling oceans during later Eocene. Basilosaurids probably exploited resources not cropped by protocetids, for example, offshore or deep-dwelling prey.

Extant Odontoceti and Mysticeti are polydont with a single set of teeth (monophyodont). Mysticetes resorb their multiple simple tooth buds while in utero. Because many early fossil Odontoceti and Mysticeti are not polydont, it is possible that the marked polydonty in extant forms is not synapomorphous. Tooth and rostrum structure in the earliest mysticetes (Early Oligocene) is consistent with filter-feeding on a mass of prey. The large †*Llanocetus denticrenatus* has large diastemata between superficially basilosaurid-like teeth which carry palmate denticles (Mitchell 1989) and it probably filter-fed as do living crab eater seals; other toothed mysticetes are interpreted as filter-feeders (Barnes & McLeod 1984, Fordyce 1989a). Fordyce (1980, 1989b, 1992) suggested that filter-feeding in Mysticeti evolved in response to availability of new food and, in turn, to new oceanic circulation patterns associated with the creation of the Southern Ocean and the final breakup of Gondwana. Migration perhaps evolved at the same time, to allow seasonal high-latitude feeding alternating with breeding in thermally less-stressful temperate-tropical latitudes.

Baleen-bearing filter-feeding mysticetes evolved by the late Oligocene, 4–5 million years after toothed mysticetes appeared. Rostra of such animals as the early cetotheres are more similar to those of rorquals than to right whales or gray whales, which suggests that gulp-feeding (Pivorunas

1979, Lambertson 1983) was used. Different sizes and proportions of rostra among early cetotheres suggest that ecological (feeding) partitioning was comparable to that of living balaenopterids. Living balaenids skim-feed (Pivorunas 1979), using long baleen in a narrow arched rostrum. Early Miocene balaenids reveal that this is an ancient behavior. It is not known when the "bottom-ploughing" feeding method of gray whales (Eschrichtiidae) evolved because no primitive members of this group are recognized. Balaenopterids appeared by the Late Miocene, dramatically separated from cetotheres in having an abruptly depressed frontal which suggests a marked functional shift in origin and action of the temporalis muscle and perhaps in "gulp-feeding."

The earliest Odontoceti probably used echolocation to help hunt single prey. Fordyce (1980, 1990) suggested that, as with mysticete feeding, echolocation evolved about the Early Oligocene in response to changing food resources (especially below the photic zone), changing oceans, and continental rearrangement. Most odontocetes have a moderately attenuated rostrum like that seen in basal Cetacea, but a short, robust, broad rostrum has evolved in some groups (†*Prosqualodon* and Globicephalinae) sometimes with marked loss of teeth. Tooth number and tooth form vary widely in the long-beaked Odontoceti. There is a general trend toward homodonty and increased polydonty. Squalodontidae have long, deep, robust rostra and stout denticulate cheek-teeth; these features suggest more than just simple grasp-and-swallow-whole, and perhaps prey such as seabirds were taken. Extremely long rostra, often with, extreme polydonty, have evolved repeatedly and convergently (†Eurhinodelphidae, †Dalpiazinidae, Platanistidae, Pontoporiidae, Lipotidae, Iniidae; see ranges in Figure 1), although details vary in different taxa. The robust, wide pterygoid lateral lamina found in many of these taxa may be a homoplasy and related functionally to the muscles for the long beak, rather than a synapomorphy. Platanistid rostra may be laterally compressed (*Platanista*) or dorsoventrally compressed (†*Zarhachis*), while †*Eurhinodelphis* has a long subcylindrical rostrum in which the bizarrely toothless tip far overhangs the mandibles. Early Miocene physeterids and Middle Miocene ziphiids perhaps fed at depth on oceanic squid, as do their extant descendants. A reduced role for teeth in processing food is shown by convergent tooth loss in diverse groups, including some Physeteridae, Ziphiidae, Kogiidae, Monodontidae, and Globicephalinae. No odontocetes are reportedly filter-feeders, bottom-ploughers, or durophagous (crushers of hard-shelled prey) feeders. There is no clear ecological (feeding) overlap with other marine mammal groups.

Diverse feeding methods were attained quickly in odontocete history. By the end of the Oligocene, temperate-latitude odontocetes showed a

range of feeding strategies comparable with those of living temperate-latitude faunas. Major changes in taxonomic and thus ecological patterns that occurred late in the Neogene may have been driven by feeding strategies. Squalodontids and eurhinodelphids became extinct, the formerly marine iniids, pontoporiids (and lipotids?), and platanistids gradually disappeared from the marine record, and monodontids disappeared from low to mid-latitudes. At about this time, the delphinids radiated rapidly, and it is possible that they ecologically displaced other groups. Delphinids are now the most diverse and widespread of the oceanic temperate-tropical smaller odontocetes, and indeed of all Cetacea.

