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REVIEW ARTICLE

Cetacean tongue mobility and function: A comparative review

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Abstract

Cetaceans are atypical mammals whose tongues often depart from the typical (basal) mammalian condition in structure, mobility, and function. Their tongues are dynamic, innovative multipurpose tools that include the world's largest muscular structures. These changes reflect the evolutionary history of cetaceans' secondary adaptation to a fully aquatic environment. Cetacean tongues play no role in mastication and apparently a greatly reduced role in nursing (mainly channeling milk ingestion), two hallmarks of Mammalia. Cetacean tongues are not involved in drinking, breathing, vocalizing, and other non-feeding activities; they evidently play no or little role in taste reception. Although cetaceans do not masticate or otherwise process food, their tongues retain key roles in food ingestion, transport, securing/positioning, and swallowing, though by different means than most mammals. This is due to cetaceans' aquatic habitat, which in turn altered their anatomy (e.g., the intranarial larynx and consequent soft palate alteration). Odontocetes ingest prey via raptorial biting or tongue-generated suction. Odontocete tongues expel water and possibly uncover benthic prey via hydraulic jetting. Mysticete tongues play crucial roles driving ram, suction, or lunge ingestion for filter feeding. The uniquely flaccid rorqual tongue, not a constant volume hydrostat (as in all other mammalian tongues), invaginates into a balloon-like pouch to temporarily hold engulfed water. Mysticete tongues also create hydrodynamic flow regimes and hydraulic forces for baleen filtration, and possibly for cleaning baleen. Cetacean tongues lost or modified much of the mobility and function of generic mammal tongues, but took on noteworthy morphological changes by evolving to accomplish new tasks.

KEYWORDS
filter feeding, ingestion, morphology, oral transport, suction feeding, swallowing

1 | INTRODUCTION

1.1 | Cetacean origins and uniqueness

For most of mammalian history, the basic body plan resembled a small, shrew-like fossorial or arboreal creature. From this origin, many remarkable groups evolved: gliding colugos and flying bats; massive herbivorous elephants, rhinoceroses, and hippopotamuses; ant-eating aardvarks and armadillos; human beings; and countless extinct forms. Perhaps no mammals departed as much from this starting point as Cetacea, which arose within Artiodactyla (McGowen et al., 2009; Thewissen et al., 2007); both are occasionally classified together as Cetartiodactyla (Prothero et al., 2021). Unlike terrestrial artiodactyls (even-toed ungulates, including hippopotamuses, pigs, antelopes, deer, giraffes, camels, and cattle), cetaceans secondarily reverted to the marine habitat of early vertebrate ancestors (Kelley & Pyenson, 2015), and thereby changed tremendously in structure, function, and ecology (Howell, 1930; Kellogg, 1928; Thewissen & Bajpai, 2001). This clade (Infraorder Cetacea: whales, dolphins, porpoises) exhibits exceptionally large

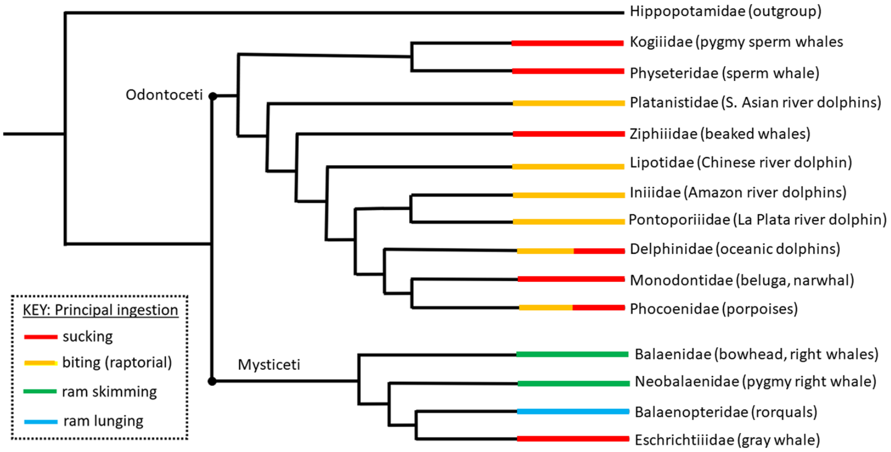

FIGURE 1 Cetacean phylogeny (Gatesy et al., 2013; McGowen et al., 2009) showing principal feeding (hence tongue use) methods: biting, suction, skim, and lunge (=gulp) feeding, or combination thereof. It might appear as if basal odontocetes used tongue-driven suction ingestion (Table 1 #6), but this figure depicts only extant taxa. Stem odontocetes likely used biting based on fossil jaws and dentition. Sucking independently evolved in multiple lineages because of aquatic effectiveness.

brains and complex social behavior. It includes the largest species known to have ever lived (Berta et al., 2015). From flukes and flippers to blowholes and baleen, cetaceans are truly atypical mammals (Pyenson, 2019). Their remarkable anatomical and physiological adaptations include vascular retia and elevated myoglobin (Reynolds & Rommel, 1999), blubber up to 50 cm thick (Werth, 2020), a heart that beats as few as two times per minute (Goldbogen et al., 2019), and elaborate nasal passages capable of producing echolocatory sonic pulses ranging from 0.2 Hz to 150 kHz (Geisler et al., 2014; Mourlam & Orliac, 2017; Pilleri, 1990).

