

MANDIBULAR AND DENTAL VARIATION AND THE EVOLUTION OF SUCTION FEEDING IN ODONTOCETI

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Comprehensive morphometric analysis of osteological and necropsy specimens indicates that blunt heads and wide jaws, both of which create a more circular mouth opening and thus improve water flow for suction feeding, are common in Odontoceti and found in all families except freshwater river dolphins (Platanistoidea), which are exclusively long-snouted. Mandibular bluntness, here termed amblygnathy, correlates with dental reduction in odontocetes; there is a further association of reduced dentition with increased body length. Examination of quantitative data reveals that many odontocetes, especially globicephaline delphinids, have a blunter cranial profile (partly from facial musculature and other soft tissues) and fewer exposed teeth for grasping prey than is generally supposed, especially when the researcher relies solely on examination of skeletal materials. Numerous teeth present in cleaned skulls and jaws remain unerupted even in adults, as verified by necropsy tooth counts, rendering tooth counts from museum specimens unreliable indicators of *in vivo* conditions. Amblygnathy and smaller, rounder mouth openings correlate with other anatomical, ecological, and behavioral traits associated with suction feeding. It is likely that odontocete suction ingestion evolved independently in multiple lineages from use of suction to transport grasped prey in long-jawed ancestors, with consequent loss of the grasp and transport step as prey are sucked directly into the oral cavity or oropharynx.

Key words: Cetacea, dentition, mandible, morphometrics, odontocete, osteology, suction feeding

In their landmark 1983 paper formally reviewing the acoustic stunning hypothesis (initially proposed by Bel'kovich and Yablokov in 1963), Norris and Møhl reviewed qualitative evidence to support the premise that odontocetes debilitate prey with intense sound pulses, including discussion of anecdotes involving behavior during foraging, limited experiments on odontocete sound generation and on the effects of shock waves on marine organisms, and comparison to sonic prey capture by snapping or pistol shrimps (Alpheidae). Norris and Møhl opened their paper (1983) by suggesting 2 major evolutionary trends, a shortening of the jaws and a loss of teeth, both evident in the fossil record from archaeocetes to Recent odontocetes. They suggest that late Tertiary (Eocene and Oligocene) and Neogene forms, which had elongate, narrow rostra and jaws bearing many teeth, were gradually replaced by a diversity of forms including many with short, blunt jaws and with marked dental reduction or total loss of teeth. Although all archaeocetes and early odontocetes display long pincer jaws with interlocking teeth along and caudal to a long, fused mandibular symphysis, many extant odontocete genera in at least 4 families

(*Kogia*, Physteridae; *Delphinapterus* and *Monodon*, Monodontidae; *Neophocaena*, *Phocoena*, and *Phocoenoides*, Phocoenidae; *Cephalorhynchus*, *Feresa*, *Globicephala*, *Grampus*, *Orcaella*, *Orcinus*, *Peponocephala*, and *Pseudorca*, Delphinidae) now possess short jaws dominated by the lingual portion. Further, although odontocetes are named and known for their teeth, some modern taxa are, ironically, functionally edentulous.

Norris and Møhl (1983) acknowledge that both trends, of cranial shortening and dental loss, have significant implications for odontocete feeding. They argue that acoustic prey stunning followed by ram (overtaking and engulfing prey) or suction ingestion is the likeliest foraging method. Although prey stunning remains hypothetical, use of intraoral or gular suction for prey capture and ingestion has since been confirmed by experimental documentation and direct observation in several odontocete species, including the long-finned pilot whale (*Globicephala melas*—Werth 2000a), short-finned pilot whale (*Globicephala macrorhynchus*—Brown 1962), beluga (*Delphinapterus leucas*—Ray 1966), killer whale (*Orcinus orca*—Donaldson 1977), harbor porpoise (*Phocoena phocoena*—Kastelein et al. 1997), pygmy and dwarf sperm whales (*Kogia breviceps* and *Kogia simus*, respectively—Bloodworth and Marshall 2005), and Cuvier's and Hubbs' beaked whales (*Ziphius cavirostris* and *Mesoplodon carlhubbsi*, respectively—Heyning and Mead 1996). In addition, a wealth of circumstantial yet substantial and consistent evidence (anatomical,

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ecological, and anecdotal) strongly supports the contention that other toothed whale and dolphin species use suction to capture and ingest prey (Werth 2000b, 2004). Suction feeding, as the term is used here, is defined as creation of negative (less than ambient) pressure via oral or pharyngeal expansion or both to capture, ingest, and transport discrete prey items. As in other vertebrate suction feeders, waterborne prey are drawn into an enlarged space, in this case from rapid retraction and depression of the hemicylindrical, pistonlike tongue. Prey items are separated before swallowing from engulfed water, which is momentarily accommodated by the expandable, elastic pharynx and (in many cases) by external throat grooves before expulsion back through the mouth, via gape closure and lingual elevation, in this bidirectional flow system.

Suction feeding is the dominant prey-capture method for aquatic vertebrates and arguably the most efficient. As a solution to biomechanical problems posed by feeding in a liquid medium, it enjoys nearly universal representation. Although it is the primitive mode for several vertebrate classes (Lauder 1985), suction feeding frequently has been adopted as an independent derivation. Among other marine mammals, suction feeding has been documented in the walrus (*Odobenus rosmarus*—Fay 1981; Gordon 1984; Kastelein and Mosterd 1989; Kastelein et al. 1994) and gray whale (*Eschrichtius robustus* [not for individual prey]—Nerini 1984; Oliver and Slattery 1985), and is suspected in sea lions as well as Ross (*Ommatophoca rossii*), bearded (*Erignathus barbatus*), and elephant (*Mirounga*) seals (Bryden and Felts 1974; King 1964, 1983).