ENVIRONMENTAL CHANGE AND PALEOZOOGEOGRAPHY

Major geological events that probably influenced cetacean evolution and distribution include (Figure 5): late stages in the closure of the Tethys seaway, with Africa and India suturing to Eurasia about the time the earliest protocetids appeared; the Paleogene opening of the Southern Ocean, culminating in the Oligocene with circum-Antarctic flow south of Australia and South America; closure of the Indo-Pacific seaway in the Neogene when Australia collided with the Indonesian arc; and closure of the Panamanian seaway in the Pliocene (references in Fordyce 1989b, 1992). Some events in cetacean history broadly correlate with these changes (Fordyce 1989b; see Figure 5).

Among living Cetacea, large species (e.g. most Mysticeti) are generally more widely distributed than small species (e.g. dolphins) (Barnes 1977, Evans 1987). In terms of evolution, large species were probably influenced only by large-scale geological changes, while small species were probably susceptible to, for example, the isolation of small basins through regression.

Many marine organisms have antitropical (or bitemperate or bipolar) disjunct distributions (Berg 1933, Hubbs 1952). North-south population pairs among large whales or taxon pairs among small cetaceans are typical (Davies 1963, Barnes 1985a). Cetacean diversity is highest in temperate latitudes and low in tropical and polar latitudes (Barnes 1977). Warm, tropical waters appear to separate populations, and Pleistocene glacial-interglacial oscillations may have separated populations (Davies 1963) for varying durations of time and brought about genetic isolation, and in some groups speciation. Even though few fossil cetaceans are known from more than one locality, some, such as the porpoise †*Piscolithax*, seem to have also had north-south taxon pairs. Further collection of specimans might show the phenomenon to be more common in the fossil record.

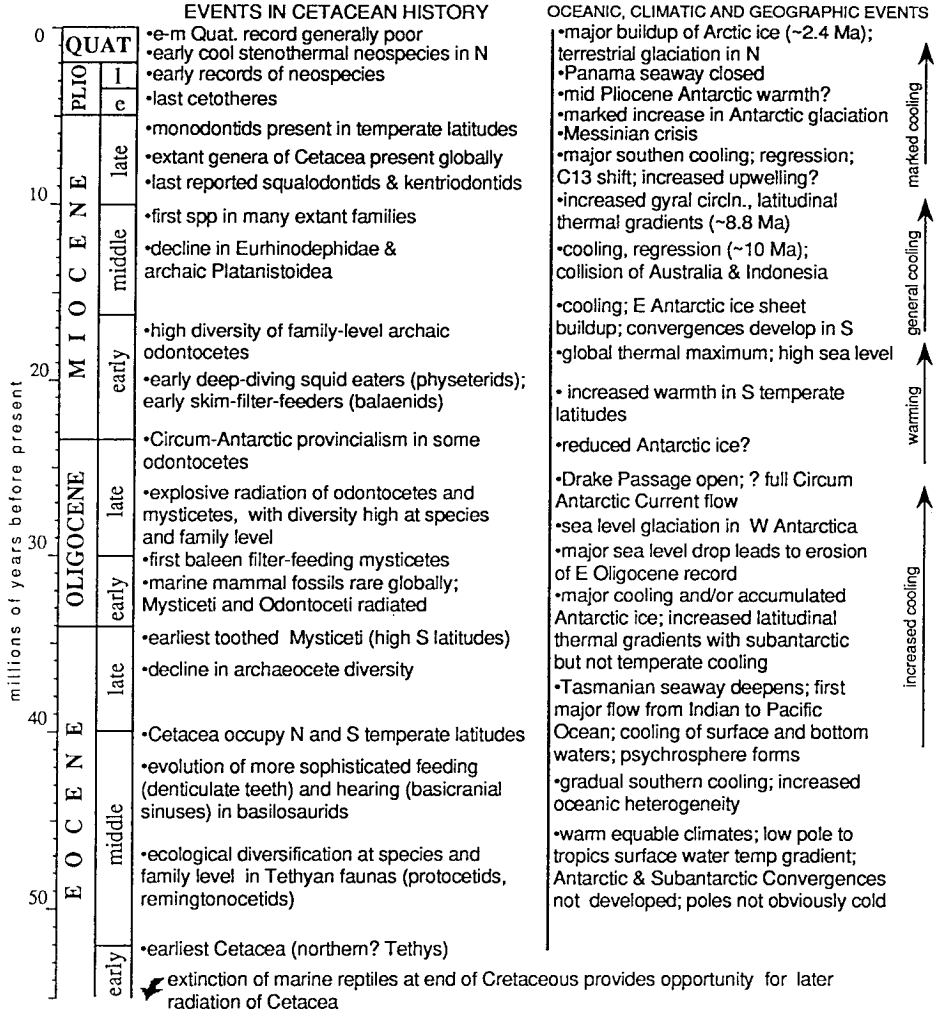

Figure 5 Events in cetacean and oceanic history, revised from Fordyce (1989). Sources of information listed by Fordyce (1989).

ACKNOWLEDGMENTS

We thank Alastair G. Watson for critical comments, and Bob Connell and Phillip A. Maxwell for their help. Wendy Smith-Griswold, former Earth Sciences Division Scientific Illustrator at the Natural History Musuem of

Los Angeles County, prepared the illustration of the fossil dolphin skeleton in Figure 2*b* from a composite of photos of various bones. Linda Staniec helped with typing and editing the manuscript.

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