These staggering departures from the traditional mammalian bauplan are paralleled by structural and functional changes in nearly every organ system. The digestive system in cetaceans involves a multi-chambered stomach featuring a unique blend of hydrolytic enzymes (Wang et al., 2016) and in some species fermentation of volatile fatty acids (Herwig et al., 1984). Cetacean dentition also differs greatly from the typical mammalian condition in gross form and enamel microstructure, in relation to their aquatic habitat and its consequences for the tongue's role in feeding (in nearly all cases swallowing prey whole without mastication). In extant odontocetes, dentition is homodont, monophyodont (emerging in a single generation, lacking deciduous teeth), and often polydont, exceeding the normal eutherian maximum of 42 teeth (Werth, Loch, et al., 2019). Further, in many cetacean species enamel is thin and exists solely in easily worn apical caps; where present, enamel is often poorly formed and lacks the complex prismatic microstructure characterizing eutherians (Werth, Loch, et al., 2019). Whales of the cetartiodactyl Parvorder Mysticeti lack teeth altogether, except as rudimentary anlagen that occasionally develop but do not erupt (Berta et al., 2016; Deméré et al., 2008). In lieu of teeth, mysticetes capture prey with a novel keratinous tissue, baleen, which hangs from the palate in paired, comb-like series of triangular plates (Pivorunas, 1976; Young, 2012).

These unusual digestive characteristics, from baleen and teeth to gastric chambers and secretions, clearly arose from cetaceans' unusual (for mammals) marine habitat. Like other marine mammals, cetaceans secondarily reverted to the aquatic habitat of long-ago piscine ancestors (Slijper, 1962). However, as air-breathing endotherms, marine mammals retain most plesiomorphic mammalian traits. Their anatomy and physiology notably differ from that of other aquatic vertebrates, especially fishes (Reidenberg, 2007; Reynolds & Rommel, 1999).

Cetaceans are the oldest marine mammals (appearing c. 50 Ma) and, judging by taxonomic, biogeographic, and ecological/trophic diversity, the most successful (Berta et al., 2015). Unlike pinniped carnivorans (seals, sea lions, and walruses), cetaceans spend their entire lives at sea, often at great depth, from polar regions to equatorial tropics (Pyenson, 2019). Unlike sirenians (manatees and dugongs), cetaceans inhabit not only shallow coastal waters but also open oceans (Fordyce, 2018). Cetaceans can swim 50 km/h and dive to almost 3000 m (Schorr et al., 2014) for nearly 4 h (Quick et al., 2020). Cetacean diets range from tiny (1–10 mm) copepods to giant and colossal squids or other marine mammals (seals and sea otters to huge mysticetes), with many fish, cephalopods, and invertebrates in between (Marshall & Pyenson, 2019; Werth, 2000b). Cetacean digestive anatomy and physiology reflect varied foraging methods and feeding mechanisms, including biting, suction feeding, and filter feeding (Figure 1; Marshall & Goldbogen, 2015; Werth, 2000b). Mysticete filtering, in which small schooling fish or zooplankton are separated from seawater by baleen, in turn is powered by ram, lunge, or suction ingestion (Werth, 2013). Suction and filter feeding require an aqueous medium (Liem, 1990; Sanderson & Wassersug, 1990, 1993; Wainwright & Day, 2007), and therefore are not found in terrestrial mammals, including non-cetacean artiodactyls. Hence the cetacean mouth notably diverges from its basal mammalian form.

TABLE 1 Tongue functions (feeding and non-feeding) in Cetacea compared to typical mammals.

Feeding-related tongue functions of generalized mammals [*not found in Cetacea]
1. Food prehension & ingestion
2. Intraoral food transport
3. *Manipulating/positioning food during mastication (chewing)
4. Securing food against teeth and palate
5. Deglutition (swallowing)
Feeding-related tongue functions unique, among mammals, to cetaceans [and some pinnipeds^{+}]
6. Suction ingestion^{+}
7. Expulsion/purging of ingested water^{+}
8. Hydraulic jetting to locate/manipulate/reorient prey^{+}
9. Creating and sustaining flow regime/gradient for filtration
10. Channeling water flow within mouth (to baleen racks)
11. Invagination into ventral gular pouch (*cavum ventrale*) during lunge feeding
12. Cleaning baleen filter
12A. via direct mechanical contact (or jaw/head motion)
12B. via suction-generated "backwash" current flow
Generalized mammalian tongue functions unrelated to solid food consumption
[*absent or < <highly limited in Cetacea]
13. *Lapping liquid/drinking
14. <<Suckling
15. <<Taste reception
16. *Respiration
17. *Vocalization
18. *Coughing
19. <<Emesis (vomiting)
20. *Thermoregulation via respiratory panting
Tongue functions of cetaceans unrelated to solid food consumption
21. Thermoregulation via lingual vascular adaptations
22. Thermoregulation via exposing palatal retia
23. Adipose tissue for insulation and seasonal nutritional stores

1.2 | Tongue origins and functions

The tongue lies at the center of the mouth, literally and figuratively. Along with its affiliated musculature arising from the hyoid (together the hyolingual apparatus), the tongue is a key structure for many vital functions (Chibuzo, 1979; Iwasaki, 2002). It lies at the crucial intersection of oral and nasal passages and plays central roles in multiple organ systems (muscular, digestive, sensory, respiratory, etc.; Herring, 1993). In mammals and other tetrapods, the tongue performs or assists numerous essential duties throughout life, beginning immediately upon birth, related to solid/liquid ingestion, transport, and swallowing in mammals (Table 1; Sokoloff & Burkholder, 2012). This is in marked contrast to fishes, which lack a muscular tongue and generally have no tongue-like analogue (Schwenk, 2000). When a tongue-like structure exists in fishes, it is usually a simple fold of the oral floor over the basihyal bone or cartilage, often stiffened with keratinized epithelium and fibrous connective tissue (Konow et al., 2011), to hold prey within the oral cavity. It may press food against marginal or palatine teeth or pharyngeal folds (Lauder, 1985), and can aid swallowing (deglutition). However, fish lack a tongue that is either protrusible or capable of shape deformation, as are tongues of many mammals, birds, reptiles, and amphibians (Iwasaki, 2002; Schwenk, 2000).