Studies using experiments, simulations, and biomechanical models (Werth 1992, 2000b) indicate that odontocete cranial and oral shape is a critical determinant of water flow and hence of suction-feeding performance. These same studies reveal a correlation in Odontoceti between suction feeding (documented or inferred from prey type and condition in stomach contents, foraging behavior, and musculoskeletal anatomy) and a cranial profile involving a short, blunt head and round mouth opening. The current study aimed to quantify such morphometric features to ascertain their prevalence in odontocetes, using osteological specimens in museum collections as well as necropsy specimens with soft tissues. An important goal of this study was to compare both tooth counts and cranial-mandibular profiles in museum versus necropsy specimens.

MATERIALS AND METHODS

Mandibular variation.—Thirty-four species representing all extant odontocete families were surveyed using osteological specimens from the Museum of Comparative Zoology (MCZ), Harvard University (Cambridge, Massachusetts), and United States National Museum of Natural History (NMNH), Smithsonian Institution (Washington, D.C.). Although many morphometric measurements were recorded, the most basic measure of head shape was found to be a simple ratio of jaw width to length (more reliable and less variable than skull width to length). Measurements of the mandible were used to calculate an index of bluntness, using the distance from the cranial tip of the mandibular symphysis to the caudal edge of the mandibular condyle as jaw length (measured directly along the jaw, not along a median axis to a point

directly between the 2 condyles; Fig. 1), and taking the distance between the 2 condylar edges (only from fused dentaries) as jaw width. In every odontocete the lower jaw is longer than it is wide, so that width divided by length provides a dimensionless number <1 ; this is termed the mandibular bluntness index (MBI). The more blunt the jaws, the higher the MBI. The survey includes only species for which at least 3 intact osteological museum specimens in proper condition (e.g., fused dentaries and no missing rami) could be found. Raw measurements were normalized by arcsine transfer to calculate mean MBI (and *SE*) for each species surveyed. Rather than computing the MBI of a species from normalized length and width measurements of every specimen, a raw MBI was produced for each jaw. Ratios within a species were normalized and the mean was calculated.

During the course of routine necropsy procedures at the New England Aquarium (Boston, Massachusetts), similar lower jaw measurements were taken, including attached soft tissues, of several recovered species also measured in the museum survey of osteological specimens, including *Delphinus delphis* (short-beaked common dolphin), *G. melas*, *Grampus griseus* (grampus or Risso's dolphin), *K. breviceps*, *Lagenorhynchus acutus* (Atlantic white-sided dolphin), *Lagenorhynchus albirostris* (white-beaked dolphin), *O. orca*, *P. phocoena*, *Physeter catodon* (sperm whale), *Stenella attenuata* (pantropical spotted dolphin), *Stenella coeruleoalba* (striped dolphin), and *Tursiops truncatus* (bottlenose dolphin). Measurements of *D. leucas* (beluga) were taken during necropsy procedures with the North Slope Borough Department of Wildlife Management in Barrow, Alaska. No research was performed on live animals.

Dental variation.—In addition to cranial bluntness, Norris and Møhl (1983) described the trend toward dental reduction in Odontoceti (see also Reilly and Shane 1986). Various ways of quantifying “toothiness” of a species were attempted, using measurements of toothrow length, tooth height, and mean spacing between teeth, along with data on mandibular length. However, simple tooth counts provided the most accessible and informative means to examine this trend. Counts were taken from each museum and necropsy specimen, recorded overall and from each quadrant (toothrow). These were analyzed to survey variation, for a given species, within museum specimens and within necropsy specimens, and particularly to note variability between museum and necropsy specimens. Dental data also were compared with published accounts of tooth number (Minasian et al. 1984; Miyazaki 2002; Ridgway and Harrison 1989, 1994, 1999).

RESULTS

Mandibular variation.—In the absence of existing terminology the word amblygnathy (Greek *amblos*, blunt, dull; *gnathos*, jaw) was coined to denote the condition of shortened, rounded jaws and rostra. An alternative existing term, brachycephaly (“short head”), normally refers to an abnormality due to pathological skull development. This study shows that many amblygnathous odontocete species exist. Fig. 1 displays the MBI (from normalized data) for all species for which measurements were obtained from at least 3 museum specimens. Sample sizes were not high (10–18 jaws for most species surveyed), yet there is little variation in the MBI within any species. Although jaw lengths and widths vary with age, sex, and other characters (e.g., general body size, which may vary by geographic distribution), MBI ratios hold remarkably constant for each species. *K. simus* has the bluntest jaws (MBI = 0.958; $n = 6$, $SD = 0.025$), and *K. breviceps* is 2nd

