

Adaptations of the Cetacean Hyolingual Apparatus for Aquatic Feeding and Thermoregulation

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ABSTRACT

Foraging methods vary considerably among semiaquatic and fully aquatic mammals. Semiaquatic animals often find food in water yet consume it on land, but as truly obligate aquatic mammals, cetaceans (whales, dolphins, and porpoises) must acquire and ingest food underwater. It is hypothesized that differences in foraging methods are reflected in cetacean hyolingual apparatus anatomy. This study compares the musculoskeletal anatomy of the hyolingual apparatus in 91 cetacean specimens, including 8 mysticetes (baleen whales) in two species and 91 odontocetes (toothed whales) in 11 species. Results reveal specific adaptations for aquatic life. Intrinsic fibers are sparser and extrinsic musculature comprises a significantly greater proportion of the cetacean tongue relative to terrestrial mammals and other aquatic mammals such as pinnipeds and sirenians. Relative sizes and connections of cetacean tongue muscles to the hyoid apparatus relate to differences in feeding methods used by cetaceans, specifically filtering, suction, and raptorial prehension. In odontocetes and eschrichtiids (gray whales), increased tongue musculature and enlarged hyoids allow grasping and/or lingual depression to generate intraoral suction for prey ingestion. In balaenopterids (rorqual whales), loose and flaccid tongues enable great distention of the oral cavity for prey engulfing. In balaenids (right and bowhead whales), large but stiffer tongues direct intraoral water flow for continuous filtration feeding. Balaenid and eschrichtiid (and possibly balaenopterid) mysticete tongues possess vascular retial adaptations for thermoregulation and large amounts of submucosal adipose tissue for nutritional storage. All cetacean tongues also function in prey transport and swallowing. These hyolingual musculoskeletal differences are unique cetacean anatomical adaptations for foraging entirely in an aquatic environment. *Anat Rec* 290:546–568, 2007. © 2007 Wiley-Liss, Inc.

Key words: Cetacea; Mysticeti; Odontoceti; tongue; hyoid; anatomy; histology; feeding; swallowing

Although tetrapod vertebrates are primarily terrestrial, several lineages have independently and secondarily reverted to a partially or entirely aquatic existence in freshwater and marine habitats, with obvious ecological, behavioral, and morphological consequences. Numerous mammals of various orders inhabit or regularly visit freshwater habitats, but with few exceptions (e.g., the duck-billed platypus, *Ornithorhynchus anatinus*), and aside from rare differences in diet and foraging behavior, feeding in aquatic monotremes, marsupials, insectivores, rodents, and ungulates does not differ notably from that of their terrestrial relatives. Such animals may find

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food in water but consume it primarily on land or above the water's surface. The same can be said for marine fissiped carnivorans, for even the truly marine sea otter and polar bear do not normally ingest prey underwater. Aquatic mammals bearing the most significant hyolingual adaptations are those that feed exclusively in, and generally under, water, including sirenians (manatees and dugong) and pinnipeds (seals, sea lions, and walrus). Much remarkable morphological convergence exists, both between these taxa and also with extant and extinct reptiles and birds adapted to aquatic life. However, no mammals demonstrate the level of separation from land seen in Cetacea, nor do any exhibit the extreme range of anatomical and physiological specialization resulting from tens of millions of years of adaptation to life in water. As truly obligate aquatic mammals, cetaceans (whales, dolphins, and porpoises) exhibit highly modified foraging methods and feeding mechanisms.

Other sources (see Werth, 2000b for review) consider aquatic mammal feeding with regard to general and specific (e.g., cranial, dental, pharyngeal) anatomy. This study focuses mainly on anatomy of the tongue, and to a lesser extent the hyoid, of cetaceans (mainly balaenid mysticetes relative to delphinid, phocoenid, and physeterid odontocetes). Following general reviews of mammalian tongue anatomy (especially the contentious dichotomy between intrinsic and extrinsic lingual musculature, which bears heavily on cetacean tongue function) and aquatic feeding, special features of cetacean hyolingual apparatus will be described and discussed. Supra- and infrahyoid myology and hyoid osteology are omitted here, as much work has been published previously, especially in Odontoceti (Table 1; see Reidenberg and Laitman, 1994, for review).

ANCESTRAL MAMMALIAN HYOLINGUAL ANATOMY

The hyolingual apparatus is specialized in many tetrapod vertebrates, especially amphibians and reptiles that capture prey by means of lingual projection. The simple crescent-shaped primary tongue of gnathostome fishes is a mere elevation of the oral floor supported by basihyal elements. It may be covered with tooth-like denticles that aid in grasping prey, but is not needed for oral transport, as items are supported and carried by buoyant water. "Higher" amphibians have a glandular field (tuberculum impar) on a longer, more mobile tongue swollen with hypobranchial musculature. In amniotes, especially mammals although less so in birds, lateral lingual swellings fill with hypobranchial musculature and there is notable intrinsic lingual musculature (fibers originating and inserting solely within the tongue body). Tongues of most mammals, excepting some cetaceans, can be protruded despite attachment to the oral floor. In most mammals, the tongue is a small muscular organ that functions in oral transport, manipulation, processing, and swallowing in addition to mechanical and gustatory sensation. In some mammals, the tongue functions in food acquisition and ingestion, thermoregulation, grooming, and vocalization.

The mammalian tongue is a muscular hydrostat, a constant-volume structure (Kier and Smith, 1985; Smith and Kier, 1989) with complex musculature—seven or

eight muscles, each with extensive, overlapping terminations in the tongue body—often allowing for dramatic shape changes. Each side of the rat tongue body comprises over 3,000 motor units (Sokoloff, 2000, 2004), providing fine neuromotor control with subsequently great diversity of response. For 70 years (Abd-El Malek, 1938), lingual muscles have been categorized according to location (e.g., intrinsic vs. extrinsic) or presumed action (e.g., protrusor vs. retrusor). Although this system forms the basis for modern studies of mammalian tongue structure and function, from cellular to system-level investigation, evidence from kinematic, electromyographic, and nerve ablation studies suggests this categorization scheme is neither functionally based nor heuristic (Sokoloff, 2004). Schwenk (2001) contested the traditional dichotomy of lingual musculature into intrinsic and extrinsic groups, and Bailey and Fregosi (2004) demonstrated in an *in vivo* rat model that at least one intrinsic lingual muscle, the superior longitudinal, is facultatively coactive with the extrinsic hyoglossus during respiration, suggesting that existing morphological and functional distinctions are too simplistic. Controversy also exists pertaining to occasional extension of intrinsic fibers outside limits of the tongue to originate or insert on nearby structures; some superior longitudinal fibers may originate medially from the basihyal (Goonewardene, 1987; Sokoloff, 1989; Levy, 1990), although this has not been reported in Cetacea. Cave (1980) suggested that all portions of intrinsic or "lingual proper" (*m. lingualis proprius*) musculature should more correctly be considered extensions or derivatives of specific extrinsic tongue muscles. As Sokoloff (2004) argued, with the exception of the extralingual portion of extrinsic muscles, mechanical effects of many tongue muscle fibers are likely similar.

Likewise positional lingual movements, typically thought to involve mainly the protrusion–retrusion axis, likely involve simultaneous deformation of tongue shape in three dimensions, including synchronized lengthening and shortening of different regions (Hiimeae and Crompton, 1985; Fuller et al., 1999), contrary to the prevailing model of simple protrusion–retrusion. The muscular hydrostat model (Kier and Smith, 1985), in linking positional and shape changes (e.g., protrusion accompanying reduced cross-sectional area), provides a more realistic conceptual approach. Activation of any lingual motor unit can alter shape, position, and stiffness. Because fiber orientations vary with tongue shape (Sokoloff, 2004), the mechanical effect of any lingual motor unit (or whole muscle) depends on integrated activity of all motor units. Multiple muscles work concurrently to provide structural support and active force for mobility. Experimental evidence (Sokoloff, 2000) suggests that within the tongue body, where many fibers insert by means of complex interdigitation, different motor unit populations, not whole muscle organs, are output elements of the tongue motor system, and that proper investigation and description of tongue function must consider neurophysiological rather than pure morphological properties (Sokoloff, 2004).

"Extrinsic" muscle fibers nonetheless chiefly effect positional changes of the tongue by originating outside it, attaching it to bones of the skull, jaws, and hyoid skeleton. All extrinsic lingual muscles are paired. The largest and most cranial, the genioglossus, originates on

TABLE 1. Published literature on cetacean hyolingual anatomy and associated function

Taxon	Hyolingual/gular anatomy	Lingual histology	Hyoid osteology
MYSTICETI			
Balaenidae	Eschricht & Reinhardt 1866 Lambertsen et al. 2005 Matthews 1938 Scammon 1874 Tarpley 1985 Werth 2004b	Tarpley 1985	Omura 1964
Balaenopteridae	Kukenthal 1889 Lambertsen 1983 Pivorunas 1977 Pivorunas 1979 Slijper 1936 von Schulte 1916		Omura 1964
Eschrichtiidae	Heyning & Mead 1997 Ray & Schevill 1974 Scammon 1874		Omura 1964
ODONTOCETI			
General	Fraser 1952 Kesteven 1941 Kukenthal 1889 Purves 1966 Raven 1942 Reidenberg & Laitman 1994 Werth 1992	Simpson & Gardner 1972 Sokolov & Volkova 1973	Oelschlager 1986 Reidenberg & Laitman 1987 Reidenberg & Laitman 1994
Delphinidae	Agarkov et al. 1975 Arvy & Pilleri 1970 Arvy & Pilleri 1972 Boice et al. 1964 Donaldson 1977 Essapian 1965 Green et al. 1980 Hosokawa & Kamiya 1965 Huber 1934 Lawrence & Schevill 1956 Lawrence & Schevill 1965 Murie 1873 Ping 1927 Reidenberg & Laitman 1994 Seagars 1982 Slijper 1936 Sokolov & Volkova 1973 Sonntag 1922 Werth 1992 Werth 2000a	Arvy & Pilleri 1970 Arvy & Pilleri 1972 Kastelein & Dubbeldam 1990 Pfeiffer et al. 2001 Simpson & Gardner 1972 Sokolov & Volkova 1973 Suchowskaja 1972 Yamasaki et al. 1976 Yamasaki et al. 1978	Reidenberg & Laitman 1994
Monodontidae	Brodie 1989 Hein 1914 Howell 1930 Kleinenberg et al. 1969 Watson & Young 1880		
Phocoenidae	Behrmann 1988 Blevins & Parkins 1973 Howell 1927 Morris 1969 Reidenberg & Laitman 1994	Behrmann 1988 Kastelein & Dubbeldam 1990 Simpson & Gardner 1972	Reidenberg & Laitman 1994
Physeteridae	Berzin 1972 Boschma 1938 Kernan & von Schulte 1918 Reidenberg & Laitman 1994 von Schulte & Smith 1918 Werth 2004a	Werth 2004a	Reidenberg & Laitman 1994
“Platanistoidea”	Arvy & Pilleri 1970 Arvy & Pilleri 1972 Li 1983 Purves & Pilleri 1976	Arvy & Pilleri 1970 Arvy & Pilleri 1972 Li 1983	
Ziphiidae	Heyning & Mead 1991 Heyning & Mead 1996 Reidenberg & Laitman 1994		Reidenberg & Laitman 1994

the caudal (medial) surface of the mandibular symphysis (unfused in mysticetes), often on mental spines or eminences, and fans out dorsoventrally to insert in the central mass of the tongue body, often with numerous discrete bellies from tongue tip to base. Inferior genioglossal fibers protract the tongue; middle genioglossal fibers depress it. The styloglossus originates on the cranial surface and apex of the styloid process and upper portion of the stylohyoid ligament, inserts on the superolateral side of the tongue and, by retracting and elevating the tongue body, aids in initiating swallowing. The palatoglossus originates on the palatine aponeurosis, inserts along the tongue's posterolateral surface (entering it from the dorsal aspect) and, like the styloglossus, aids in swallowing by elevating the caudal portion of the tongue and closing the oropharyngeal isthmus. The hyoglossus originates on the hyoid body and superior border of the greater cornu, fans out to insert on the sides of the tongue, mingling with internal fibers, and depresses and (to a lesser extent) retracts it. A distinct pharyngoglossus is occasionally described as originating along the superior pharyngeal constrictor and inserting between palatoglossal and styloglossal fibers along the side of the tongue; this may be a separate head of the palatoglossus.

"Intrinsic" lingual fibers existing solely within the tongue body include those running in all three planes. Vertical fibers of the *m. linguae verticalis* run dorsoventrally (superoinferiorly in humans) and so flatten the tongue upon contraction, whereas transverse fibers of the *m. linguae transversus* compress and narrow the tongue body. Superior and inferior longitudinal fibers of the *m. linguae longitudinalis* span the length of the tongue body from tip to base and shorten or bend it, allowing it to expand laterally and dorsoventrally.