Apart from instances where highly specialized tongues are used to detect and ingest food, the vertebrate tongue arguably reaches a zenith of structural and functional complexity in mammals, which depend on the tongue's key roles in suckling and mastication (Abd-el-Malek, 1955). These uniquely mammalian activities (although herbivorous dinosaurs and other reptiles possibly used rudimentary mastication) require complex, rhythmic lingual motion (Rossignol et al., 1988). The basic mammalian tongue is a highly mobile muscular hydrostat: an incompressible, constant-volume structure supported by fluid pressure (Kier & Smith, 1985; Livingston, 1956) capable of changing shape and overall position while remaining rooted to its anchoring hyoid apparatus and oral floor (Herring, 1993). Muscles that alter the tongue's shape mainly exist solely within the tongue body; these so-called intrinsic muscles (*m. lingualis proprius*) include vertical, transverse, and longitudinal fibers (Figure 2), the latter often in dorsal and ventral bundles (Sanders & Mu, 2013; Schwenk, 2001). Paired extrinsic muscles insert within the tongue yet originate outside and chiefly alter tongue position (Goonewardene, 1987; Levy, 1990). These include the genioglossus (originating on the interior of the mandible to protract the tongue), hyoglossus (from the hyoid, acting to retract and depress the tongue), paired styloglossus (from stylohyal bones, to retract and elevate either side of the tongue), and palatoglossus (from the hard palate to retract and elevate the tongue; Lawrence & Schevill, 1956; Werth, 2007a). The supporting bony hyoid includes two paired cornua (horns), a greater horn comprising paired thyrohyal bones extending laterally from a median unpaired basihyal, and a lesser horn comprising paired ceratohyals, with multiple elements joined by flexible synovial joints. Extending superiorly from each ceratohyal is an ossicular chain (epihyal, stylohyal, and tympanohyal) that connects to the skull base near the ear region (Reidenberg & Laitman, 1994). In cetaceans, a robust interhyoid (ceratohyoid) muscle connects greater and lesser horns. The hyoid also attaches via muscular connections (Figure 2) to the mandibular rami and symphysis, the styloid or mastoid process of the cranial temporal bone, the sternum, the larynx, and sometimes the scapula or other structure of the shoulder (Howes, 1896; Omura, 1964).

The mammalian tongue plays crucial roles in moving and positioning food into and within the mouth relative to the teeth, lips, cheeks, and oropharyngeal isthmus of fauces, the opening to the pharynx (Herring, 1993). The strong yet mobile mammalian temporomandibular joint allows for strong mechanical advantage and bite forces (with robust jaw adductors; Lautenschlager et al., 2016), as well as precise mandibular movements relative to the upper jaw

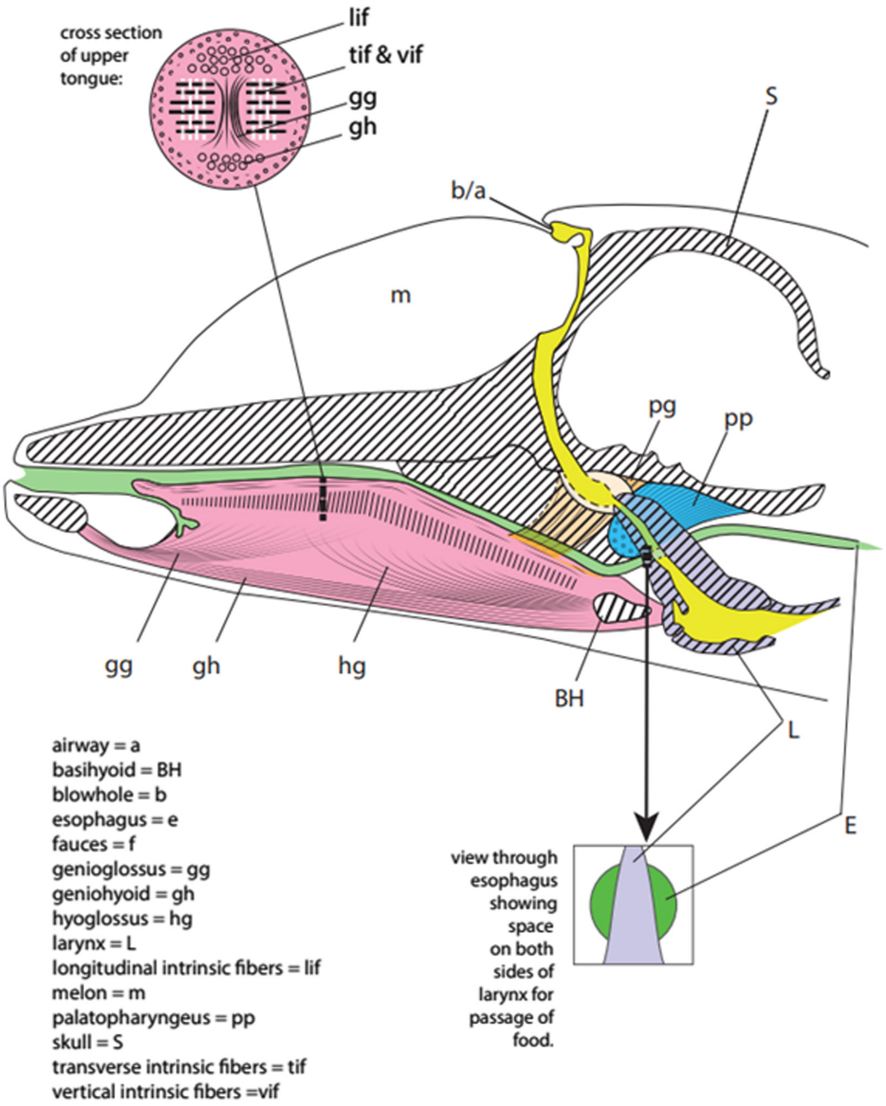

FIGURE 2 Schematic diagram of a representative odontocete (bottlenose dolphin, *Tursiops truncatus*) head in parasagittal section, with inset showing transverse (cross) section of tongue body, depicting positions of the tongue, jaws, esophagus, larynx, sternum, palatopharyngeal sphincter, and orientation of extrinsic tongue and main gular muscles. Relative to other mammals, cetaceans have few intrinsic lingual muscle fibers (existing solely within the tongue); extrinsic lingual fibers are largely similar to other mammals (including mysticetes). Cetaceans have no free soft palate; a palatopharyngeal sphincter binds the larynx. (Catherine Musinsky redrew this illustration).