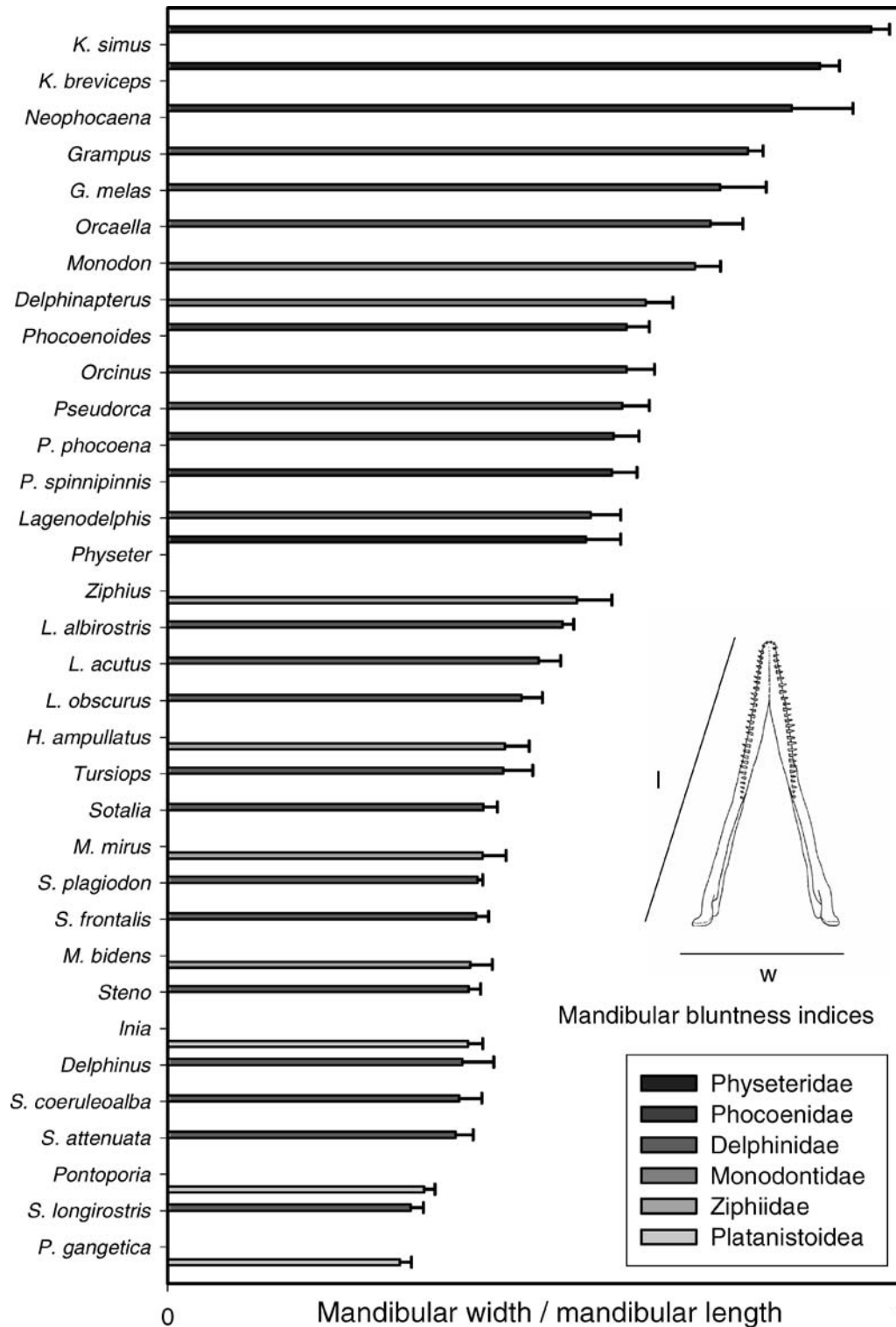


FIG. 1.—Mandibular bluntness index (MBI), a simple dimensionless ratio (scale = 0–1) of mandibular width (*w*) to length (*l*), shown for the 34 species included in this morphometric analysis (error bars = 1 *SD*).

(MBI = 0.888, *n* = 7, *SD* = 0.027). The finless porpoise (*Neophocaena phocaenoides*; MBI = 0.850, *n* = 8, *SD* = 0.048) and Risso’s dolphin (MBI = 0.790, *n* = 11, *SD* = 0.021) also demonstrate considerable amblygnathy. Species surveyed with the narrowest jaws are Ganges susu (*Platanista gangetica*; MBI = 0.316, *n* = 6, *SD* = 0.016), long-snouted

spinner dolphin (*Stenella longirostris*; MBI = 0.331, *n* = 14, *SD* = 0.017), and franciscana (*Pontoporia blainvillei*; MBI = 0.349, *n* = 9, *SD* = 0.015). Considerable diversity exists in all families, especially Delphinidae (with some of the most and least amblygnathous species; e.g., *Grampus* and *S. longirostris*), except Monodontidae, of which both species are

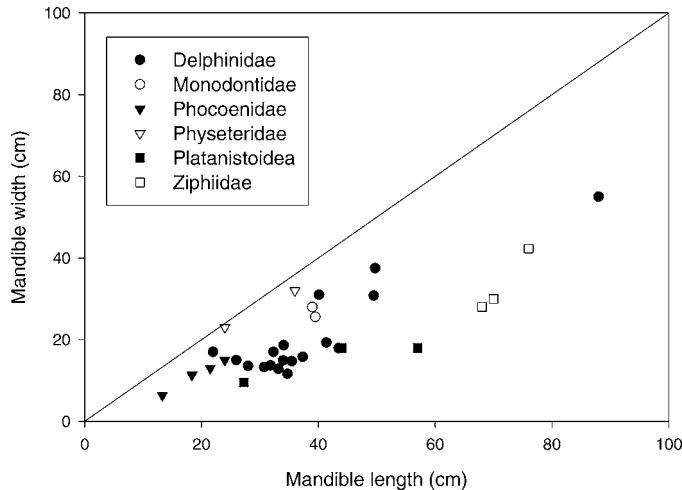


FIG. 2.—Plot of mandibular width versus length for all odontocetes (designated by family or superfamily) surveyed for this study. The central line with slope of 1 is not a regression line but is shown for evaluation of amblygnathy (“blunt-headedness”); it represents the condition in which lower jaw width equals length (i.e., mandibular bluntness index = 1.00).

blunt-jawed. Consideration of age and other life history data available for osteological specimens reveals no allometric progression with growth. Determination of various alternative indices within species was attempted, using museum collection data on sex, age, and distribution, but did not yield significantly different results. Fig. 2 shows a plot of mean mandibular length versus mean width for all odontocetes for which measurements were obtained, with species arranged by family. A line with slope = 1 represents the hypothetical condition of lower jaws with length equal to width (e.g., MBI = 1.00). Species closer to this 1:1 line have blunter jaws, those farther away narrower. Placement along the x and y axes obviously pertains more to size than shape. However, there is a solid overall correlation between jaw width and length (all families; $r^2 = 0.832$). Porpoises (Phocoenidae) display such a significant linear relationship ($r^2 = 0.963$), but other families (especially Delphinidae) show greater diversity.