All lingual muscles receive motor input from the hypoglossal nerve (XII) except the palatoglossus, which as a palatal muscle is innervated by the pharyngeal branch of the vagus nerve (X), with some motor fibers from the cranial accessory nerve (XI). Extrinsic and intrinsic muscles alike are served by the lingual artery, with the styloglossus receiving blood from the ascending pharyngeal and ascending palatine arteries, and the palatoglossus from the tonsillar branch of the facial artery and ascending pharyngeal artery.

ADAPTING THE BASIC MAMMALIAN TONGUE TO AN AQUATIC ENVIRONMENT

Because all mammals arose from terrestrial ancestors whose food was not supported by a current of water, the basic (terrestrial) mammalian tongue is adapted for manipulating food. Land-dwelling tetrapods often use inertial (gravity-based) food transport, relying on rapid, jerking cranial movements to direct food to the rear of the oral cavity, where it is swallowed. Cetaceans can, like other aquatic animals, use hydrodynamic and hydraulic forces for prey manipulation and transport and also, unlike terrestrial animals, use water-dependent forces for initial prey capture and ingestion. It is much harder to grasp items, especially evasive but even nonmotile prey, in water than in air, for swirling currents of this heavy, dense, viscous, compressionless fluid tend to push swimming or floating items ahead and just out of the reach of the mouth. As a result of these functional

and evolutionary influences, the cetacean hyolingual apparatus is divergent both from other mammals and other marine (mainly piscine) vertebrates. Just as it is easier to clean particles from a swimming pool with a dip net or vacuum tube than by attempting to grasp them individually, many aquatic mammals have adopted tried-and-true methods of suspension and suction feeding, although others (including almost all aquatic mammals outside Cetacea) rely on prehension. Once prey is acquired, its buccal transport is different than in air, as water's buoyancy can be used to convey items for swallowing, even in species that seize and hold prey with teeth. Prey processing is likewise simplified, as most cetaceans swallow whole prey intact and undisturbed, without mastication (the killer whale, *Orcinus orca*, is a notable exception). Because food is often swallowed in large portions, cetacean digestive tracts may be complex, with multiple gastric chambers to enhance physical and chemical digestion.

Other generalizations can be made pertaining to cetacean feeding, especially in ways they differ from other aquatic animals. As endotherms, cetaceans maintain elevated body temperature and must avoid undue heat loss. As obligate air-breathers, they dwell near and periodically return to the surface. They have no pharyngeal or other ventilatory slits, so that all water entering the mouth must be swallowed or expelled the way it entered, except in balaenid mysticetes that achieve unidirectional water flow for continuous filter feeding. Strong pharyngeal and laryngeal musculature prevents water from entering the trachea (Reidenberg and Laitman, 1987; 2007a, this issue; 2007b, this issue). Sexual dimorphism may affect feeding as manifested in dental differences. Many species undertake long migrations that carry them far from productive feeding grounds, necessitating long bouts of fasting, up to half a year, such that they must build up plentiful nutritional stores for extended periods of time and maximize intake during periodic feeding. The feeding apparatus is obliged to accommodate both neonate/juvenile suckling and adult feeding or else undergo a transformation between adolescent and adult phases of life history. All of these circumstances influence cetacean hyolingual anatomy.

Cetaceans subsist on virtually every animal life form, including other marine mammals, found in every marine environment from intertidal or littoral benthic zones to neritic, pelagic, and abyssal habitats of all ocean basins. Their food ranges from tiny zooplankton to large nekton (e.g., squid, sharks, bony fishes) and is obtained at all levels of the water column, including the surface and bottom. Prey ranges from nonmotile to highly evasive and can be solitary or gregarious, and soft or hard. Because of the broad taxonomic and ecological diversity within Cetacea, it is useful to adopt a functional approach and thereby consider three general feeding types: filter feeders, suction feeders, and raptorial ("predatory") feeders, the latter involving prey prehension. These groupings cross taxonomic boundaries, although the chief phylogenetic division of Cetacea relates to feeding (hence old subordinal names Filtrales and Raptoriales), and ecological or taxonomic classifications of cetaceans according to diet and feeding type have been proposed (Tomilin, 1954; Gaskin, 1976). It must be emphasized, however, that cetaceans are versatile opportunists whose feeding preferences vary according

to seasonal migrations and circumstances of prey availability, abundance, distribution, and depth.

Filter Feeding

Although filter feeding—straining small prey or particulate organic matter suspended in water—is presumed to be the primitive mode of chordate feeding (Lauder, 1985), it is a secondary derivation for aquatic mammals, as it was for many large Mesozoic reptiles. By feeding near the bottom of a trophic pyramid and thus reaping rewards of greater energy per unit biomass consumed, filter feeders attain giant body size (or, conversely, support huge populations of smaller animals, as in the krill-eating crabeater seal, *Lobodon carcinophagus*). Baleen whales eat whole organisms, whereas many tiny suspension feeders, with correspondingly diminutive filters, feed on detritus (fragmented organic debris). However, like other strainers, mysticetes are not selective; they locate patchy food sources and swallow whatever is trapped. Tiny filter feeders must contend with difficulties of moving in a dense, viscous fluid, but mysticete kinematics depend on inertial (both hydraulic and hydrodynamic) rather than viscous forces. Baleen whales are often described as grazers, yet this term is properly reserved for animals that consume herbage, algae, or phyto- rather than zooplankton, so that carnivory is an appropriate if unlikely term for mysticete feeding, although the presence of volatile fatty acids and symbiotic bacteria in mysticete forestomachs suggests microbial fermentation (Herwig et al., 1984).

The mammalian Suborder Mysticeti comprises three families of baleen whales, each of which uses a distinct type of filter feeding (Werth, 2000b, 2001, 2004b). Like other aquatic tetrapods, most mysticetes are intermittent filter feeders, engulfing a single mouthful of water at a time and trapping food in a baleen sieve before expelling the water, unlike lower vertebrates and invertebrates that generally pump or push water continuously and unidirectionally (Sanderson and Wassersug, 1993). Members of Balaenopteridae, commonly called rorquals (from Norwegian “furrowed whale,” referring to throat pleats) use ram gulping from forward propulsion (using muscular contraction of the tail) to engulf a mouthful of water and prey (schooling fish, krill, or other micronekton) in a rapid lunge. The gray whale (Eschrichtiidae), which draws in benthic invertebrates by means of suction ingestion from rapid oral expansion (using muscular contraction of the tongue), also is an intermittent filter feeder yet can feed while stationary. A third family, Balaenidae (right and bowhead whales), uses continuous, unidirectional ram filter feeding. Balaenids slowly skim copepods and other minute zooplankton that deposit on finely fringed baleen by a steady stream of water flowing through the mouth.

Suction Feeding

Suction ingestion is used not only by the gray whale but also by other marine mammals (e.g., walrus; Gordon, 1984) that capture, ingest, and transport discrete prey items with suction generated by means of oral and pharyngeal expansion (Werth, 1992, 2000a,b, 2004a, 2006a,b). Whereas gray whales consume quantities of aggregating organisms with consequent need for filtra-

tion, certain odontocetes vacuum larger and ordinarily more evasive solitary prey, retaining items while engulfed water is expelled before deglutition. Suction feeding has been documented in floating or otherwise stationary marine mammals, often at the bottom of the water column (Werth, 2000a), demonstrating that this is not merely “ram” feeding in which a predator relies on rapid locomotion to overtake and engulf prey. Although simple in principle, suction feeding requires modifications to the hyolingual apparatus and often to the skull and jaws (see MacLeod et al., 2007, this issue). Mammalian suction feeders are largely teuthophagous (consuming cephalopods) yet variation exists in prey type, size, and activity; mesopelagic and benthic fishes and invertebrates are taken. This solution to the problems of aquatic prey capture has been independently adopted by nearly all aquatic vertebrates and has evolved multiple times in Odontoceti (Werth, 2006a).

Raptorial Feeding

An obvious if somewhat less effective method of obtaining food underwater involves seizing or grasping items with jaws using forward or lateral movements of the head, neck, or entire body. This raptorial foraging (sometimes described as predatory feeding; Owen, 1980), encompasses ram prey capture as well as snapping or biting. It is the simplest and thus probably the original mode of prey capture in aquatic mammals, necessitating few changes from the terrestrial body plan, so that the most recently evolved aquatic mammals, including most members of the Order Carnivora, rely on raptorial feeding. However, some highly derived odontocetes have retained or secondarily adopted this method, making marine mammal raptors a large and diverse group that combines generalists with extreme specialists.

Thermoregulation

In addition to its role in feeding, the tongue of mysticetes and possibly odontocetes also functions in thermoregulation. All cetaceans possess a thick layer of insulating blubber that precludes radiative cooling, but a greater concern for large whales may be cooling off (Gaskin, 1982). Many mysticetes feed in productive cold waters at high latitudes. In balaenids the rotund, stocky body, lacking dorsal fins, and squarish flippers (as opposed to the high aspect ratio flippers of balaenopterids) are suited to reducing heat loss by minimizing exposed surface area, yet these features make it difficult to radiate excess heat and thereby lower elevated body temperature during periods of high locomotor activity, as during migration, mating, and feeding. As a high surface area “external” organ (often exposed to cool water, especially during long bouts of feeding), the tongue is ideally suited for thermoregulation.

MATERIALS AND METHODS

A total of 99 cetacean specimens, including 8 mysticetes in 2 species and 91 odontocetes in 11 species, were examined for this study (Table 2, listing only 10 specimens per species), including 20 additional Atlantic white-sided dolphins, 4 common dolphins, and 14 harbor porpoises not listed in Table 2. Several other species were studied more qualitatively or cursorily for compar-

TABLE 2. Primary dissection specimens used in this study (all measurements taken post mortem)

Genus species	Common name	Source	Specimen ID code	Sex	Age	Length (cm)	Mass (kg)		
MYSTICETI									
<i>Balaena mysticetus</i>	Bowhead whale	NSB	93.B6	F	A	1499	?		
		NSB	93.B12	F	J?	1010	?		
		NSB	93.B16	F	A	1105	?		
		NSB	95.B6	F	J	964	?		
		NSB	95.B7	F	A	1372	?		
		LSU	88.KK1F	F	F	150	?		
		LSU	90.B4F	F	F	390	?		
<i>Eubalaena glacialis</i>	North Atlantic right whale	NEAq	MH.89.424.Eg	M	I	454	900		
ODONTOCETI									
<i>Delphinus delphis</i>	Common dolphin	NEAq	MH.85.422.Dd	M	A	203	92		
		NEAq	MH.87.428.Dd	F	A	183	88		
		NEAq	MH.87.445.Dd	F	A	214	133		
		NEAq	MH.87.448.Dd	M	A	252	208		
		NEAq	MH.87.564.Dd	M	J	176	64		
		NEAq	MH.88.419.Dd	F	J	151	59		
		NEAq	MH.88.420.Dd	M	A	207	136		
		NEAq	MH.89.529.Dd	F	A	186	127		
		NEAq	MH.90.502.Dd	F	A	166	97		
		NEAq	MH.90.609.Dd	M	A	221	155		
		<i>Globicephala melas</i>	Long-finned pilot whale	NEAq	MH.88.425.Gm	M	A	364	485
				NEAq	MH.89.416.Gm	F	A	359	483
				NEAq	MH.89.440.Gm	F	J	326	472
				NEAq	MH.89.522.Gm	F	A	390	494
				NEAq	MH.91.635.Gm	M	J	325	431
<i>Grampus griseus</i>	Risso's dolphin	NEAq	MH.86.044.Gg	M	A	338	440		
		NEAq	MH.87.474.Gg	F	A	319	426		
		NEAq	MH.89.524.Gg	F	A	282	410		
<i>Kogia breviceps</i>	Pygmy sperm whale	NEAq	MH.86.202.Kb	F	A	336	398		
		NEAq	MH.89.517.Kb	M	J	291	344		
		NEAq	MH.90.555.Kb	M	A	347	410		
<i>Lagenorhynchus acutus</i>	Atlantic white-sided dolphin	NEAq	MH.87.295.La	M	A	184	185		
		NEAq	MH.87.417.La	M	I	137	32		
		NEAq	MH.87.418.La	M	A	217	198		
		NEAq	MH.87.436.La	F	A	164	133		
		NEAq	MH.87.442.La	M	A	252	294		
		NEAq	MH.87.443.La	M	A	255	207		
		NEAq	MH.87.446.La	F	J	156	109		
		NEAq	MH.87.464.La	M	A	235	204		
		NEAq	MH.87.542.La	F	A	227	178		
		NEAq	MH.87.561.La	M	A	181	165		
		NEAq	MH.89.444.La	M	A	233	178		
		<i>Lagenorhynchus albirostris</i>	White-beaked dolphin	NEAq	MH.89.515.Oo	M	A	663	?
				NEAq	MH.86.296.Pp	M	A	144	52
<i>Orcinus orca</i>	Killer whale	NEAq	MH.87.419.Pp	F	A	157	63		
		NEAq	MH.87.421.Pp	F	A	153	59		
<i>Phocoena phocoena</i>	Harbor porpoise	NEAq	MH.87.424.Pp	M	J	129	38		
		NEAq	MH.87.425.Pp	M	A	145	47		
		NEAq	MH.87.432.Pp	M	A	156	60		
		NEAq	MH.87.450.Pp	F	A	143	47		
		NEAq	MH.87.462.Pp	M	A	150	56		
		NEAq	MH.87.468.Pp	M	J	132	39		
		NEAq	MH.87.471.Pp	F	A	168	71		
		<i>Physeter macrocephalus</i>	Sperm whale	NEAq	MH.88.522.Pc	F	I	375	?
				NEAq	MH.90.651.Pc	M	A	1286	?
				NEAq	MH.91.673.Pc	M	A	1432	?
		<i>Stenella coeruleoalba</i>	Striped dolphin	NEAq	MH.86.026.Sc	F	A	218	231
				NEAq	MH.88.546.Sc	F	J	189	164
				NEAq	MH.89.415.Sc	M	A	239	186
NEAq	MH.89.426.Sc			M	A	232	177		
NEAq	MH.89.427.Sc			F	A	225	163		
<i>Tursiops truncatus</i>	Bottlenose dolphin	NEAq	MH.87.431.Tt	M	A	251	204		
		NEAq	MH.90.469.Tt	F	A	234	187		