for unilateral dental occlusion (i.e., on one side of the jaw at a time; Crompton & Hiiemae, 1970). This cyclic, rhythmic masticatory motion, with tongue and jaws moving in orbital loops, depends on precisely occluding tribosphenic molars bearing complexly matching cusps and basins with cutting and shearing surfaces (Crompton, 1971; Crompton & Hiiemae, 1970; Hiiemae & Crompton, 1971, 1985). Although other animals orally process food to increase its surface area for faster, more efficient digestion and nutrient absorption, no processing comes close to mammalian mastication's effectiveness in breaking hard or fibrous foods into consistently smaller fragments. During mastication the tongue plays a key role in moving food and positioning it against the palate (Table 1 function #3). Various mammalian clades exhibit unusual tongues related to specialized diet and foraging ecology. This includes nectar feeding in some bats, in which the tongue carries fluid into the mouth (Tschapka et al., 2015), and myrmecophagy (eating ants, termites, or similar insects) in several orders of mammals with long, sticky tongues (Doran, 1975; Doran & Baggett, 1971; Reiss, 1997).

The mammalian tongue plays a key role during suckling (Table 1 #14) by creating two seals: anteriorly between the tongue and nipple, and posteriorly between the tongue and soft palate, which stiffens by contraction of the tensor veli palatini muscle (Lawrence & Schevill, 1956). Rapid depression of the lingual dorsum (i.e., dorsal surface) between these seals increases intraoral cavity volume, creating a negative (subambient) pressure gradient into which milk readily flows (German et al., 1992; German & Crompton, 1996; Mayerl et al., 2021; Thexton et al., 1980, 1998, 2004). Suckling must be distinguished from sucking. In sucking, rapid retraction and depression of the hyolingual apparatus also generates intraoral suction (Table 1 #6), but without the anterior seal. Juvenile and adult cetaceans (and some pinniped species) have exploited, with little modification, this generic sucking mechanism of swift, piston-like posteroventral tongue motion to generate intraoral suction for prey ingestion and transport (Table 1 #6; Johnston & Berta, 2011; Wainwright et al., 2007, 2015). However, it is unlikely that cetacean sucking stems from retained neonatal suckling (Table 1 #14) because cetaceans [likely] never truly suckle like typical mammals, as will be explained.

Both mastication and suckling are complex, highly choreographed processes involving rhythmic contractions of numerous tongue and jaw muscles (Rossignol et al., 1988; Vinyard et al., 2011), with sequential firing cycles governed by neural central pattern generators (Lowe, 1981, 1990; Lund et al., 1998; Lund & Kolta, 2006). Conserved tongue movement patterns (Thexton et al., 1998, 2004) may relate to the anatomical and neuromotor control mechanisms of suction feeding in varied cetacean lineages (Figure 1). The uniform ubiquity of mastication and suckling in diverse lineages provides strong evidence that both processes arose early in therian evolution and have been deeply conserved. Yet as is often the case, Cetacea diverged profoundly. Tongue mobility and function, particularly loss of mastication and neonatal suckling, offer prime examples of cetaceans' uniqueness.

Cetacean tongues include the largest muscular organs that exist or presumably ever existed (Werth, 2000b). In bowhead and right whales (Balaenidae), the tongue averages 4%–6% of total body mass (Omura, 1958). In an average 50 ton (50,000 kg) whale, the tongue weighs 2000–3000 kg and reaches 5 m in length and >1 m in width and height. In large rorquals (Balaenopteridae), including blue and fin whales, the tongue is of similar size (5+ m long) and mass (2500–3500 kg), although it is more flaccid than firm in adult rorquals (Carte & MacAlister, 1868).

Not only are cetacean tongues unusual for their extraordinary size, but their highly modified or wholly novel functions also set them apart from tongues of other mammals. In this comparative, comprehensive review, we describe tongue structure and function within all cetacean lineages relative to other mammals, including artiodactyl relatives and other aquatic animals. We outline numerous tongue functions, distinguishing processes related to feeding on solid food from functions unrelated to solid food (Table 1). We highlight ways in which diverse cetacean tongues perform functions unique among mammals (or any organisms), or in some cases shared with a few pinniped taxa (Kienle et al., 2022; Kienle & Berta, 2016). This list includes functions that rely on direct physical contact, on hydraulic forces generated by tongue movement, or on hydrodynamic effects created by water flow along tongues (Table 1). Along the way, we summarize ways in which tongues of all odontocete and mysticete lineages evolved to exhibit unusual morphology, histology, and mobility (Table 2).

2 | FEEDING-RELATED FUNCTIONS OF CETACEAN AND GENERAL MAMMAL TONGUES

Tongues play a central, starring role in the lives of mammals. Tongue structure typically reflects multiple roles in varied activities. In addition to central roles in feeding, mammalian tongues generally perform or assist in several non-feeding functions (Section 3; Table 1).

2.1 | Vertebrate ancestors

Although some fishes possess a tongue-like fold on the oral floor, a proper muscular tongue did not evolve until the origin of tetrapod vertebrates (Schwenk, 2000). Extant amphibian tongues develop during metamorphosis and likely arose from occipital somites (Iwasaki, 2002). Fleshy, mobile tongues of amphibians and amniotes contain skeletal musculature. In many frogs and salamanders, an elongated, prehensile ballistic tongue bears a sticky tip that is rapidly and forcefully protruded to catch prey (Schwenk, 2000). The origins of novel hyolingual muscles and skeletal elements in amphibians (Fabrezii & Lobo, 2009) are hypothesized to be key innovations that led to complexly structured and highly mobile tongues found in most tetrapods today. Conversion of aquatic suction feeding to tongue-based prey prehension (Liem, 1990; Noel & Hu, 2018) and ingestion in some fishes (Heiss et al., 2018; Michael et al., 2015) likely also prompted lingual evolution. At the same time, the tetrapod tongue's exceptional mobility and importance in feeding presumably led to its simultaneous use in numerous non-feeding roles, as outlined in Section 3.