Dental variation.—Overall, as the MBI increases, tooth number decreases; that is, as jaws get blunter, they have fewer teeth (Fig. 3). Both museum and necropsy specimens in intact, unharmed condition display great variability in dental tallies (Fig. 4; showing mean number of erupted adult male teeth with range of high and low tooth counts, not counting teeth that have fallen out or broken pre- or postmortem). In general, species with fewer teeth (or more amblygnathous jaws = higher MBI) display less variation in tooth counts. However, all phocoenids surveyed show extensive variation in dental number. Some delphinids (particularly those with few teeth; e.g., *Grampus* and *Orcinus*) show little variation in tooth count; other delphinids (e.g., *Delphinus*) have major variation, with a span of almost 70 teeth from low to high count. There is also significant variation within some genera, especially *Stenella*, because *S. attenuata* and *S. plagiodon* (136–148 teeth) show far less dental variability than *S. coeruleoalba* (176–216 teeth)

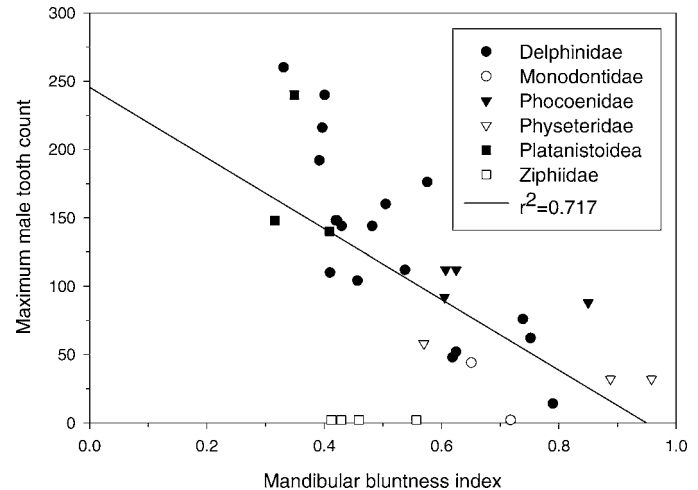


FIG. 3.—Total maximum male tooth number plotted against calculated mandibular bluntness index for all odontocetes (designated by family or superfamily) surveyed. Tooth count numbers include erupted teeth in all jaws, derived from Miyazaki (2002) and Ridgway and Harrison (1989, 1994, 1999). Regression analysis does not include ziphiid specimens surveyed.

and *S. longirostris* (184–260 teeth). Again, such counts were only taken from unharmed male specimens of adult body size (or with presence of other data confirming adult status). Much of this variation was apparent solely from inspection of museum osteological specimens, although it was also observed in whole (fresh or frozen) necropsy specimens. However, frequent disparity between necropsy and museum specimens was noted (not specifically depicted in Fig. 4, although included in the overall range of variation), with museum specimens routinely yielding greater tooth counts, in some cases substantially so (approximately 14% discrepancy), especially in long, narrow-jawed (i.e., nonamblygnathous) species with many teeth.

DISCUSSION

Mandibular variation.—Results of this analysis indicate that many amblygnathous odontocete species exist (Figs. 1 and 2), supporting the hypothesis of Norris and Møhl (1983) of an evolutionary trend toward mandibular bluntness. Although some amblygnathous odontocetes are commonly displayed in captivity (e.g., the beluga), they generally remain less well known than long-snouted species such as *T. truncatus* or *D. delphis*, which for the general public and even some mammalogists remain the embodiment of odontocetes, as snapping, grasping, long-snouted raptorial predators similar to gars, gavials, and diving birds.

Figure 2 makes apparent several points. First, there is clear variation in head shape throughout suborder Odontoceti as depicted by these basic measurements. Body size notwithstanding, several toothed whales and dolphins have narrow jaws; others do not. Two physeterids of the genus *Kogia* lie almost on the line with a slope of unity. Second, although certain families tend to cluster at a given distance away from this line, there is, as

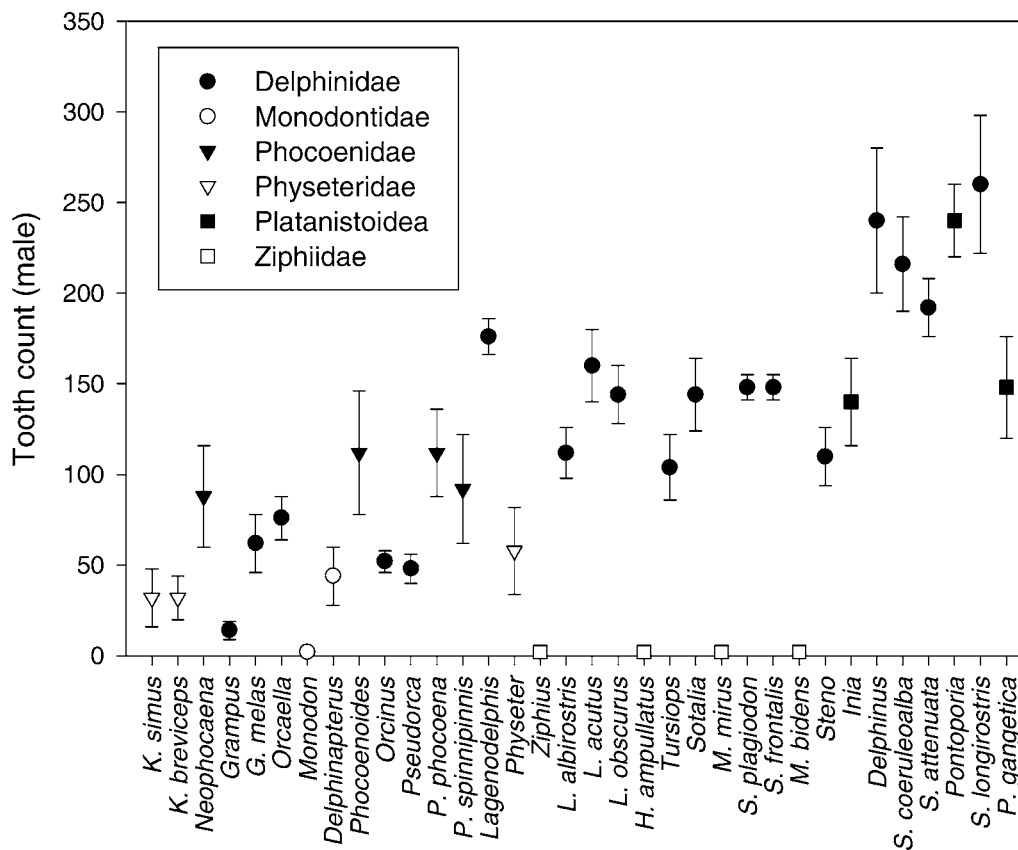


FIG. 4.—Variation in erupted adult male tooth count (all data from this study), showing mean tooth number and minimum and maximum tooth count, from both necropsy and cleaned osteological specimens, for species arranged (left to right) by mandibular bluntness index. Note that some species display great variation in dentition. Tooth counts are typically higher in museum specimens, likely because of counting of numerous conspicuous unerupted teeth.