Source: NSB = North Slope Borough (Alaska) Department of Wildlife Management/Alaska Eskimo Whaling Commission, Barrow, AK; LSU = Louisiana State University School of Veterinary Medicine, Department of Anatomy and Fine Structure, Baton Rouge, LA; NEAQ = New England Aquarium, Boston, MA. Specimen ID code is accession catalogue number assigned by donor source to each necropsied specimen. Sex: F = female, M = male. Age: F = fetus, I = infant, J = juvenile, A = adult, ? = unclear. Length = total body length, measured in centimeters, from rostral tip of snout to fluke notch. Mass = total body mass in kg; ? = unknown.

ative analysis yet also are not listed in Table 2, including humpback (*Megaptera novaeangliae*), fin (*Balaenoptera physalus*), and minke (*Balaenoptera acutorostrata*) whales; Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales; the beluga (*Delphinapterus leucas*); and spinner (*Stenella longirostris*) and Atlantic spotted (*Stenella frontalis*) dolphins.

All dissection specimens were obtained in accordance with federal statutes governing possession and disposition of marine mammal material. No animals were killed for this study. Specimens were obtained post mortem from beach strandings or, in the case of bowhead whales, Inuit subsistence hunting, and were examined fresh or frozen, hauled out on the beach (or ice) or in a necropsy laboratory (freezer storage at -10°C). Specimens were dissected during standard necropsy procedures to obtain tissue samples, examine for parasite infestation, and determine cause of death, or during Inupiat butchering. No remarkable pathological or anatomical conditions were observed in any specimen. All specimens were whole carcasses, including fetuses, that were dead when retrieved but otherwise fresh and in good condition. Structures were photographed, videotaped, and sketched with scale bars for later study and measurement; measurements were taken of structures in situ. To allow for more detailed study, heads of smaller carcasses were removed immediately cranial to the insertion of the flipper, at the atlanto-occipital joint dorsally but including all hyoid and laryngeal musculature ventrally. The sternohyoid muscle was removed as close to its origin on the sternum as practicable, and as many fibers retained as possible. Other muscles were later removed for weighing, closer inspection, and microscopic analysis. Several whole heads were frozen and bisected along the midsagittal plane with a band saw to reveal intact, undissected internal structures. Vasculature was closely studied for potential thermoregulatory function. Whenever possible fetal specimens were whole-body formalin perfused through umbilical vessels for fixation and preservation for later study. Limited histological study was done.

The tongue was typically split longitudinally into two halves with a median sagittal section. One half was sliced into serial segments with uniform transverse sections; the other was dissected from the medial side or sectioned in other planes. To quantify proportional contributions of extrinsic and intrinsic musculature to the tongue body, attempts were made to compare weights of various muscles as fractions of the total tongue weight, within species as well as relative to other cetaceans and other mammals for which comparable data exists. Calculation of rough estimates by measuring the proportion of fat to muscle in sample cross-sectional area was unsatisfactorily attempted. Later comparisons used cross-sectional areas, with photographs of transverse tongue sections, in which distinct muscle bundles were delineated as clearly as possible with string or thread, and digitized to calculate the percentage of total tongue body area taken up by a given muscle along the length of the tongue.

Terminology presented here is consistent with the Nomina Anatomica Veterinaria (1983), using the suffix *-hyoid* or *-glossus* to denote a muscle and *-hyal* to denote a skeletal element of the hyoid apparatus. The terms *origin* and *insertion* are used in the classic sense, where *origin* suggests a more stable (and generally more proximal) attachment and *insertion* a more mobile (and dis-

tal) one, although it must be emphasized that such conditions depend on function.

RESULTS

Descriptions of the tongue's gross morphology and musculature are arranged taxonomically with concomitant functional division into feeding types.

Mysticeti (Filter Feeding)

Mysticete tongues appear similar externally, but as the threefold (familial) variation in diet and foraging ecology correlates with major differences in hyolingual morphology, each family will be treated separately.

Balaenidae. In external shape and appearance the balaenid tongue is prominently elevated and muscular, with a smooth surface and cream, pink, or gray coloration with darkly pigmented tip. It occupies the entire oral cavity and is largely connected to the oral floor. The exceptionally massive tongue is the world's largest muscular organ, averaging 4–6% of total body mass (Omura, 1958), so that in an average 50 ton or 50,000 kg whale, the tongue weighs 2,000–3,000 kg and reaches 5 m in length and > 1 m in width and height. There is a large central furrow or sulcus in the dorsal midline, a cranial spoon-shaped concavity and small free tip, limited longitudinal folds or plicae, and in younger animals a scalloped, papillated margin. In all ages, including fetuses, the tongue is not protrusible but has a sublingual fat pad, a boomerang-shaped bumper of adipose and loose connective tissue just below the tongue's slightly free cranial tip, above the origin of the genioglossus. Internally there is profuse adipose tissue, not only between myofascicles and in the midline lingual septum, but in a thick layer of subdermal fat surrounding the entire tongue body (Fig. 1). This is apparent dorsally but is most pronounced on lateral surfaces. The tongue is much more muscular below the median septum. The tongue is highly vascularized ventrally, with many large valved veins and tributaries, and both anastomotic and periarterial venous retia (Fig. 2), yet there are almost no peripheral blood vessels, especially near the dorsum. Numerous foliate papillae can be found on the dorsum near the root of the tongue.

The high quantity of adipose and loose connective tissue makes the balaenid tongue soft and pliable, but unlike the flaccid rorqual tongue it always holds its shape, even in death. Extrinsic lingual muscles (especially genio- and hyoglossus) extend great distances into the tongue body and insert there over large areas (Fig. 1). The genioglossus has separate regions with distinct fiber orientations; some of the middle or oblique genioglossal fibers wrap around the heavily vascularized hyoglossus, which passes far cranially as a long, rod-like muscle. Limited intrinsic fibers are scattered below the dorsum but otherwise notably sparse except far caudally, near the tongue root, where vertical and transverse fibers are apparent (Fig. 3). Discrete longitudinal intrinsic fibers cannot be distinguished from extrinsic fibers inserting in the tongue body. For much of the tongue body's length only clear ribbon-like insertions of extrinsic lingual muscles, especially the genio- and hyoglossus, are visible amid abundant fatty tissue (Fig. 1).



Fig. 1. Serial transverse sections through tongue of adult bowhead whale (*Balaena mysticetus*; approximately 50, 200, and 350 cm from cranial tip; scale bar in top photo = 10 cm) showing extraordinary profusion of adipose tissue and insertion of genioglossus, whose fibers

appear as thin, dark bands or ribbons as they fan out to insert in tongue body. Most caudal section (lower right photo) also shows some fibers of styloglossus (far left of photo) and hyoglossus (bottom left and bottom right of photo).

Balaenopteridae. The floppy tongue of adult rorquals, commonly said to have the same mass as an elephant, is much more loosely defined and weakly muscular than in other mysticetes. It is extraordinarily flaccid (distinct yet deformable), as is the oral floor, with broad, flattened mylohyoid and geniohyoid. After death, in the absence of normal muscle tonus, the tongue typically

droops within the mouth or partly inverts to its invaginated caval position. The cavum ventrale, named and described by von Schulte (1916), is an intermuscular fascial cleft extending under the mouth, throat, and chest. The slick walls of this space slide freely over adjacent surfaces, and the cavum enlarges to form a giant, bulging vestibule as it receives engulfed water and the dis-

placed tongue and oral floor. Dissection of fetal and adult rorquals (see also Pivorunas, 1979) reveals major changes in the tongue as it transforms from a solid, muscular structure in suckling juveniles to the deformable, flaccid sheet of adults. From birth until weaning the paired lingual musculature separates from the midline septum and muscle fiber is gradually replaced with adipose and elastic connective tissues as the increasingly saccular organ flattens and spreads laterally, so that distinct muscle groups (e.g., genioglossus) may remain, but

only diffusely, with loose insertions in the tongue body among profuse connective tissue fibers. Intrinsic lingual muscle fibers are likewise scattered and poorly developed, much more so than in neonate rorquals. The adult rorqual's lingual flaccidity, then, is a combined product of loss of muscle fibers and muscle connections, loss of fascia that bind myofibrils in discrete muscle organs with defined contractile pathways and actions, and gain of elastic fibers and fat.

Eschrichtiidae. Although smaller than in balaenids, the gray whale (*Eschrichtius robustus*) tongue is more robust, firm, and muscular than in other mysticetes, with well-defined muscles with clear fiber orientations and connections, and with less adipose and connective tissues than in balaenids and balaenopterids. The hyoglossus of *Eschrichtius* is particularly large. As in balaenids, vascular retia are abundant in the gray whale tongue (Heyning and Mead, 1997).

Hyoid. The mysticete hyoid is remarkable neither in relative size nor form, consisting of a single fused body with basihyal and paired, wing-like thyrohyals (greater cornua) completely ankylosed with no visible sutures, with a large median cranial notch between parallel protuberances where paired stylohyal elements (lesser cornua) attach (Fig. 4). There may also be a single or paired projections from the caudal edge of the basihyal, serving as a point of insertion for the *m. sternohyoideus*, but there is great individual variation (Omura, 1964); there is often a prominent median projection in sei, Bryde's, and minke whales (*Balaenoptera borealis*, *B. edeni*, and *B. acutorostrata*), and on these three species, the distal end of the thyrohyal is often flat, rather than thickened as in other rorquals or nearly cylindrical and massive in balaenids. Likewise the stylohyal elements, flat and narrow in *Balaenoptera* and somewhat thicker in *Megaptera*, are large and cylindrical in balaenids and

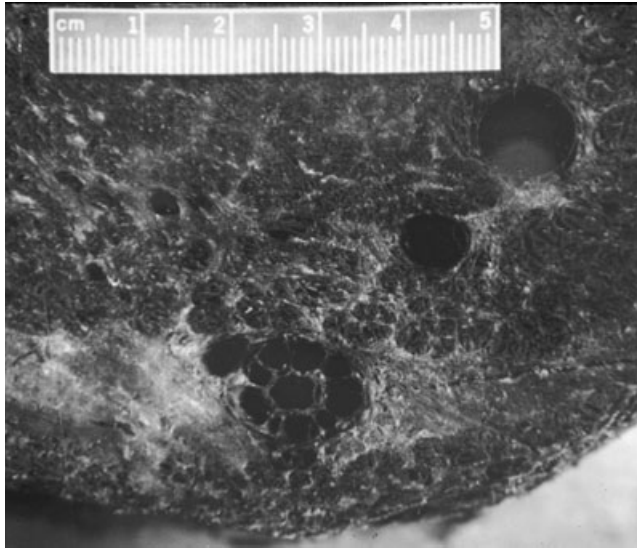


Fig. 2. Tongue root of fetal bowhead whale (*Balaena mysticetus*) in transverse section showing vascular adaptations for thermoregulation, including periarterial venous rete (bottom) and isolated peripheral vein (top right), both within fibers of the hyoglossus.



Fig. 3. Midsagittal section through dorsum of tongue at caudal root in adult bowhead whale (*Balaena mysticetus*; scale bar in 1 cm² grid) showing transverse and vertical intrinsic fibers interspersed with sheets of adipose tissue and (below) more densely concentrated fibers of hyoglossal insertion.