2.2 | Closest cetacean ancestors

Paleontological evidence indicates that Cetacea arose about 50 million years ago during the early Eocene (Mchedlidze, 1984; Thewissen et al., 2009). The closest sister group of cetaceans appears to be *Indohyus* within the extinct Raoellidae, a family of small, digitigrade, likely amphibious artiodactyls (Thewissen, 1998). In size and form *Indohyus* was similar to tragulid artiodactyls (chevrotains), though in lifestyle it may have more closely resembled raccoons (Thewissen et al., 2007). Molecular analysis (McGowen et al., 2014) confirms the fossil link between cetaceans and non-cetacean artiodactyls. Cetaceans' closest living relatives, as judged by morphological and molecular analysis, are the two extant species of Hippopotamidae: the only members of the cetartiodactyl Suborder Whippomorpha, along with cetaceans. Hippopotamus tongues are not notable in anatomy or histology (Goździewska-Harłajczuk et al., 2020; Jackowiak et al., 2006), nor are hyolingual or oral and pharyngeal regions of other artiodactyls closely related to cetaceans (Greaves, 1991). Some artiodactyls (notably giraffids) possess notably long, prehensile tongues commonly used to strip foliage from vegetation (Cave, 1980). Tongues of some artiodactyls are large, perhaps for improved drinking and thermoregulation in camelids or for prolonged mastication and regurgitation in bovids (Márquez et al., 2019). Otherwise artiodactyl tongues are typical of most mammals in form and function (Olson, 2020).

Indohyus has been proposed as the "missing link" sister group uniting cetaceans to other artiodactyls (Thewissen et al., 2009).

TABLE 2 Fundamental cetacean feeding types with corresponding principal aspects of lingual anatomy and mobility.

Family	Biting ingestion	Suction ingestion	Skimming ingestion	Lunging ingestion	Key tongue anatomy	Main tongue mobility
Physeteridae (sperm whales)		■			Rounded, wide; lg GG, HG, hyoid	Rapid depression/retraction and reset; gular expansion
Kogiidae (pygmy and dwarf sperm)		■			Rounded, wide; like Physeteridae but smaller; lg GG, HG, hyoid	Rapid depression/retraction and reset; gular expansion
Ziphiidae (beaked whales)		■			Hemicylindrical; long, flat; lg HG and hyoid; papillae	Rapid track-like retraction and anterior reset
Platanistidae (S. Asian river dolphins)	■				More typical mix of extr-/intrinsic muscles, papillae	Highly mobile; capable of shape deformation
Iniidae (Amazon river dolphin)	■				More typical mix of extr-/intrinsic muscles, papillae	Highly mobile; capable of shape deformation
Pontoporiidae (La Plata river dolphin)	■				More typical mix of extr-/intrinsic muscles, papillae	Highly mobile; capable of shape deformation
Lipotidae (Chinese river dolphin)	■				More typical mix of extr-/intrinsic muscles, papillae	Highly mobile; capable of shape deformation
Monodontidae (beluga and narwhal)	▒	■			Like Delphinidae but shorter, wider; lg GG, HG	Less mobile and firmer than Delphinidae
Delphinidae (oceanic dolphins)	■	■			Flat w/papillae, esp in young; obv. extr/intrinsics	Extensible shape/positional changes, <"river" dolphins
Phocoenidae (porpoises)	■	■			Short, wide, like Monodontidae but w/papillae	Easily retract; <<mobile than Delphinidae
Balaenidae (bowhead and right)			■		Massive, elevated; firm and muscular, w/retia and fat	Limited mobility for channeling water flow, swallowing
Neobalaenidae (pygmy right)			■		Like balaenid but <<smaller; all muscle, no fat	Limited mobility for water flow, swallowing
Eschrichtiidae (gray whale)		■	░	░	Firm, muscular; lg GG, HG, hyoid	Rapid retraction/depression and reset
Balaenopteridae (rorquals)			░ [sei whale]	■	Floppy, flaccid, saccular in adults; lg. GG	Passive invagination, protraction to return to resting position

Note: Several families include diverse morphotypes and ecotypes; darker shading of boxes indicates more frequent behavior. Only extant taxa are included here (fossil forms are described in the text).

Abbreviations: GG, genioglossus; HG, hyoglossus.

There is no indication from fossils of *Indohyus* or other raoellids that the tongue, jaws, or other oral structures were unusual in size or other aspects (Thewissen et al., 2007). Based on their morphology and phylogenetic relationships and ancestry, raoellids were probably herbivorous or omnivorous. Stable isotope analysis of ^{18}O indicates *Indohyus* was semiaquatic in habitat, but ^{13}C values suggest it rarely fed in water (Marx, Hocking, et al., 2016), meaning that its tongue was not yet adapted to aquatic feeding.

2.3 | Archaeocetes

Based on their jaw and dental structure, the first cetaceans (Archaeoceti) probably masticated food like typical mammals (Uhen, 2010). There is no direct evidence regarding tongues of early cetaceans (Thewissen et al., 2009), but fossil teeth and jaws indicate that early cetacean tongues departed little from those of immediate terrestrial ancestors (raoellid cetartiodactyls) in form or function (Thewissen & Williams, 2002). All evidence suggests the first cetaceans were biters, as are most modern dolphins, whose tongues are like those of most mammals in morphology and mobility (Figure 2; Donaldson, 1977).