previously noted, diversity within most families. Ziphiids (beaked whales) and platanistoids (river dolphins, as a superfamily) lie far from the line, but delphinids (oceanic dolphins) are scattered at varying distances from it. A group of small delphinids with jaws 20–40 cm long (of genera *Lagenorhynchus* and *Stenella*) displays tremendous diversity (see also Perrin 1975). These species show almost no diversity in jaw width (about 16 cm in adults), but as jaw length varies so too bluntness changes, creating a spread of delphinids (of close body size, not obvious from Fig. 2) nearly perpendicular to the line of equality, thus indicating almost maximal variation. Such variation in closely related species of similar body size may be due to character displacement from a rapid evolutionary radiation. It would be interesting to note what amount of ecological diversity (in feeding method), if any, parallels this morphological diversity, and if it points to the causes and consequences of divergence in competitive exclusion. Delphinids may have divided food resources and habitats, evolving distinct foraging strategies with concomitant feeding ecology and morphology.

A 3rd point to be gained from the varying extents of diversity between families seen in Fig. 2 is that an amblygnathous profile consistent with suction feeding arose multiple times (Fig. 5). Many families have amblygnathous species. This correlates with other anatomical findings (hyoid size, shape, and flexibility; relative cross-sectional area and

proportional weight of lingual and gular muscles, etc.—Werth 1992, 2000b) showing there is no single suction-feeding family; varying extents of amblygnathy within families support the claim of multiple independent origins of suction feeding in this suborder. Dolphins and porpoises possess a variety of short or long, projecting rostra. The only taxon not presumed to include suction feeders is the superfamily Platanistoidea, which consists of exclusively long-snouted snappers, demonstrating ecological and morphological uniformity (Fig. 2). However, the monophyly of “Platanistoidea,” including extant families Platanistidae, Iniidae, Lipotidae, and Pontoporiidae, is far from certain (Geisler and Sanders 2003; Rice 1998); this may represent a poly- or paraphyletic assemblage of relict dolphin lineages that convergently evolved morphological and ecological specializations in adapting to a riverine habitat (Cassens et al. 2000; De Muizon 1994; Messenger and McGuire 1998). Regardless of the taxonomic status of river dolphins as 1 or several lineages, the point remains that amblygnathy (and hence suction feeding), now found in most odontocete families, is not a plesiomorphic trait conserved from a common ancestor in most families and lost in river dolphins, but rather an apomorphy that arose independently.

It must be emphasized that suction feeding can be used to varying degrees depending on prey type, size, and elusiveness. Although some odontocetes (e.g., beaked whales and narwhal

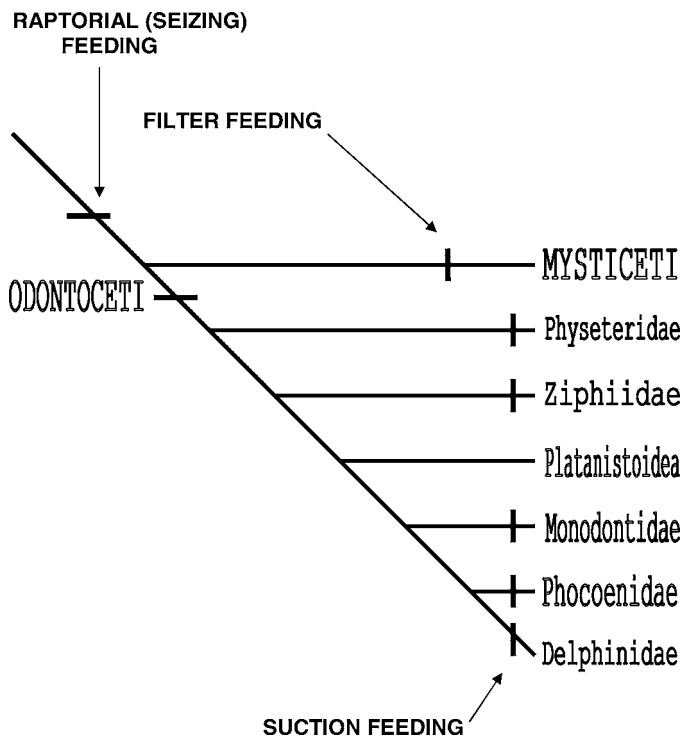


FIG. 5.—Phylogenetic tree (based on Cassens et al. 2000) indicating multiple origin of suction feeding (rightmost vertical crossbar) in extant odontocete clades. See text for discussion of status of Platanistoidea.

[*Monodon*]) may be obligate suction feeders, other species are likely to employ suction feeding among a variety of foraging methods. Likewise morphological and behavioral specializations for suction feeding probably have evolved to varying degrees in different taxa. However, because all odontocetes use the same anatomical mechanism (rapid, pistonlike hyolingual retraction to create a region of negative pressure in the oral cavity or oropharynx into which water and prey are drawn), it is less expedient to describe different degrees of suction-feeding development than different degrees of morphometric development, as by the dental and mandibular analysis presented here.

Creation of another index that so simply and usefully describes the shape of a species' head and jaws was attempted, such as a ratio of mandibular height to length (to show vertical bluntness), or of widths between most anterior versus posteriormost teeth, but the MBI seems to be the best index. Mandibular values were used instead of rostral–cranial measurements for several reasons, including availability and ease of measurement (smaller size and clear landmarks) and consistency with and comparison to earlier measurements of dissection specimens. Unlike the occasional separation of left and right dentaries already alluded to, upper jaws are always well fused but their tips may be broken or missing. Specimens in museum collections are occasionally represented solely by intact lower jaws. Finally, although diversity in mandibular osteology ought mainly to represent modifications for feeding, the entire cranial complex or a portion thereof is much more likely to reflect myriad functional influences.