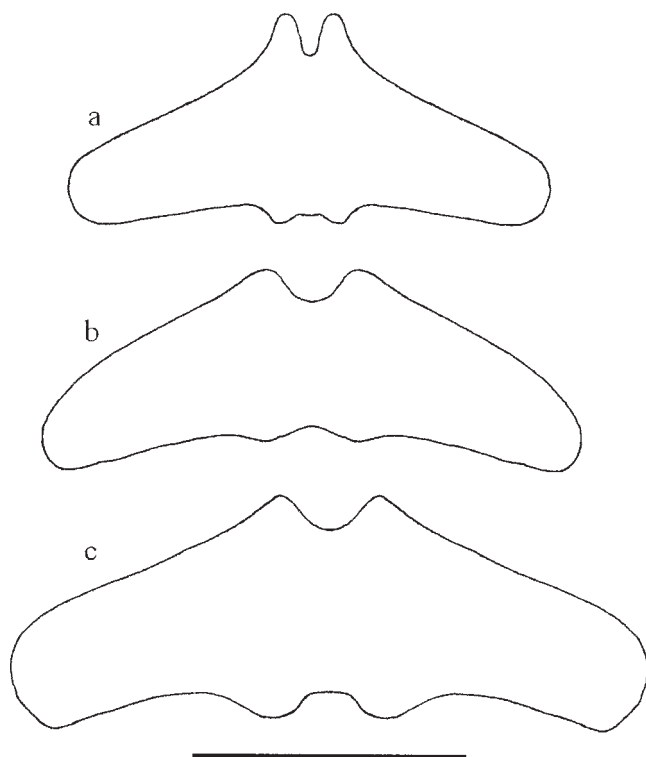


Fig. 4. Schematic outline of hyoid bodies (combined basihyal and thyrohyal elements), in dorsal view, of humpback whale (*Megaptera novaeangliae*; a), North Atlantic right whale (*Eubalaena glacialis*; b), and gray whale (*Eschrichtius robustus*; c). Scale bar = 50 cm.

in *Eschrichtius*. Although the fused hyoid body is often concave from the dorsal aspect, there is no species-specific regularity, with much individual variation (Omura, 1964). In most mysticetes, hyoid bones are smooth, but they are very rugosely corrugated as well as significantly larger and thicker in *Eschrichtius*, and to a lesser extent (with fewer and smaller muscle scars and surface ridges) in *Megaptera*, *Balaena*, and *Eubalaena*. Although balaenopterid tongues undergo major developmental changes, the hyoid does not seem to alter similarly, although the elements do not fuse until late in adolescence, before puberty, and perhaps later in balaenids than other mysticetes (Omura, 1964).

Odontoceti (Suction and Raptorial Feeding)

In all species, the tongue is firm and highly muscular, without large accumulations of adipose or loose connective tissues that characterize mysticete tongues. Because there are fewer differences in odontocete hyolingual morphology than in mysticetes, all toothed whale, dolphin, and porpoise families are treated together.

Tongue. The tongue's epithelial mucosa is composed of flat, stratified squamous cells with a horny, parakeratotic corium that is approximately 18 cells thick (Pfeiffer et al., 2001) except at the tongue apex. Although the dermal corium possesses many collagen fibers it lacks the elastin typical of other mammals and as such is rather inflexible and nondeformable (Werth, 1992). Keratin intermediate filaments are numerous, forming cir-

cular whorls. The density of the keratinized lingual tunic, described by Murie (1873) as a "leathery-like envelope," the strong development of ventral mucosa, fascia, and other connective tissues surrounding the extrinsic muscle bundles, and the density of the musculature itself and corresponding low degree of glandular, lymphatic, and adipose tissues all serve to stiffen the tongue body and root (Ping, 1927; Arvy and Pilleri, 1970, 1972; Simpson and Gardner, 1972). In their report on the histology of the long-finned pilot whale (*Globicephala melas*) tongue, Pfeiffer et al. (2001) reported that epidermal keratinocytes resemble those of cetacean skin in other body regions, including cytoplasmic lipid droplets around nuclei of stratum spinosum cells, a lingual feature not seen in terrestrial mammals. Pigment granules are not evident, stratum corneal cells contain nuclear remnants (parakeratosis) and small multivesicular bodies, and nuclei of stratum basale keratinocytes possess numerous deep clefts. There are few true surface papillae (vallate or other) along the dorsum, although spherical groups of nonkeratinized cells within connective tissue papillae penetrate the multilayered epithelium, especially along fissures near the tongue root. These resemble taste buds and may be chemosensory. There are no obvious mechanosensory receptors. Mucous and serous lingual glands are found but are less widespread than in typical terrestrial mammals, as is typical of cetaceans (Slijper, 1962; Sokolov and Volkova, 1973; Donaldson, 1977).

Numerous deep, parallel longitudinal folds or fimbriated plicae, each with smaller transverse folds, run along the sides of the tongue (Fig. 5); these also are covered with a thick epithelium, albeit smoother and less keratinized. There is a short frenulum under the tip, with a protuberance at the genioglossal origin. Caudally, there is no clear demarcation between the tongue and oropharynx, although the abrupt junction of genioglossal fibers with the oropharyngeal connective tissue sheath can be taken as the caudal limit of the tongue. A fringe of large (2–5 mm) marginal papillae is frequently seen along the cranial and lateral edges of the tongue body (Yamasaki et al., 1976). Although these papillae (Fig. 5) are found primarily in neonate and juvenile individuals (Kastelein and Dubbeldam, 1990) and appear late in fetal development, they persist throughout life in several species (Sonntag, 1922; Ping, 1927; Yamasaki et al., 1976; Donaldson, 1977), predominantly suction feeding taxa.

There are scattered intrinsic lingual muscle fibers (*m. lingualis proprius*), notably vertical and superficial longitudinal fibers, mostly in the rostral half of the tongue (Fig. 6). Intrinsic fibers are more prominent in neonates than in adults; extrinsic muscles constitute most tongue musculature in juveniles and adults. Foremost among these is the large, complex genioglossus, whose fan-shaped fibers are arranged in three characteristic bundles of vertical (most cranial), oblique (middle), and longitudinal (caudal) fibers, although these heads are less distinct than in most mammals (Evans and Christensen, 1979), and less so in physeterids than in delphinids and phocoenids (Lawrence and Schevill, 1965; Sonntag, 1922). The largest odontocete extrinsic lingual muscle, the genioglossus, takes origin along the ventral and medial margins of the mandible, running from the midline symphysis dorsal or internal to the genioid tendon, to the more caudal region where genioglossal

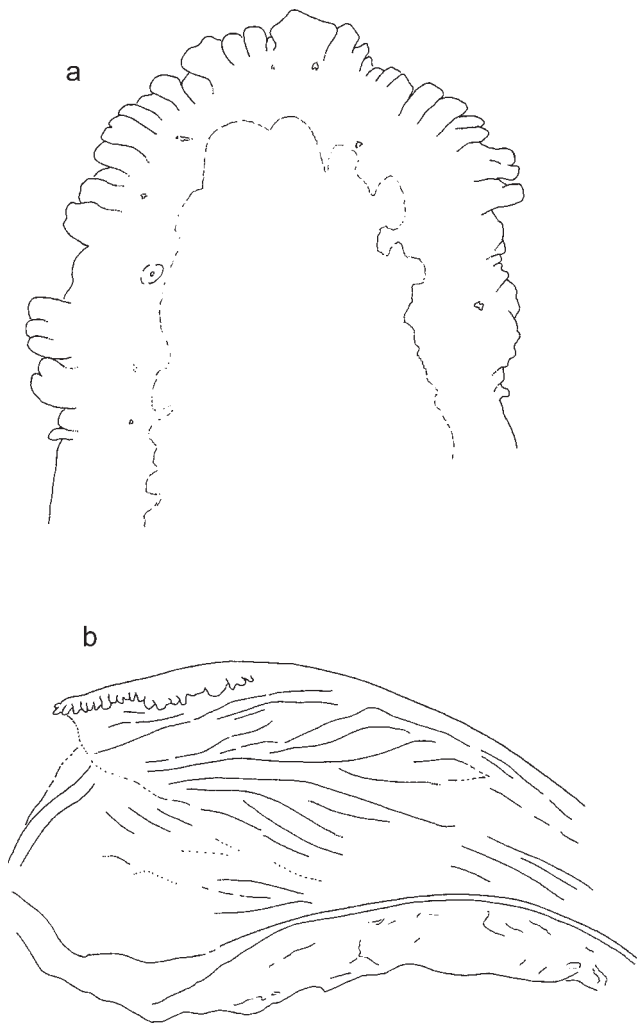


Fig. 5. Morphological features of adult Atlantic white-sided dolphin (*Lagenorhynchus acutus*) tongue: fringe of marginal papillae along cranial tip, presumed to create better seal against palate during water ingestion/expulsion (a); extensive lateral longitudinal plicae (folds), increasing degree and range of lingual excursion (b).

fibers mingle with mylohyoid fibers on tough connective tissues of the lateral ramus of the jaw. Some genioglossal fibers have no attachment to the jaw, originating instead from the ventral surface of the mucosa lining the mouth. A loose, quasitendinous cranial connection between left and right bellies of the genioglossus and the geniohyoid origin may be formed by fibers from either muscle or, more likely, is a stronger region of the extensive connective tissues separating both muscles. Genioglossal fibers then pass caudally and medially onto the ventral aspect of the tongue, joining medially into a long raphe that rises vertically and spreads to constitute the bulk of the tongue musculature, especially rostrally, but along the entire tongue length (Figs. 6–9). In most odontocetes, especially of Delphinidae and Phocoenidae, a few medial genioglossus fibers continue caudally to fan out ventrally around the oropharynx, caudal to the tongue, in some cases mingling with palatoglossus fibers that descend to enter the tongue laterally at its root. Other medial genioglossal fibers insert on the cranial

midline of the hyoid body between ceratohyals. This thin connection is barely perceptible and easily removed. Dolphins of the genera *Stenella* and *Delphinus* lack the vestigial caudal connection to the hyoid. Where the genioglossus inserts into the tongue, its fibers are largely indistinguishable from other extrinsic contributors. In *Physeter*, *Kogia*, and *Globicephala* (sperm and pilot whales) the three genioglossal heads are especially distinct at their insertions (Werth, 2004a). A similar although not so pronounced condition exists in *Grampus griseus* (Risso's dolphin) and *Orcinus orca* (killer whale).

The large and broadly shaped hyoglossus (Figs. 6–8) has an extensive origin on the hyoid skeleton, from the thyrohyal (just deep to the mylohyoid) and basihyal to the ceratohyal. It passes cranially ventral to the palatoglossus and dorsal to the styloglossus, with which it inserts on the ventral surface of the tongue. Lawrence and Schevill (1965) described medial and lateral heads of the paired hyoglossus, with the medial portion inserting as described above and the lateral section attaching to the palatoglossus as it wraps around the oropharynx; they concluded that the hyopalatinus muscle of previous authors is equivalent to this lateral head and discounted the possibility of a ceratohyal origin for the medial portion of the hyoglossus, although this origin is supported by *L. acutus* in this study as well as findings of others (von Schulte and Smith, 1918; Howell, 1927, 1930). Both hyoglossal divisions were distinct in the Atlantic white-sided dolphin (*Lagenorhynchus acutus*) as well as in most other species examined, although the lateral head was found to insert not so much on the pharynx as the sides of the tongue body, especially dorsally along the palatoglossal insertion. Minor variation exists in the site and extent of hyoglossus origins. In *Physeter*, *Kogia*, and *Globicephala* the medial portion of this muscle also originates from the proximal part of the stylohyal, at its joint with the ceratohyal; in these species the width (and range of insertion) of the hyoglossus is relatively much greater (Fig. 8).

The narrow yet robust, paired styloglossus originates on the proximal (lateral) end of the stylohyal, in a small triangular region along the flat cranial stylohyal surface, passing ventrally and cranially (deep to the genioglossus) as flat, laterally compressed straps, to insert in a fan-like spread on the lateral and ventral aspect of the tongue cranial to the hyoglossus insertion. Inserting fibers of the styloglossus mingle with those of other extrinsic and intrinsic lingual musculature. The styloglossus is thicker and rounder in *Physeter macrocephalus* (sperm whale) than in other odontocetes (Werth, 2004a) but also thick in larger delphinids (*Globicephala*, *Grampus*, *Orcinus*; Murie, 1873; Werth, 2000a), the beluga, *Delphinapterus leucas* (Watson and Young, 1880), and other documented or presumed suction feeders. In such species, the styloglossus inserts more ventrally at the base of the tongue body rather than along its sides.