The earliest known archaeocetes, of the Family Pakicetidae, include several genera of fox- to wolf-sized animals known from fragmentary skull, jaw, and tooth fossils (Mchedlidze, 1984). Teeth of the smallest pakicetids were similar to those of modern fish-eating mammals (Thewissen, 1998), whereas those of larger pakicetids resemble teeth of hyenas (Thewissen et al., 2011). It is not known if pakicetids, and other early archaeocetes, were ambush predators, chase hunters, or carrion scavengers, or if they used some combination of foraging methods (Uhen, 2010). However, cranial and postcranial osteology, such as limb proportions and pachyosteosclerosis (Uhen, 2004, 2010), along with trophic data from stable isotopes (Clementz et al., 2014), indicate that raoellids and pakicetids were adapted to amphibious or semiterrestrial lifestyles. They likely moved well in and near water, and could feed on aquatic or semiaquatic prey (Thewissen et al., 2009). Pakicetids may have been similar to otariid pinnipeds (sea lions and fur seals) in their ability to move on land and in water (Thewissen, 1998).

As early archaeocetes became better adapted to aquatic life, and their teeth and jaws departed from terrestrial forms, their tongues likely also shifted functions toward suction ingestion and swallowing large prey whole, without processing. (We have not provided a cladogram like Figure 1 showing archaeocete taxonomy because their phylogeny remains unresolved.) Ambulocetids were considerably larger archaeocetes (Marx, Lambert, & Uhen, 2016). Their skulls and body form, with smaller hindlimbs, and orbits and external nares beginning to migrate dorsoposteriorly, suggest they were most likely similar to crocodilians, and perhaps were aquatic ambush predators. Skeletal, dental, and isotopic analysis indicate that later remingtonocetids and protocetids were even more at home in water. They probably fed in deeper waters and spent all of their time away from land (Thewissen et al., 2017). Finally, the even larger and more diverse basilosaurids, with two subfamilies, the very long (to 18 m) yet slender, mosasaur-like basilosaurines and smaller (4–6 m) killer whale-like dorudontines, were all well adapted for fully aquatic life (Fordyce, 2018). A main way in which basilosaurids, like other earlier archaeocetes, differed from modern cetaceans was their large, triangular teeth, with numerous accessory cusps and serrated denticles (Uhen, 2004). These teeth, along with skull characters such as a large temporal fossa and robust attachment sites for jaw musculature, strongly suggest that archaeocetes, unlike crown cetaceans (Neoceti), masticated prey (Uhen, 2010). Fossilized stomach contents reveal that their diet included fish (Thewissen & Williams, 2002). It has been speculated (in part due to fossilized stomach contents, but also the lack of grasping forelimbs) that archaeocetes likely swallowed smaller prey whole (Bianucci, 2005; Thewissen et al., 1994, 2007). Although nothing is known about early cetacean tongues, morphological (dental and skeletal) and paleoecological data suggest they departed little from tongues of terrestrial ancestors, although they may have ingested and transported prey via suction (Werth, 2006a).

2.4 | Neoceti (crown Cetacea) tongues

All modern crown cetaceans (Neoceti) form a monophyletic group that in turn comprises two monophyletic sister clades, the Parvorder Odontoceti, with 80 currently recognized species of toothed whales, dolphins, and porpoises in 30 genera of 10 families, and the Parvorder Mysticeti, with 16 recognized species in six genera of four families (Berta et al., 2015). Odontocetes and mysticetes presumably diverged ~34 Ma (Fordyce, 2018). Cetacean tongues vary considerably but are commonly flat, with few if any surface ridges, folds, or papillae (Werth, 2007a). Lingual mobility and function will be outlined for each family in turn, but cetacean tongues are generally less mobile and more firmly anchored to the oral floor relative to typical mammals (Kleinenberg et al., 1969; Sonntag, 1922; Werth, Lillie, et al., 2018). Generally, odontocete tongues retain typical lingual musculature, though with notably fewer intrinsic fibers than most mammals (Figure 2; Werth, 2000b, 2007a). Insertions of genioglossal and hyoglossal fibers, both of which fan out into the tongue body in multiple bundles (typically three and two, respectively), often comprise a majority of tongue volume (Werth, 2007a; Figure 2). There may be scattered connective tissues, especially in larger species (Werth, 2007b). Adipose tissues are common in mysticete tongues (Werth, 2007a), as are fascial planes and spaces between bundles or compartments of muscle fibers (Werth, Lillie, et al., 2018).

In most mammals, the tongue plays five distinct roles related to feeding on solid food (Hiiemae, 2000; Hiiemae & Palmer, 2003): (1) food acquisition, prehension, and ingestion (i.e., bringing from outside the mouth into the mouth; Table 1 function #1); (2) Stage I and Stage II intraoral transport (carrying food from lips to teeth, and from teeth to tongue root/fauces for swallowing; Table 1 #2); (3) manipulating and positioning food within the mouth during mastication

(Table 1 #3); (4) securing food against the palate or dentition, even in the absence of mastication or other oral processing (Table 1 #4); and (5) swallowing food (Table 1 #5). Of these five fundamental functions, mastication (Table 1 #3) does not occur in any crown cetacean, but as described in the following sections, all other feeding-related tongue functions occur to varying extents. Prey processing of any kind (i.e., comminution) occurs only in a few odontocete species (notably killer whales, *Orcinus orca*, and false killer whales, *Pseudorca crassidens*) that bite or tear large prey items prior to swallowing. Killer whales use their tails to slap and stun herring corralled into large bait balls (Jourdain & Vongraven, 2017); scattered but unsubstantiated accounts from people diving or fishing nearby claim whales can be observed ingesting stunned fish individually, then "filleting each with their tongues (i.e., separating flesh from bone) and spitting out the bones" (McBride, 2021). Terrestrial mammals often use gravity or inertial tongue/head movements to transport food posteriorly (Lauder, 1985; Schwenk, 2000); these are unnecessary if food is neutrally buoyant in water, so cetaceans instead often rely on hydraulic or hydrodynamic means to propel food intraorally (Table 1 #2) with tongue-generated negative or positive pressure, as explained below.