Dental variation.—The correlation of blunt jaws with reduced dentition generally holds for all odontocete families (shown independently in Fig. 3). Families form small phylogenetic or functional clusters except for Delphinidae which, with the greatest variation in both variables, shows a division into 2 major groups which may be called globicephalines (wider jaws and fewer teeth) and delphinines (narrower jaws and more teeth), a division that parallels Nishiwaki's (1963) taxonomic scheme. Mandibular and dental data are consistent with division of Delphinidae into these 2 subfamilies, and possibly a split of Delphininae into further subgroupings of long-snouted genera (*Delphinus*, *Sotalia*, *Sousa*, *Stenella*, *Steno*, and *Tursiops*) and others with shorter, nonprojecting rostra and shorter beaks (*Cephalorhynchus*, *Lagenodelphis*, *Lagenorhynchus*, and *Lissodelphis*). Genera included in the Globicephalinae include *Feresa*, *Globicephala*, *Grampus*, *Orcaella*, *Orcinus*, *Peponocephala*, and *Pseudorca*. There is a further correlation between dentition and body size. Three families of large odontocetes (Physeteridae [sensu lato, not including *Kogia* in separate Kogiidae], Ziphiidae, and Monodontidae, all at the bottom of graph in Fig. 3) have few teeth, whereas smaller dolphins and porpoises have many more teeth. Dental data (including erupted teeth in all jaws, upper and lower, both sides, in males only) in Fig. 3 are not derived from specimens used in this study, because some teeth were missing, but instead are taken from Minasian et al. (1984), Ridgway and Harrison (1989, 1994, 1999), and Miyazaki (2002). Published tooth counts may include unerupted teeth (often a significant proportion of the total), as in the sperm whale (*Physeter*), in which maxillary teeth almost never erupt.

The claim that blunter jaws correlate with reduced dentition may seem axiomatic or circular, yet this is not the case. Shorter jaws obviously have fewer teeth simply by virtue of limited space, yet the index of amblygnathy (Fig. 3) takes into account not merely mandibular length but width. As jaws become blunter, width may increase while length remains constant. Rather than a simple physical or ontogenetic connection between jaws and dentition, there is a strong association in that both reflect modifications for feeding. Amblygnathy improves water flow for suction feeding, because the optimal form for waterborne prey ingestion involves a more circular, terminal oral aperture, as occurs with a short, blunt head, instead of an open, notched ("Pac-man") gape (Werth 2000b). This in turn relieves a species from the need to possess elaborate dentition for use in prey grasping. Note that presence of any teeth whatsoever in highly amblygnathous species may represent a wholly different use. Once freed from grasping function, teeth could have been maintained by strong selective pressures as a secondary sexual character for intraspecific fighting or display (Heyning 1984; Kato 1984; Kleinberg et al. 1969; McCann 1974; Werth 2000b). If female instead of male dentition were used in Fig. 3 several species would show no teeth at all; beaked whales typically have male mandibular tusks but are otherwise edentulous. The opposite scenario, of use of teeth as a secondary sexual feature preceding and leading to adoption of suction feeding, is less plausible. Regarding a possible correlation between body size and

dentition, the simplest inference is that larger toothed whales and dolphins generally have fewer teeth because they are suction feeders.

Interpretation of morphometric data.—Two cautions must be appended. The 1st, more obvious reservation is that amblygnathy may not always be associated with suction feeding, as is taken for granted here. The foregoing analysis is intended to demonstrate morphological variation and explain it in terms of feeding. However, there may be feasible explanations for the evolution of blunt heads unrelated to feeding. Slender heads and narrow jaws may have been retained to streamline fast-swimming taxa; this feature may have been lost in slower species with no evolutionary pressure for or functional advantage of a streamlined contour. Conversely, amblygnathy might be adaptive for opening breathing holes in ice in polar species (*Monodon* and *Delphinapterus*), or for ramming predators or other combatants (Carrier et al. 2002). Bryden (1988) suggested that blunt heads may function like bulbous ship bows to reduce drag and improve speed. The possibility that bluntness reflects adaptation for prey stunning also must not be overlooked. However, abundant evidence exists to support the contention that blunt heads and small, round mouth openings evolved in relation to prey capture, particularly suction feeding (Werth 1992). Amblygnathy correlates with other anatomical traits (e.g., throat grooves, enlarged hyoid, reduced dentition, and cervical fusion), ecological (e.g., teuthophagy), and behavioral traits (e.g., intact, unharmed prey) associated with suction feeding (Werth 1992, 2000b). In light of this consilience, especially correlation with nonstructural characters such as prey condition, suction feeding seems a highly likely explanation. The sole exception to this association is the blunt-jawed killer whale (*Orcinus*; MBI = 0.625). However, preliminary inspection of videotaped feeding (Werth 1992) indicates that juvenile killer whales can generate impressive suction. It is not known whether adults retain this ability, but *Orcinus* may capture small prey using suction despite its toothy jaws and wolflike reputation. Still, amblygnathy in this species is more likely due to its propensity to swallow whole or tear pieces from large prey.

The 2nd caveat is subtler. It must be stressed that the view of amblygnathy presented here does not take into account soft tissues. The values of osteological indices such as the MBI are manifold: measurements are simple, quick, and can be taken or repeated at any time. Museum specimens are generally plentiful and geographically widespread, making access to data easy. Fresh or preserved odontocete specimens (whole or partial) are rarer, and tooth counts vary significantly between dissection and osteological material (Fig. 4) because, for unknown reasons, some unerupted teeth remain covered with gingiva even in adults, leading to higher museum tooth counts. Thus dentition of prepared skulls is hardly representative of live odontocetes. Tooth counts from museum collections seem generally to be inflated relative to necropsy tooth counts; soft tissue study reveals a different story (Fig. 4). Morphologists must interpret osteological data with caution. The beluga presents a good argument for this point. Although *Delphinapterus* (a monodontid) has a moderately high MBI (0.651) it

possesses in reality a much blunter head because of its pronounced, deformable melon and its highly mobile lips, which when pursed transform the notched gape into a round mouth opening (Brodie 1989). Although its skull appears dolphinlike, in life this species looks nothing like a long-snouted dolphin. *Delphinapterus* undergoes developmental changes relating to amblygnathy, as its cranial profile changes progressively and markedly from neonate to juvenile to adult (Brodie 1989). The extent to which this modification results from soft tissue growth is unknown, although independence of MBI calculations from age (for this and all other species) shows that the melon, lips, and other soft tissues have a profound effect on head shape.