The palatoglossus, a thick, paired muscle originating on tough connective tissues of the oropharynx (Fig. 9), is often mistaken for a pharyngeal constrictor muscle, although the palatoglossus is cranial to the constrictors and clearly shows connections to the tongue as well as to other extrinsic lingual muscles. Palatoglossal fibers from each side meet dorsally in a tendinous raphe where the pharynx is tightly bound to the bony palate. From their broad origin here palatoglossal fibers fan out to as-

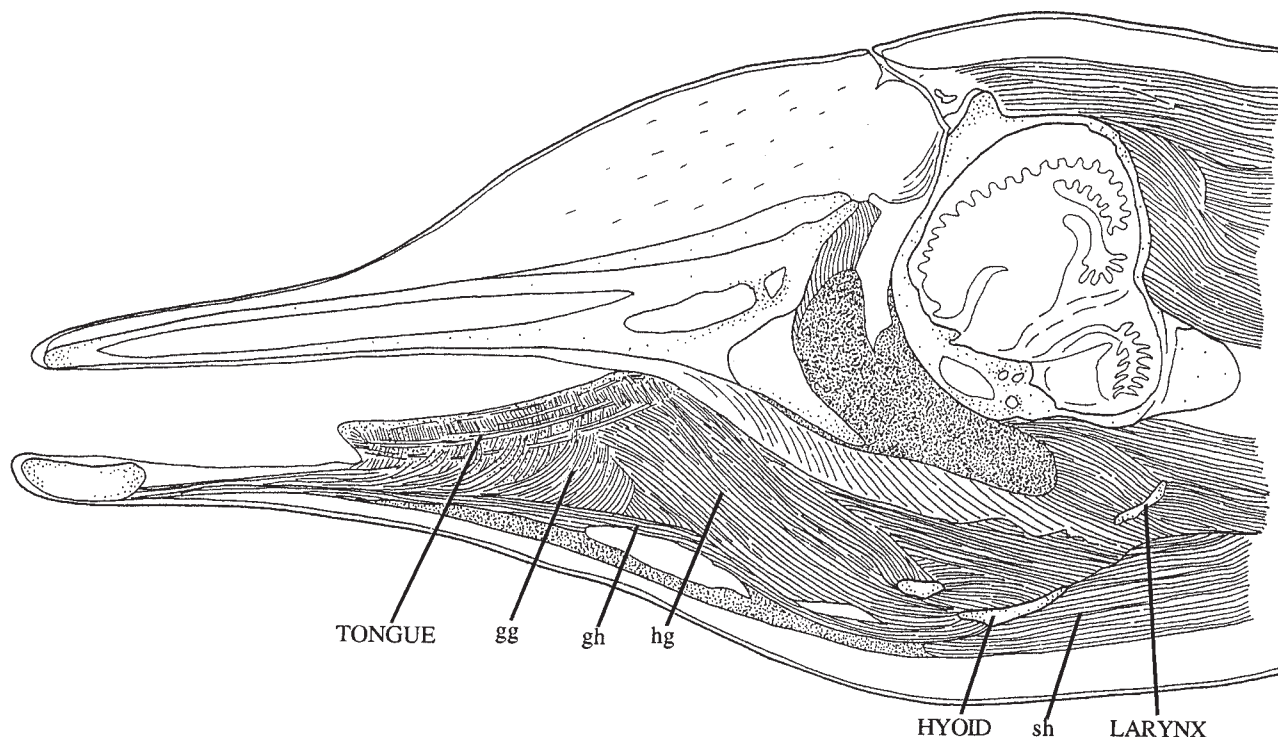


Fig. 6. Parasagittal section of the head and neck of common dolphin, *Delphinus delphis*, 2.5 cm from median plane. Stylohyal and thyrohyal elements are visible, as is palatopharyngeal sphincter; larynx and nasal passages are mostly out of view. Note smooth palate, arrangement of intrinsic lingual musculature, and large sublingual

space below geniohyoid (gh), as well as large sternohyoid (sh) and hyoglossus (hg) and hyoid insertion of the genioglossus (gg). The tongue normally resides in this caudal position, closely applied to entrance of oropharynx.

sociate with lateral portions of hyoglossus and genioglossus ventrally. The palatoglossus does not penetrate deep into the tongue root; its scattered fibers are mostly superficial. A thick, elastic band of connective tissue completely covers the palatoglossus from the dorsum of the pharynx down along sides of the tongue, finally meeting ventrally at the most lateral extent of the genioglossal insertion (Fig. 9). Lawrence and Schevill (1965) discussed merits of previous authors' identification of probable palatoglossal fibers as either palatopharyngeus and genioepiglotticus muscles, among others. They do not discount the possibility of palatoglossal fibers being misconstrued as the former (especially the thyrohyal portion), but they mostly dismiss the latter as a caudal insertion of the genioglossus. No discrete pharyngoglossus could be found in any species examined for this study.

As in other mammals, odontocete proper or intrinsic lingual musculature consists of fibers named for their predominant orientation in three planes. Fibers generally originate on connective tissues in the lamina propria of the coarse, fibrous tunic surrounding the tongue, or on similar structures (e.g., median septum) within the tongue. Intrinsic fibers in the odontocete tongue do not deviate from the standard mammalian condition in arrangement and distribution yet are more sparse than in many mammals (including phocids), although not to the extent seen in Mysticeti. Vertical and transverse fibers are plentiful cranially but rarer in the caudal half of the tongue body and root. Longitudinal fibers are rarer still, especially ventrally, appearing as thin, scat-

tered fibers that can easily be (and often are) mistaken for fibers of the genioglossus and hyoglossus (Fig. 6). Dissection of neonate and fetal material in many species supports the claim that intrinsic fibers have greater representation in younger odontocetes (Werth, 1992).

Amounts and arrangements of connective tissue fibers in odontocete tongues are unremarkable relative to other mammals, although a marked concentration of dense fibers (mostly collagenous but some elastic) along the ventral part of the median septum encapsulates a long, firm, rod-like body of adipose cells. This finding is strikingly reminiscent of the lyssa of the dog tongue, presumed to be a stretch receptor (Chibuzo, 1979). A ventral sublingual space of loose areolar tissues (Fig. 6) provides little resistance and allows for rapid tongue retraction. In delphinids, this opening is 8–10 cm long, 4–5 cm wide, and 2–3 cm high, taking the shape of a horizontal, flattened cylinder with a median longitudinal axis. The cranial limit of the cavity is near the middle of the tongue body; caudally it reaches almost to the hyoid. This space seems to be related to the large amount of fascial and general connective tissues surrounding the geniohyoid. Many lingual veins extend close to the lateral surface of the tongue; an extensive network of large lingual veins lies in close proximity to (nearly surrounding) paired lingual arteries.

Hyoid. The odontocete hyoid skeleton (Fig. 10; see Reidenberg and Laitman, 1994, for a thorough review)

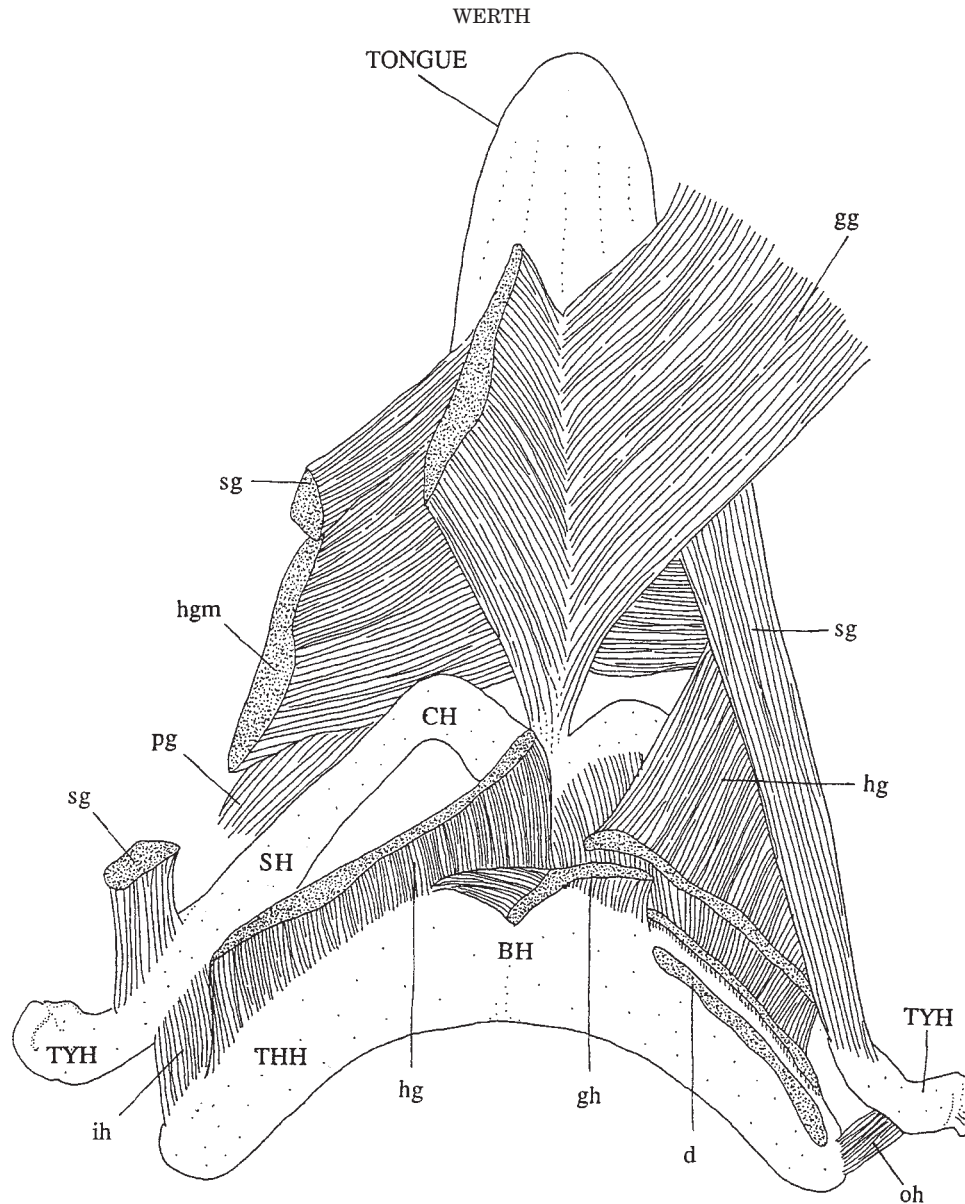


Fig. 7. Deep dissection of bottlenose dolphin (*Tursiops truncatus*) gular musculature in ventral view, with sternohyoid (sh) removed and hyoglossus (hg) and styloglossus (sg) cut and folded to side to reveal deeper stylohyal (SH, from which most interhyoid [ih] muscle has been removed).

consists of five well-developed elements with two paired arches or horns. The first and more cranial and dorsal cornu (homologous to the lesser horns of humans), comprising the tympanohyal, stylohyal, and ceratohyal elements, is a suspensory portion connecting the hyoid body (basal portion of flattened basihyal with thyrohyal "wings") to the tympanic and periotic bones near the stylomastoid foramen, and by means of ligamentous attachment to the paroccipital process of the exoccipital. Suspensory elements are not as flattened as the robust basal elements and are joined by flexible synovial joints except for epihyal-stylohyal fusion (Reidenberg and Laitman, 1994). The tympanohyal, a small cartilaginous segment at the proximal end that rarely ossifies, joins the stylohyal bone, a long, curved, three-sided rod with a prominent dorsal ridge or protuberance where the stylo-

glossus muscle originates. The stylohyal in turn attaches distally to a thin yet flexible cylindrical rod of cartilage, the ceratohyal. Normally, the only ossified segment of this arch is the stylohyal. Existence of the tympanohyal as a separate element in this chain has been questioned (Lawrence and Schevill, 1965; Oelschlager, 1986).