2.5 | Neoceti feeding methods

Odontocetes and mysticetes vary in general foraging methods and feeding mechanisms (Hocking, Marx, Park, et al., 2017; Kienle et al., 2017; Marshall, 2018; Marshall & Goldbogen, 2015; Marshall & Pyenson, 2019; Werth, 2000b), as outlined in Table 2 and shown in Figure 1. Although there is much variation, odontocetes are categorized as either biting (AKA raptorial or seizing) or suction feeders (Kawamura, 1974, 1980; Nemoto, 1959, 1970; Tomilin, 1954; Werth, 2000b). For the type of ingestion that precedes filter feeding, mysticetes are classified as suction, skim, or lunge feeders (Werth, 2001). Note that lunge (AKA gulp) feeding is often ram-driven: that is, an animal swims forward with open jaws and overtakes prey (Arnold et al., 2005), capturing it either within the oral cavity proper and/or with grasping or filtering structures (for cetaceans, teeth or baleen). However, lunges are often accompanied by complex behaviors and bodily rotations affecting water engulfment (Cade et al., 2016; Goldbogen et al., 2006, 2011, 2013, 2017; Goldbogen, Calambokidis, Friedlaender, et al., 2012; Kosma et al., 2019) which might be sensed by mechanoreception (Pyenson et al., 2012). Skim feeding is typically ram-driven; biting also can be ram-driven, although it need not be (Werth, 2000b). Although suction feeding is often combined with rapid, open-mouthed forward locomotion, the physical impetus for prey movement into the mouth depends on generation of negative (subambient) pressure (Table 1 #6), and hence incurrent flow (Werth, 2006b). As such, suction ingestion can occur if an animal is stationary. This is also true of biting ingestion but not for mysticete lunge or skim ingestion. Skim ingestion may by accompanied or aided by tongue- and baleen-based generation of intraoral flow regimes (Bernoulli and Venturi effects; Table 1 #9) that preclude compressive bow waves, but alone appear insufficient to generate proper (below ambient) suction (Lambertsen et al., 1989).

Importantly, the sole feeding-related function of the cetacean tongue that is largely the same as in other mammals (Herring, 1993; Hiiemae & Crompton, 1985) is propulsive clearing of food through the fauces (oropharyngeal isthmus) during swallowing (Table 1 #5; Werth, 2007a). In cetaceans this process generally involves a single prey item (normally a fish, squid, or benthic invertebrate), but may involve an accumulated prey slurry (typically in mysticetes) or prey fragment in rare cases in which odontocetes bite prey (Werth, 2000b).

2.6 | Neoceti dental evolution

The decline of cetacean tooth number and dental complexity, in both gross form and enamel microstructure, highlights the notable absence in Cetacea of mastication, a typical hallmark of Mammalia. This profoundly altered tongue mobility and function. In several taxa odontocete teeth are secondary sexual features (prominent or erupted solely in males) used for display or male–male combat. This is especially true in beaked whales, Ziphiidae (Heyning & Mead, 1996), and the narwhal, *Monodon monoceros* (Nweeia et al., 2009). In these and other odontocete species, teeth may be reduced in size and number or entirely absent, such that some "toothed whales" are literally or functionally edentulous (Werth, Loch, et al., 2019). Teeth often project entirely outside the oral cavity in ziphiids, where they can play no obvious role in feeding; they may be covered in epizoic barnacles (Werth, 2000b). Several long-snouted oceanic and river dolphin taxa are notable for their high number of teeth, in some cases far exceeding the typical eutherian maximum of 42 teeth (Werth, Loch, et al., 2019). However, polydonty is the exception rather than the norm for Odontoceti.

2.7 | Odontoceti, archaic and extinct families

There are at least 20 described odontocete families with no living representatives (Marx, Hocking, et al., 2016). Because many are known only from limited, fragmentary fossil remains including teeth, portions of the jaw(s) and braincase, and vertebrae or other postcranial bones, there are virtually no indications of tongue structure or function (Mchedlidze, 1984). However, some conjectures can be made based on tooth and jaw structures in relation to other cetaceans and other mammals: namely, that extinct odontocetes likely used tongues to grasp prey (Table 1 #1) and in some taxa to ingest them via suction (Table 1 #6). There are at least eight families of early (mainly Oligocene) basal odontocetes, notably agorophiids, patriocetids, and xenorophids; there are in addition at least six basal odontocete genera yet to be assigned to families (Fordyce, 2018). All have, as far as is known, long jaws with heterodont dentition, suggesting they masticated prey (likely fish) using mobile tongues similar to those of most terrestrial mammals (Table 1 #3; Marx, Hocking, et al., 2016). Members of at least three known families of eurhinodelphinoids (mostly Miocene) had long bony rostra, similar to those of billfish, with peg-like teeth in the lower jaws and caudal portion of the upper jaws (Marx, Hocking, et al., 2016). Members of at least four extinct (mostly Miocene) platanistoid families (including squalodontids, squalodelphinids, and allodelphinids) had shark-like triangular teeth, whereas both families of the extinct Miocene squalodontoids, including prosqualodontids, had teeth that were intermediate between shark-like triangles and the earlier heterodont dentition of archaeocetes and stem odontocetes (Marx, Hocking, et al., 2016; Thewissen, 1998); these all probably sliced prey and used less mastication (Table 1 #3) than earlier odontocetes, based on the palate and dentition (Werth, 2000b). Several lineages of extinct delphinoids, including kentriodontids (Oligocene–Pliocene) and albireonids (Miocene–Pliocene), as well as numerous genera, families and other enigmatic fragmentary odontocete fossils *incertae sedis* appear to have had peg-like, conical teeth presumably used to grasp prey in the manner of modern dolphins (Table 1 #4); their tongues likewise probably functioned similarly to those of extant dolphins (Marx, Hocking, et al., 2016; Uhen, 2010). Only one known delphinoid, *Odobenocetops* (the sole species of the Late Miocene to Early Pliocene Odobenocetopsidae, but perhaps a member of Monodontidae), departed notably from this morphotype and ecotype: *Odobenocetops* ("walrus whale") is named for its striking convergence to *Odobenus*, the walrus (De Muizon & Domning, 2002). By all indications this odontocete was a suction feeder (De Muizon, 1993) that sucked benthic bivalves from the substrate, perhaps even out of their shells, exactly as walruses do (Table 1 #6; Fay, 1982; Gordon, 1984; Kastelein et al., 1991, 1994; Kastelein & Mosterd, 1989; Oliver et al., 1983, 1985). Like *Odobenus*, *Odobenocetops* had a prominently vaulted palate, strongly indicative of a large, highly mobile tongue (Table 1 #1); other shared walrus-like features (large tusks, flexible neck, dorsally-directed eyes) suggest suction feeding like that of *Odobenus*.