Beaked whales serve as another warning against sole reliance on osteological data. Calculation of MBI suggests ziphiids are not amblygnathous, yet the rostral beak is often dwarfed by a huge forehead (as in *Hyperoodon*) overlying the upper jaw. Even ziphiids with pronounced snouts have significantly restricted lateral gape due to large gums and extensive lower lips or large, flat teeth (males only) that block much of the sides of the mouth, or encircle and nearly occlude the jaws in the strap-toothed whale (*Mesoplodon layardii*). Such structures have been envisioned as a trough for food transport or as guard rails to contain unwilling prey on the path to the throat (Baker 1972; Heyning and Mead 1996; Tomilin 1954). Still, another line of reasoning may explain ziphiids' long heads and apparent suction-feeding prowess. It could be argued that amblygnathy is not wholly relevant to a species' suction-feeding capabilities, for, again, the overriding concern is the shape of the opening through which prey are drawn. As jaw length increases a greater volume of water can be sucked into the oral space. Many fish with extremely long heads and narrow jaws are nonetheless noted for impressive suction capacities (Bergert and Wainwright 1997), especially syngnathid fishes (e.g., pipefish and sea horses). Cranial shape is mainly important in creation of a round mouth opening. By itself a blunt jaw will not necessarily improve suction generation except inasmuch as it reduces lateral water influx. The real relevance of amblygnathy in odontocetes is that by shortening the rostra and jaws it correlates with smaller mouths and in fact serves to create a better suction opening.

Oral openings and the special case of the sperm whale.—That this opening rather than jaw and head shape is a better index of suction-feeding performance is illustrated by the sperm whale (*Physeter*), whose suction feeding (Werth 2004) is at odds with its unlikely morphology. The MBI of *Physeter* (0.57) is far below those of amblygnathous dwarf and pygmy sperm whales, *K. simus* (0.958) and *K. breviceps* (0.888), known suction feeders (Bloodworth and Marshall 2005). However, numerous anatomical, behavioral, and ecological findings (including presence of intact, unharmed, and even live prey in stomach contents—Clarke 1955) are consistent with suction prey ingestion in sperm whales (Werth, 2004). How can elongate jaws of *Physeter* be reconciled with its suspected suction feeding? This exception stems from the unique oral anatomy of physeterids. *Kogia* species are often misidentified as sharks (Caldwell and Caldwell 1989), not only because of their size,

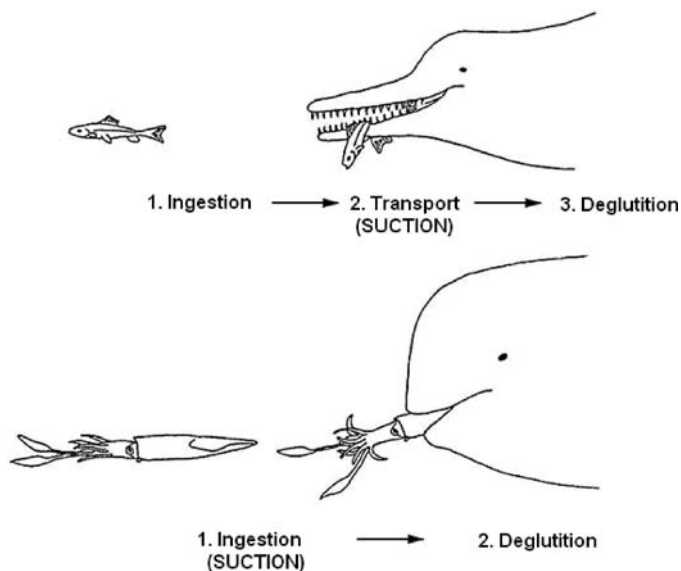


FIG. 6.—Major stages in the evolution of odontocete suction feeding and cranial shape, with comparison of prey capture in the Amazon river dolphin or boto (*Inia geoffrensis*, above), in which prey are caught and grasped by elaborate dentition of long jaws, then transported via suction to the posterior of the oral cavity for swallowing, and a pilot whale (*Globicephala*, below), an amblygnathous odontocete with blunt head, short jaws, and reduced dentition, which sucks prey directly into the oral cavity (Werth 2000a), eliminating the transport step.

prominent dorsal fin, sharp teeth, and white bracket-shaped gill-like coloration, but because of their short, underslung jaws. *Physeter*'s mandible is long and narrow, yet the high incidence of healthy sperm whales with congenitally deformed or broken and rehealed mandibles and worn or barnacle-ridden teeth suggest its jaws and dentition often play little or no role in feeding (Clarke et al. 1988; Slijper 1962). *Physeter* has no oral cavity delimited by lips or cheeks; it cannot create a round mouth opening without a proper mouth. Analysis of the sperm whale's oral, gular, and hyolingual anatomy (Werth 2004) shows that the oropharyngeal isthmus (between palatoglossal folds or fauces) presents a round opening analogous to the proper oral orifice. The short, unusually positioned tongue (caudal to toothrows) and extremely large, flexible hyoid are situated so as to generate sufficient gular suction pressures by lingual retraction and depression to suck prey and water through this opening rather than into a true oral cavity. *Physeter* represents the extreme condition of open lateral gape (missing lips and cheeks), but it is possible that other odontocetes also suck prey directly into the oropharynx. In some species with erupted dentition (especially ziphiids), teeth lie partially or wholly outside the oral cavity and can play no role in seizing or holding prey (Kleinenberg et al. 1969). This is significant because all other suction-feeding vertebrates suck prey into the oral cavity rather than into the oropharynx. Unlike cetaceans, other suction feeders did not evolve from long-jawed terrestrial ancestors that secondarily reverted to an aquatic existence.