The second and more caudal and ventral cornu (homologous to the greater horns of humans) is a broad basal portion with paired thyrohyals projecting laterally or laterodorsally from a single median basihyal. As these elements are normally fully ankylosed in adults, with but a small ridge demarcating their margins, this large fused unit comprises a flattened, crescent-shaped structure spanning the throat and lying inferior to the laryngeal aditus (Reidenberg and Laitman, 1994). Bone growth continues until late in life in cetaceans, and

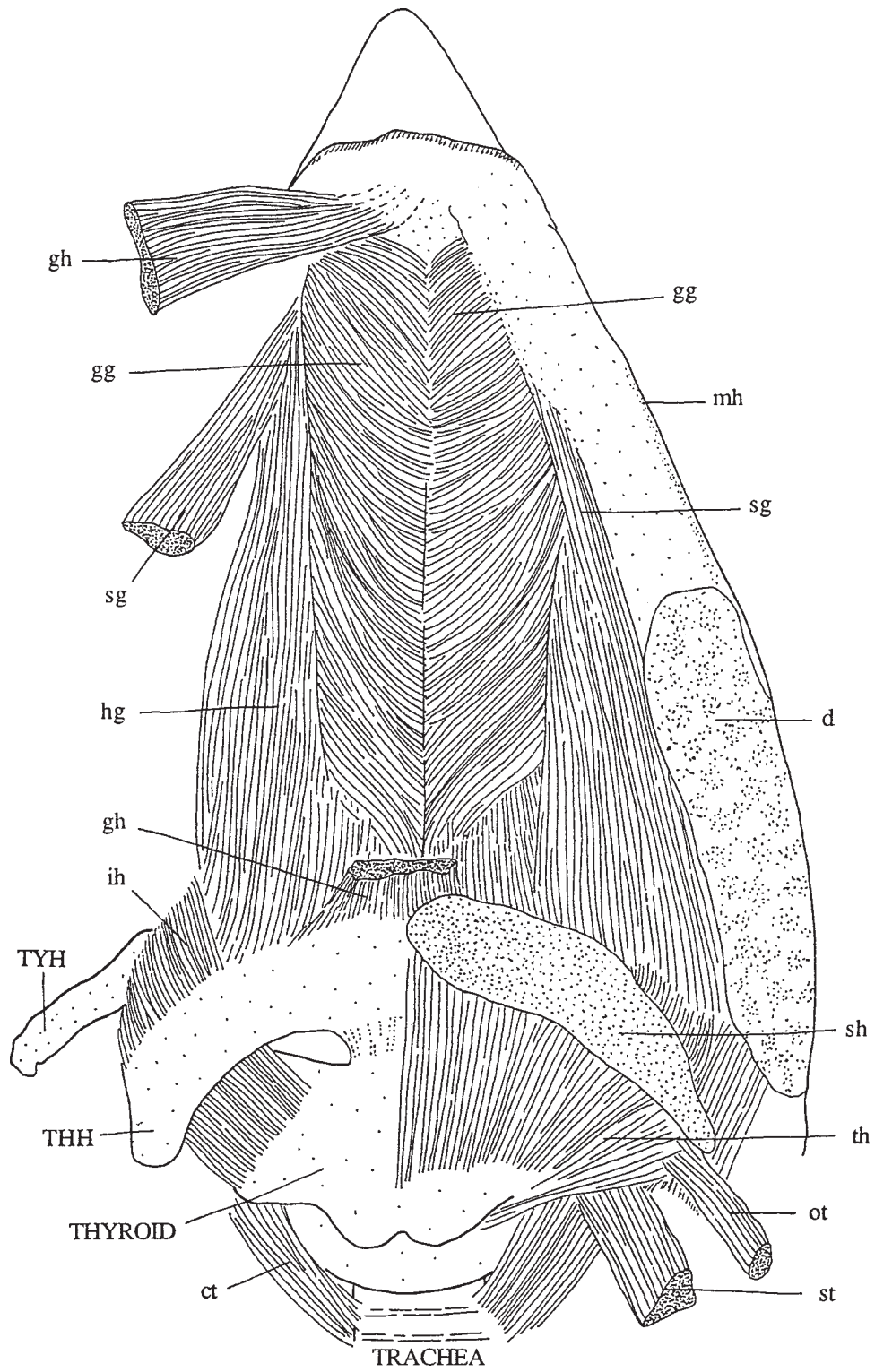


Fig. 8. Ventral view of hyolingual apparatus of long-finned pilot whale, *Globicephala melas*, with huge sternohyoid (sh) muscle removed to show strong muscular and tendinous connections between robust hyoid and larynx. Note fatty digastric (d, cut), extensive hyoglossus (hg), and wide genioglossus (gg).

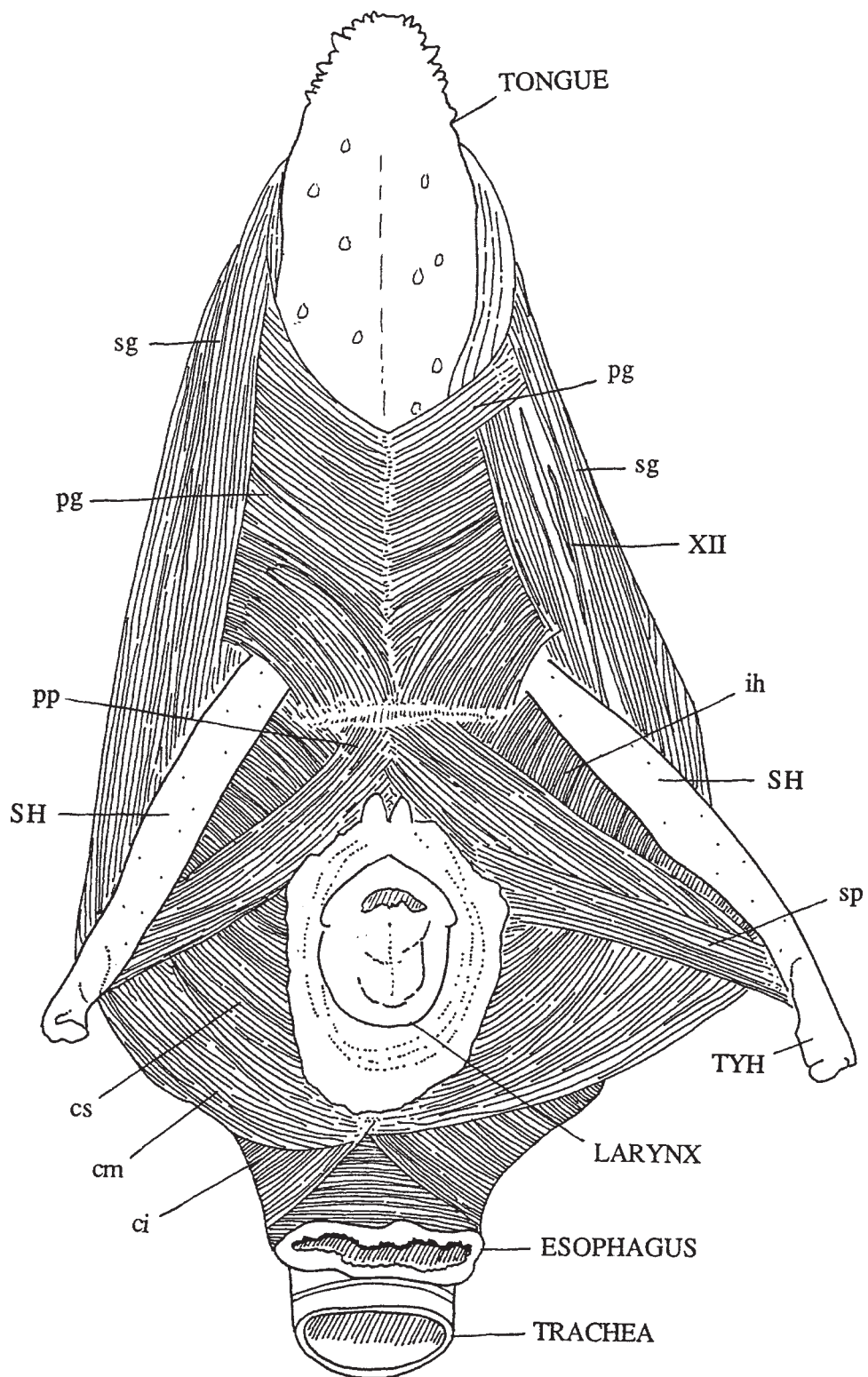


Fig. 9. Dorsal view of hyolingual apparatus of *Globicephala melas*, with larynx removed from intranarial position and hyoid severed at its attachment to skull. Note palatoglossal (pg) fibers, which meet in median raphe, large styloglossus (sg) and pharyngeal constrictors (ci, cm, cs), and hypoglossal nerve (XII) passing cranially before it dives ventral to tongue.

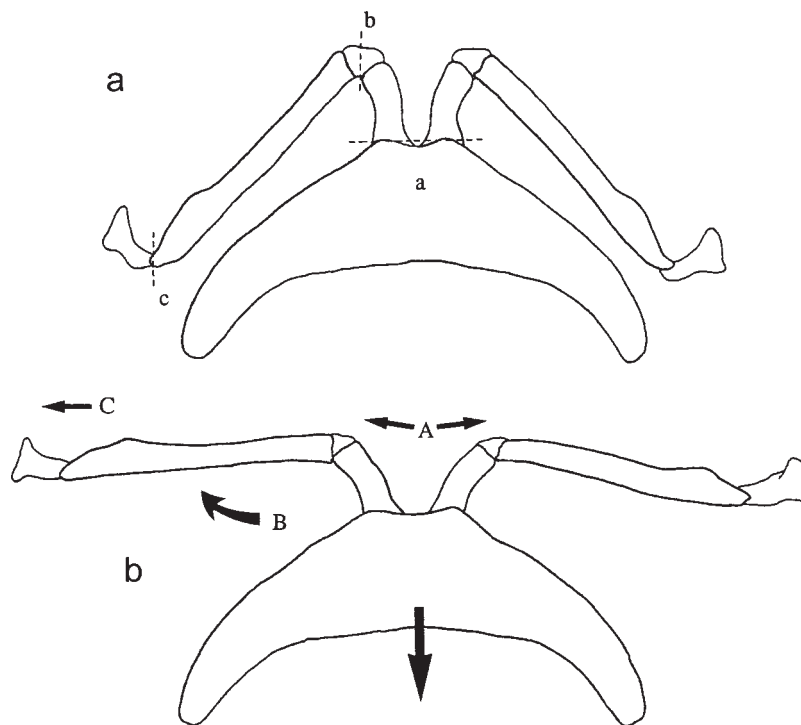


Fig. 10. Schematic diagram showing degree and range of motion in "flexed" and "extended" harbor porpoise (*Phocoena phocoena*) hyoid, showing [top] joints: **a**: basihyal and ceratohyal; **b**: ceratohyal and stylohyal; **c**: stylohyal and tympanohyal; and [bottom] joint exten-

sion by means of sternohyoid contraction, "opening" hyoid apparatus and allowing for greater caudal excursion of the hyoid body with concomitant retraction of extrinsic lingual musculature originating there.

hyoid ossification centers are notable for their fusion at a relatively early age (Flower, 1885; Lawrence and Schevill, 1965), although this is less definite in physterids, in which the robust hyoid elements typically remain distinct for an extended period.

The odontocete hyoid is thus a large and strong yet flexible and jointed structure (Fig. 10). An interhyoid muscle (also called ceratohyoid muscle, among other names; see Reidenberg and Laitman, 1994) extends between the two hyal arches, and a massive sternohyoid originates on the sternum and inserts on the hyoid body. The hyoid connects to the larynx, which is bound in an intranarial position by a sphincter of pharyngeal muscles originating from the pterygoid bones and palate (Reidenberg and Laitman, 1987, 2007a, this issue). There is little variation in hyoid shape within Delphinidae and only a slight progression in size, although *G. melas* has a substantially wider hyoid. Hyoids of *Physeter* and *Kogia* (juvenile and adult; Fig. 11) are relatively larger than in other odontocetes; they possess greatly flattened, rounded thyrohyal elements and robust stylohyals. The massive physterid hyoid is particularly impressive when compared with mysticetes of similar body size.

Comparative Analysis of Lingual Musculature

Analysis of proportional weights reveals that the genioglossus is twice as massive in the sperm whale as in the harbor porpoise (99% more muscle mass) and more than twice as massive (138%) as in the Atlantic white-sided dolphin (Werth, 2004a). In contrast, other lingual muscles are relatively smaller contributors to the total tongue

mass in documented or suspected suction feeders compared with raptorial feeders. The styloglossus occupies 9% of total tongue mass in *Physeter* compared with 21% in *P. phocoena* and 23% in *L. acutus*. The palatoglossus occupies 6% of total tongue mass in *Physeter* compared with 15% in *P. phocoena* and 17% in *L. acutus*.

Comparison of relative cross-sectional areas (areas of individual muscle organs relative to total tongue area as analyzed from serial sections) also reveals that extrinsic lingual muscles occupy a proportionally greater volume of the tongue in suction and filter feeding cetaceans than in raptorial feeders. In odontocetes the genioglossus is most extensive at the midpoint of the tongue body's length, where fibers of all three heads may comprise a third of the tongue's total cross-sectional area. At this midpoint, the genioglossus occupies 33% of the tongue's cross-sectional area in *Physeter* compared with 13% in *Lagenorhynchus acutus*. Comparable figures for the hyoglossus are 12% in *Physeter* and 3.5% in *L. acutus*. However, the styloglossus and palatoglossus, which do not extend as far cranially, are proportionally larger in raptorial feeders. At a point equaling 80% of the tongue body's total length (from the cranial tip), the styloglossus and palatoglossus occupy 6% and 7%, respectively, of the total tongue area in *Physeter* and 12% and 15% in *L. acutus*.

Extrinsic muscles are most extensive and intrinsic muscles occupy the least tongue volume in all mysticetes studied. Precise proportional mass data were not reliably available for mysticetes studied. However, at least in the bowhead, *Balaena mysticetus*, the genioglossus and hyoglossus are notably large, contributing an estimated 18% and 12%, respectively, of the fatty tongue's

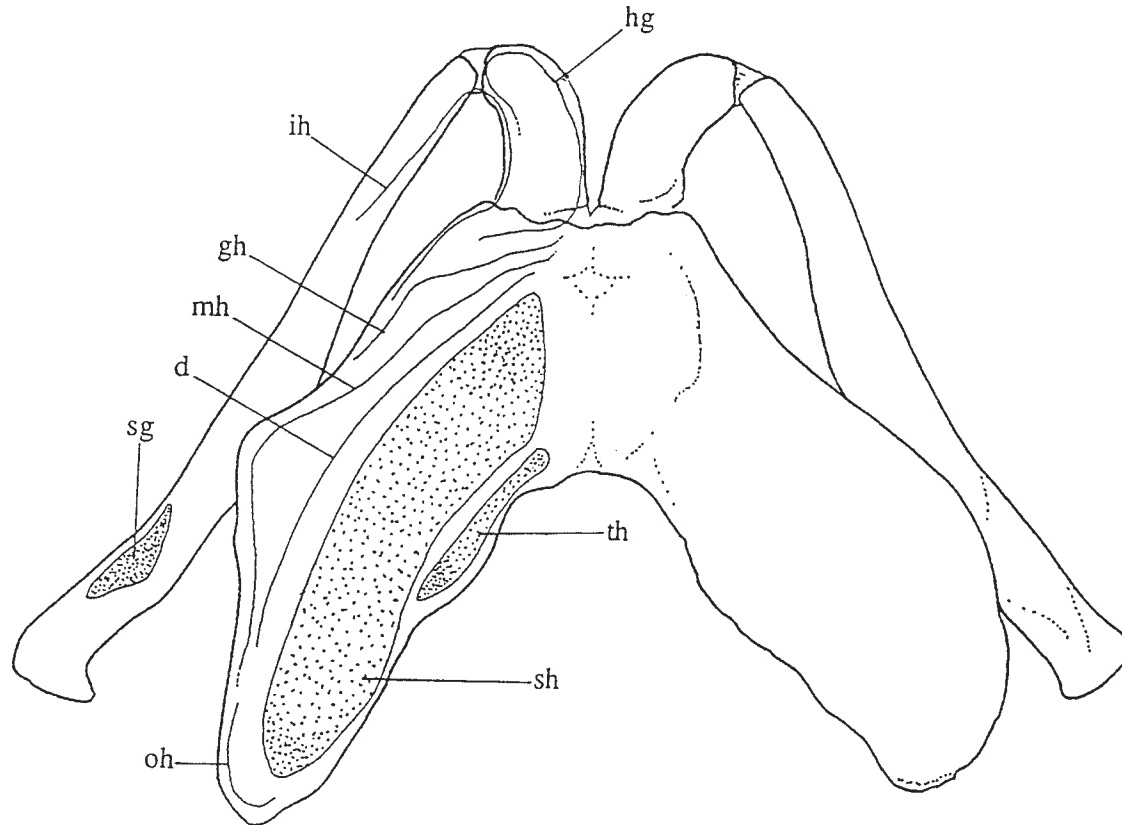


Fig. 11. Hyoid structure and muscle origins (ventral) in pygmy sperm whale, *Kogia breviceps*. Note robust stylohyals (SH) and enlarged, flattened thyrohyals (THH) as well as exceptionally large sternohyoid (sh) muscle origin. Scale bar = 5 cm. Abbreviations in all figures follow Lawrence and Schevill (1965): b, buccinator; BH, basihyal; CH, ceratohyal; ci, constrictor pharyngeus inferior; cm, constrictor pharyngeus medius; cs, constrictor pharyngeus superior; ct, cricothyroideus; d, digastricus; gg, genioglossus; gh, geniohyoideus;

hg, hyoglossus; hgm, hyoglossus [medial]; ih, interhyoideus (ceratohyoideus; Reidenberg and Laitman, 1994); mh, mylohyoideus; oc, orbicularis oculi; oh, occipitohyoideus; or, orbicularis oris; ot, occipitohyoideus; pg, palatoglossus; pp, palatopharyngeus; sc, sphincter colli profundus and primitivus; sg, styloglossus; sh, sternohyoideus; SH, stylohyal; sp, stylopharyngeus; st, sternothyroideus; th, thyrohyoideus; THH, thyrohyal; TYH, tympanohyal.

overall mass. These muscles are likely to be as massive if not more so in *Eschrichtius*. Although fiber interdigitation often makes it difficult to discern purely intrinsic from extrinsic lingual musculature, results from comparative myological analysis of the right whale, *Eubalaena glacialis*, reveal that along the entire length of the tongue (as indicated by transverse sections), intrinsic muscles occupy no more than 18% and as little as 6–9% of tongue's total cross-sectional area. These findings can be contrasted with those of a documented suction-feeding odontocete, *G. melas*, in which intrinsic lingual muscles occupy 26% of the tongue's cross-sectional area near its cranial tip, reach a zenith of 37% near the longitudinal midpoint, and decline to 22% near the tongue's caudal root, or with those of an evident raptorial species, *D. delphis*, in which intrinsic musculature occupies 45–69% of tongue area along its length (greatest values again near longitudinal midpoint).

DISCUSSION

Filter Feeding

Balaenopterid whales (genera *Balaenoptera* and *Megaptera*) display the most extreme morphological speciali-

zation and most highly modified tongue of any aquatic mammal. Along with the loose tongue and oral floor, balaenopterid feeding relies on other adaptations including accordion-like longitudinal elastic throat pleats; wide-opening jaws with locking joint to create a hydrostatic seal and prevent opening during rapid locomotion; frontomandibular stay to store kinetic energy for jaw closure; and unfused mandibular symphysis with Y-shaped fibrocartilage arms extending along mandibular rami (Pivorunas, 1977). During engulfment, the rorqual tongue folds inward into the cavum ventrale with subsequent massive gular expansion. This pouch, which receives engulfed water and the displaced bag-like tongue, extends over the thorax to the umbilicus, momentarily giving the normally slim body a tadpole shape. The total volume of a large, hypothetical blue whale (*Balaenoptera musculus*) has been calculated to increase 600 percent during feeding, from roughly 5,550 to 35,700 cubic feet, with perhaps 1,000 tons of water engulfed in a single gulp (Storro-Patterson, 1981). Pivorunas (1979) gave a more conservative estimate of at least 60 m³ (approximately 70 tons) of water ingested in one gulp, an amount of water equal to roughly 50% of a blue whale's total body volume. This remarkable

capacity for gular distention is seen in all rorquals. Rather than expanding a space to create negative pressure and draw water in, rorquals unlock their jaws and relax adductor musculature to open the mouth (at least 30°, and up to 90°), which suddenly fills with water in much the same way as a bag is opened by rapidly pulling it through air, by both mandibular depression and slight cranial elevation (Arnold et al., 2005; Kot, 2005). Positive inertial pressure forces open the space into which water and prey flow; seawater is passively enveloped rather than displaced forward or sucked internally (Orton and Brodie, 1987). Smaller rorquals may retract the tongue to varying degrees to pull in a water stream that fills the oral sac toward the rear rather than sides (Pivorunas, 1979), avoiding a wave of resistant pressure that could disperse prey at the entrance to the mouth and thus interfere with capture. Because the expansive pouch allows huge quantities of water to enter, pressures build only when the incurrent stream slows (Pivorunas, 1979).

Lambertsen (1983) elucidated the dynamic inversion of the balaenopterid tongue into the intracaval position. Experiments with the head of a minke whale (*Balaenoptera acutorostrata*, a species whose tongue is bulky relative to other rorquals) demonstrated that, when the mouth fills with water, the loose tongue folds into the cranial portion of the cavum, between its inner and outer walls, initiating distention of the capacious oral pouch. The inverted tongue acts as an elastic sac whose lumen is continuous with the buccal cavity and whose walls are formed by the now-invaginated tongue and nonlingual intermandibular lining. The mouth balloons out in pelican-like manner as distensible pleats expand. Lambertsen (1983) speculated that closure and expulsion occurs by active contraction of jaw adductors (especially temporalis) and elastic recoil of the pouch. Contraction of lingual musculature is not implicated in water expulsion and return of the tongue to its resting (extracaval) position. Rather, Orton and Brodie's biomechanical study of the throat wall (1987) outlined three sources that deflate the pouch and expel water: dynamic pressure of water coming to a stop at the front of the mouth, stored elastic energy in blubber and other tissues around the cavum, and possibly active contraction of muscle underlying blubber.

In contrast to balaenopterids, balaenids are slow, rotund cruisers that filter a constant current of water through a mat of long, finely fringed baleen to skim dense swarms of tiny zooplankton (Watkins and Schevill, 1979; Lowry and Frost, 1984; Mayo and Marx, 1990; Lambertsen et al., 2005). Water enters through a large cranial cleft, the subrostral gap, between left and right baleen racks, flows through the oral cavity over the tongue, then flows laterally between baleen plates and passes out a gutter-like groove or depression, the orolabial sulcus, at the rear of the lower lip. Because this flow path becomes constricted, water exits the mouth at higher flow velocity than it enters, creating a Bernoulli effect that in turn induces perpendicular (medial to lateral) Venturi flow from the center of the oral cavity through the baleen filter, creating slight suction pressure toward the anterior of the mouth, confirmed by physical and mathematical modeling, that precludes formation of an compressive bow wave to alert and disperse prey (Werth, 2004b). The meager, isolated balaenid lin-

gual muscles described here relate to the limited role of the tongue (in contrast to rorquals and the gray whale) in capturing prey. Nonetheless, kinematic analysis of open-mouth behavior (Werth, 1990) reveals that the firm, elevated balaenid tongue sweeps laterally to deflect or channel water to the baleen racks, as suggested by Nemoto (1959) and Gaskin (1982), potentially to aid in creation of favorable flow currents or preferentially to divert prey-laden water to one side of the mouth. Foliate papillae may act as taste buds, as proprioceptors to determine tongue position, or as pressure or mechanoreceptors to detect water flow or contact with prey or baleen.

The gray whale (*Eschrichtius robustus*) uses benthic suction feeding, turning on its side and skimming the bottom while rapidly depressing and retracting the tongue to stir sediments and suck in prey, primarily molluscs and gammaridean amphipods, that are winnowed from a single mouthful of muddy water with stiff, short, coarse baleen (Murison et al., 1984; Nerini, 1984; Oliver and Slattery, 1985; Nelson and Johnson, 1987). Although *Eschrichtius* occasionally scrapes prey from strands of kelp or skims fish and squid in open water (even gulping like rorquals; Sund, 1975), it is the only mysticete to ingest food with strong, internally generated suction pressures, as was first documented in a young captive observed to suck in fish and squid with expansion of gular grooves and subsequent oral water expulsion (Ray and Schevill, 1974). Although not examined directly for this study, the more distinct, traditional arrangement of gray whale lingual musculature doubtless reflects this species' suction ingestion, as does the thicker, more rugose hyoid, indicating a strong, expansive hyoglossus muscle.

Extrinsic lingual musculature is commonly implicated in positional changes of the tongue, whereas intrinsic fibers are thought to be primarily although not totally responsible for deformational shape changes. The profusion of extrinsic fibers in mysticetes was not unexpected in fetal and neonate animals, in which lingual retraction and depression might be expected to aid in suckling, yet this finding applies to adults as well, which have prominent genioglossus and hyoglossus muscles with presumably similar function. The tongue may function as a plow to preferentially direct prey-laden water to one side of the mouth in balaenids, and it can expel water from the mouth in all mysticetes, but it is unlikely that the tongue plays other roles in foraging, especially as the mouth closes for engulfment in intermittent filter feeders. However, lingual movements are likely significant once prey have been captured but not yet swallowed, especially when prey are tiny (as in Balaenidae) and may become entangled in fine baleen fringes instead of dropping off in a pile of fish or krill or a slurry of copepods. Retention of prey by baleen is straightforward, but the matter of how food is removed from this filter may depend on any of three potential mechanisms that each rely on some degree of tongue mobility (Werth, 2001). The simplest idea is that the tongue elevates and retracts to scrape trapped items from the baleen mat directly. Lingual depression and retraction would then allow a bolus of prey collected on the central furrow to be swallowed. A second mechanical hypothesis depends on observations of Southern right whales shaking or "flapping" lips between filtering bouts to indirectly dis-

lodge prey. Right whale “nodding” behavior (Mayo and Marx, 1990) suggests a third possibility of hydrodynamic reverse-flow “backwash” by means of brief re-entry of water into the mouth. Rapid tongue depression coupled with jaw abduction and perhaps outward rotation could create sufficient negative pressure to draw cleansing water in. The ensuing current would transport prey to the middle of the oral cavity, where they would accumulate and be transported to the oropharyngeal isthmus for swallowing. All solutions depend on some degree of lingual mobility, and tongue movements of all three hypotheses involve changes in position rather than shape, which fits myological findings of right and bowhead whales that extrinsic lingual muscles are greater contributors to the tongue body than are intrinsic muscles that exist solely within it.