The evolution of odontocete head and jaw shape.—A substantial portion of Norris and Møhl's (1983) evidence for

prey stunning comprised qualitative osteological data demonstrating that many Recent odontocetes possess blunt heads and short jaws and that the fossil record reveals clear evolutionary trends toward these conditions. Although the hypothesis of acoustic prey debilitation stands as an alternative to suction feeding, it does not rule out the latter; it is conceivable that both phenomena occur together, although examination of some data (Mackay and Pegg 1988; Zagaeski 1987) casts doubt on the prey-stunning claim. Norris and Møhl (1983) also suggested progressive dental reduction, in some cases leading to loss of functional teeth and to reduction in size and complexity as well as in number; examination of data presented here supports this claim. Although these findings indirectly support prey stunning by demonstrating that long pincer jaws with numerous teeth are not necessary for prey capture in many extant odontocetes, examination of the data argues strongly that not only jaws and dentition have changed but also skull size and shape. Norris and Møhl (1983) did not attempt to explain this critical discovery. It might be asserted that cranial modifications reflect the evolution of the melon, nasal sacs, and diverticula, and other structures presumed to play a role in odontocete sound generation and transmission, but an alternative explanation is that these changes, by altering gape profile, improve water flow patterns (Werth 2000b) and thus suction-generation capability. Stunned prey could simply be overtaken and swallowed, but suction ingestion has been documented in numerous odontocetes without need for prey stunning.

The evolution of odontocete suction feeding.—Norris and Møhl (1983) included mention of fossil taxa, whereas this study quantified diversity of extant taxa. The paleontological record shows that the presumed common ancestor of Odontoceti, a dorudontine basilosaurid archaeocete, did not possess a blunt head and small, round mouth, but instead had a long, notched gape filled with large, multicusped teeth (Barnes and Mitchell 1978; Uhen 2002, 2004). It is clear therefore that blunt heads and jaws were not inherited (and later lost in certain taxa) but rather arose within the suborder, apparently numerous times (Fig. 5). Archaic representatives of every extant odontocete family possessed long jaws and slender rostra (Kellogg 1928) unsuited to suction feeding. Also, most extremely long-snouted odontocetes appeared early in the fossil record and are now extinct; in fact, all extinct odontocete families had representatives with blunt rostra, except perhaps for the Oligocene Agorophiidae. It may be more parsimonious to assume amblygnathy and suction feeding evolved once within Odontoceti, yet examination of paleontological data strongly indicates that amblygnathy, and hence suction feeding, evolved in each family.

Experimental evidence (Werth 2000b) shows that gars and other long-snouted fishes use suction to transport prey from the jaws to the pharynx, and I suggest that odontocete suction feeding arose from this initial step (Fig. 6). Loss of elongate jaws and rostra, coincident with reduction in dental number, size, and complexity in several independent lineages—in some cases functional teeth are wholly absent—strongly suggests that certain modern toothed whales and dolphins eliminated the transport step and now use suction to ingest prey into the

shortened mouth or directly through the palatoglossal arch into the oropharynx. An alternative view, that odontocete suction feeding evolved from retention of anatomical and behavioral features associated with suckling (e.g., marginal lingual papillae—Kastelein and Dubbeldam 1990), is weakened by the fact that no cetacean suckles like a typical mammal because milk is forcibly ejected into the infant's mouth and perhaps pharynx. Structures associated with adult suction feeding (enlarged hyoids, gular grooves, etc.) bear no relation to suckling (Werth 2000b).

Kinematic study of suction feeding in captive *G. melas* (Werth 2000a) confirms that this species employs lateral suction to ingest prey items at the side of the head, especially when both whale and food are at a pool wall. Although this behavior was less frequent than instances in which items were sucked from a spot anterior to the mouth (whales commonly turned and rolled so as to position floating or sinking items directly anterior to the mouth), videotaped sequences demonstrate the ability of this species to suck items into the side of the mouth. (Use of suction is unequivocal because nonliving items moved rapidly [from a mean distance of 14.1 cm] into mouths of stationary whales.) As in other amblygnathous odontocetes, notably *Delphinapterus*, pilot whales have large buccinator and orbicularis oris muscles enabling them to limit gape on one side of the mouth and produce a circular opening on the other (Werth 2000b). Belugas have also been observed to “pucker” or purse their lips to reduce or round the mouth opening (Brodie 1989). Although these findings preclude concerns that odontocetes make poor candidates for suction feeding based on their “notched” gape profile, they also suggest that odontocetes may take active measures to alter the mouth opening in ways that cannot be appreciated from studies on nonliving specimens. Additional data must be obtained, especially from species not included in this study, to render the analysis more complete. Similar measurements from fossil material would prove useful in evaluating the evolutionary history of odontocete crania, jaws, and dentition with respect to the evolution of feeding methods (e.g., Adam and Berta 2002).

ACKNOWLEDGMENTS

Pivotal research support was provided by staff of the Mammal Department, MCZ (J. Chupasko, L. Code, M. Rutzmoser, and J. Winchell), and by the Marine Mammal Department, NMNH (J. Mead and C. Potter). Additional assistance and access to necropsy specimens came from the New England Aquarium's Curatorial Laboratory (G. Early, B. Cooper, and J. Boggs) and the North Slope Borough (Alaska) Department of Wildlife Management (T. Albert, C. Brower, J. C. George, M. Philo, and R. Suydam). Two anonymous reviewers provided valuable suggestions that greatly improved the content and presentation of this paper, as did discussions with N. Pyenson, P. Adam, B. Beatty, L. Barnes, and M. Uhen.

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Submitted 18 August 2005. Accepted 26 October 2005.

Associate Editor was Eric A. Rickart.