Suction Feeding

The anatomical mechanism of suction feeding involves rapid, piston-like retraction and depression of a flat, hemicylindrical tongue, creating an empty space of negative (less than ambient) pressure to draw in water and prey. Ingested water in this bidirectional flow system is momentarily accommodated by the expandable, elastic pharynx and in many cases by external throat grooves, and possibly by the stomach as well. Influx this far caudally (and internally) is doubtful, because it could result in digestion of undesirable quantities of seawater, yet Harrison et al. (1967) showed that the odontocete forestomach can forcibly eject ingested water, and cetacean excretory capabilities are sufficient to counter this osmotic load. Generation of suction by pulmonary expansion and subsequent inhalation is untenable in odontocetes due to the virtually permanent patent airway, effectively separating the oropharynx and trachea. Expansion of the hyoid complex for suction feeding occurs by means of joint extension from contraction of infrahyoid (mainly sternohyoid) musculature. The ceratohyoid (interhyoid) fixes the first arch to the second as the latter is retracted and, with tongue protractors (e.g., genioglossus and geniohyoid), returns the hyoid to its normal flexed position. Ventral rotation at the hyoid’s dorsal attachment to the skull adds additional mobility, again contributing to lingual depression and retraction.

The tongue of suction feeders is a large, firm, muscular hydrostat with an extensive system of lateral longitudinal folds or plicae attesting to its marked mobility. The tongue has a smooth, flat dorsum and does not taper but maintains uniform height and width, making it a perfect hemicylindrical piston. According to Sonntag (1922), odontocetes are unique among mammals in the unusually caudal position of the tongue; Donaldson (1977) suggests this limits entry of water into the oropharynx. In *Physeter* (with a highly caudal tongue, posterior to tooth rows) prey are likely sucked directly into the oropharynx (Werth, 2004a, 2006a). Marginal papillae that are common in tongues of suction feeders are present in most newborn mammals, where they create a tight seal between the tongue and the roof of the oral cavity for suckling (Chibuzo, 1979). Retention of this neonatal feature is strongly suggestive of sucking activity in certain adult odontocetes. Sokolov and Volkova (1973) also propose a receptor function for these “fimbriae,” but preliminary histological analysis (Werth,

1992) does not support their claim. Ping (1927) and Sonntag (1922) speculated that lingual papillae might also serve as mechanoreceptors. Sokolov and Volkova (1973) suggested lingual glands may function in extrarenal salt excretion.

The tongue is normally held in a retracted position and is surrounded by a sheath of slick, smooth fascial layers that permit it to move readily in a craniocaudal line. Heyning and Mead (1991) reported that the ziphiid tongue slides extremely easily, as if on a lubricated track. The ventral sublingual opening, which appears hollow in frozen bisected specimens, may be filled in life with areolar tissue or serous fluid and may serve as an area into which the tongue and its ventral extrinsic muscles move when depressed. The fascia of this sublingual space may promote gular expansion as well as lingual mobility, allowing greater suction pressure and water influx.

Throat grooves are found in large suction feeding odontocetes (*Physeter*, ziphiids) where gular expansion from engulfment of large quantities of water would otherwise be prohibited by thickness and rigidity of the overlying blubber (Boschma, 1938; Hubbs, 1946; Clarke, 1956; Ross, 1987). Heyning and Mead (1991, 1996) confirmed that these folds are distensible and controlled by contraction of superficial ventral musculature (perhaps the sphincter colli [panniculus carnosus] profundus or primitivus, or even a novel offshoot of these muscles) in ziphiids, suggesting they may serve as active rather than merely passive expanders of the pharynx. They also found that ziphiid intrinsic lingual musculature is quite complex and that certain gular muscles (i.e., interhyoid and sternohyoid) are relatively larger in beaked whales than in other putative suction-feeding odontocetes, correlating with their larger hyoid skeletons.

In all cases, water ingested by means of suction exits the mouth by means of gape closure and lingual elevation. The familiar ability of captive odontocetes to spray water onto a trainer or audience member, over great distances (6 m) and with great accuracy (Essapian, 1965; Donaldson, 1977), demonstrates that large volumes of water can be held in the oral cavity or oropharynx and expelled by tongue elevation and protraction. Captive pilot whales were similarly observed to expel water immediately after suction ingestion of prey (Werth, 2000a). Expulsion of a concentrated stream of water also suggests the capacity of odontocetes to form a rounded mouth opening, as useful in sucking as in spitting. That *Tursiops* (bottlenose dolphin) and *Orcinus* (killer whale) can spray not only powerfully but accurately, as detailed by Essapian (1965), is testament to the mobility and neural control of extrinsic lingual musculature, and to the ability of some odontocetes (*Delphinapterus*, Brodie, 1989; *Globicephala*, Werth, 2000a) to use limited facial musculature (e.g., buccinator, orbicularis oris) to close one or both sides of the mouth. Martin (1990) suggested such squirting capabilities may aid belugas in dislodging benthic prey. Although the tongue’s cranial free tip is small relative to other mammals it is apparently not as immobile as commonly thought. Caldwell and Caldwell (1972) and Donaldson (1977) described lingual protraction in *Tursiops* and *Orcinus*, especially evident in juveniles or adults learning new and difficult tasks, as with humans. They described an incident in which a leaping bottlenose dolphin accidentally bit its protruded tongue

upon falling into the water, leaving a line of punctures that clearly demonstrate marked lingual mobility in this species.

Oral and gular movements visible during pilot whale suction feeding (Werth, 2000a) suggest that lingual, hyoid, and/or mandibular motions aid in prey transport. The tongue likely retracts to carry prey items to the faucial pillars for swallowing; these motions might also reposition prey in the oral cavity. The tongue functions in deglutition, by forcing prey into the oropharynx (possibly by a second tongue retraction, immediately after lingual retraction for suction generation and prey ingestion; as noted earlier *Physeter* probably uses a single retraction) while simultaneously or subsequently expelling water. Concurrent tongue elevation and sealing of the tip against the palate would force excess water out of the oral cavity, preventing swallowing of excess water with food. It is presumed that the tongue plays a critical role in repositioning grasped prey before swallowing. Kleinenberg et al. (1969) and Donaldson (1977) proposed that the tongue reorients food, as it is pressed to the palate, with lateral and cranio-caudal movements, so that items can be transported to the rear of the oral cavity and swallowed in the proper orientation to avoid damage from projecting fins and spines. Kinematic analysis of suction feeding in *Globicephala* (Werth, 2000a) shows that, at least this species, and probably others (including beaked whales; Madsen et al., 2005), uses locomotor maneuvers (e.g., body rotation) to ingest prey head first, so that fins or spines do not catch in the throat, yet when grasping prey by the tooth rows use a combination of prehensile lingual movements and tongue-generated suction currents to reposition prey so that they are likewise swallowed head first.

Raptorial Feeding and Comparative Conclusions

In some aquatic birds a modified tongue may, with the beak, perform this grasping function, yet raptorial odontocetes typically use dentition to seize and hold prey. It is likely that raptors use gular suction to transport prey to the rear of the oral cavity for swallowing, and that suction ingestion evolved from use of suction to transport prey with loss of the grasp and transport steps (Werth, 2006a). Experimental evidence (Werth, 2006b) indicates that suction feeders benefit from adoption of a blunt head with a small, circular mouth opening; paleontological and osteological evidence (Norris and Møhl, 1983; Werth, 2006a) reveals precisely such a trend in odontocete cranial evolution. Nonetheless even raptorial feeders could use, in combination with other foraging methods, intraoral suction with small gape (jaws opened slightly) for prey acquisition, expanding gape and grasping prey when they are close. Use of some amount of suction for prey transport, and potentially even for prey ingestion, in all odontocetes may explain why odontocete lingual variation involves differences of degree rather than kind.

Nonetheless comprehensive comparative analysis of attachments, positions, and actions of lingual and hyoid musculature in this and previous studies (Heyning and Mead, 1996; Werth, 1990, 1992, 2000b,a) indicates significant differences between suction feeding versus raptorial odontocetes in the size, shape, thickness, cur-

vature, and flexibility of the hyoid, as well as in the proportional weight and relations of the sternohyoid, genio-glossus, and hyoglossus, which are substantially greater relative contributors to the total mass of the tongue in *Physeter*, *Kogia*, *Globicephala*, and *Grampus*, all known or suspected suction feeders.

Proportional weight comparisons ultimately proved unsatisfactory because total weights of whole extrinsic muscles (not merely the portion projecting inside the tongue body) were used and because varying amounts of lingual connective and adipose tissue were included, rendering comparisons between cetacean species and especially between suborders difficult. Comparison of relative cross-sectional areas (areas of individual muscle organs relative to total tongue area as analyzed from serial sections) proved more fruitful, indicating that, while extrinsic lingual muscles follow strikingly similar paths of insertion in all cetaceans, they occupy a proportionally greater volume of the tongue in suction and filter feeding cetaceans than in raptorial feeders, with obvious functional implications. This holds true for all extrinsic musculature, but again the difference is most pronounced with the genio- and hyoglossus. Drawing functional inferences from such limited cross-ordinal data is dubious, especially when considering the imprecise histological and functional separation of classic extrinsic and intrinsic lingual muscles previously noted, but the simplistic conclusion that raptorial cetaceans rely more heavily on lingual shape changes for prey capture, ingestion, and transport seems warranted.

Thermoregulation and Other Functions

Cetacean (especially mysticete) tongues show not only muscular but also vascular adaptations, including classic periarterial venous retia (Fig. 2) that prevent or facilitate heat loss. Such retia were not observed in roqual and odontocete tongues dissected for this study but are readily apparent in balaenid and gray whales. Counter-current retial vessels near the tongue root ensure that warm blood cools before it can lose heat in the blubberless mouth, and likewise that cool venous blood returning to the body core is simultaneously warmed; these synchronous counteractions together prevent hypothermia in frigid water. When blood pressure rises during periods of high activity, central arteries expand to close adjacent periarterial veins, forcing blood to flow through surface rather than deep lingual veins, allowing for temporary cooling, as also occurs in cetacean fins, flippers, and flukes (Schmidt-Nielsen, 1997). There are reports of whales swimming open-mouthed in waters devoid of plankton, and the balaenid palate likewise bears highly vascularized retia to regulate heat loss in frigid polar waters (Heyning et al., 1993).

Vascular adaptations have been reported in the gray whale tongue (Heyning and Mead, 1997), which has an extensive network of heat-exchanging retia arranged as a bilateral pair of bundles, each with over fifty retia laid in parallel, that converge at the base of the tongue. These lingual retia are far larger than other retia in *Eschrichtius* associated with locomotor appendages. Because veins within each lingual rete are small and thin-walled, they collapse when the large, flaccid tongue is dissected, especially when the specimen is neither small nor fresh, and so had previously escaped detection by anatomists. Heyn-

ing and Mead (1997) also took infrared temperature measurements from the oral cavity of a captive juvenile gray whale, confirming that little heat is normally lost through the tongue, even though it is highly vascularized and lacks insulating blubber. Simple vasoconstriction of lingual vessels would prevent heat loss yet impair muscle contraction, and the vivid pink tongue of this live whale indicated normal blood flow. Lingual (and palatal) retia may be a universal feature of mysticetes (Heyning, 1998; Heyning and Mead, 1998), as the mouth is a critical site for heat exchange during filtration. Absence of such vascular adaptations in odontocete species surveyed for this study (including large *Physeter*) suggests either less of a need to prevent oral heat loss in toothed whales or, alternatively, different thermoregulatory control surfaces, such as locomotor appendages.

The high adipose content of balaenid tongues not only aids in insulating this susceptible organ but also reflects seasonal fat storage. These whales feed in summer at high (boreal or austral) latitudes, migrating to warmer waters in lower latitudes during winter, where some mating and all calving (largely because small calves have much higher relative surface area) but little feeding occurs, such that there are prolonged periods (up to 6 months) of fasting. How much the tongue contributes to caloric storage in balaenids is unknown, but gross anatomical evidence from bowhead whales butchered during subsistence hunting by Inupiat Eskimos at Point Barrow, Alaska, during both spring and fall migrations (to and from summer feeding in the Beaufort Sea, respectively) strongly suggest that this amount is substantial (Werth, previously unpublished data). Further study including quantitative analysis of the role of fat storage in the tongue of balaenids and other mysticetes is ongoing. The rorqual tongue may also serve as a seasonal nutritive store of adipose tissue (Howell, 1930; Tarpley, 1985).

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