2.8 | Odontoceti, Physeteridae

The tongue of the sperm whale, *Physeter macrocephalus*, is in absolute size the largest of odontocetes, reaching 1 m long in adult males (Tomilin, 1967), but is proportionally smaller than those of all other cetaceans because it resides only at the rear of the

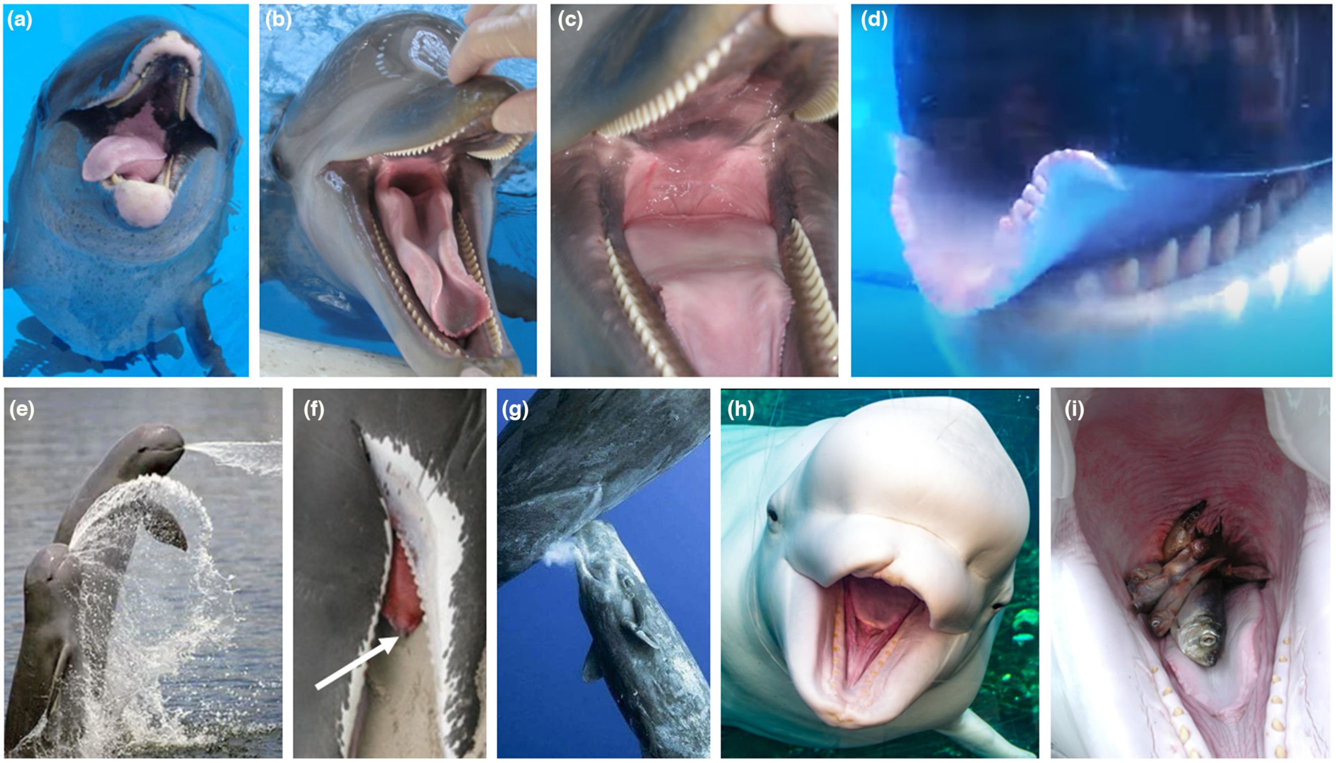

FIGURE 3 Tongue mobility and function in diverse odontocetes. (a–c) Bottlenose dolphin, *Tursiops truncatus*, showing typical large, flat, hemicylindrical muscular delphinid tongue with (a) free tip moved laterally outside mouth, (b) curled, e.g., to channel milk during nursing, and (c) retracted to seal water from entering pharynx. (d) Shows video screen grab of captive killer whale, *Orcinus orca* with marginal papillae, lingual protrusion, and ability to roll and change tongue shape. (e) Shows frequent behavior of Irrawaddy dolphins, *Orcaella brevirostris*, using tongue to rapidly suck in and powerfully squirt out large volumes of water for suction ingestion and hydraulic jetting to corral or uncover prey. (f) Shows short tongue in posterior oral cavity of sperm whale, *Physeter macrocephalus* (arrow pointing to tongue tip). (g) Shows sperm whale calf nursing as mother ejects milk. (h) Shows ability of beluga, *Delphinapterus leucas*, to purse its lips to form circular opening for suction feeding, and (i) with tongue retracted to swallow fish after expelling water. Photo credits (a, d): Pinterest (CCY); (b, c, i): Joy S. Reidenberg, (e): reddit (CCY); (f): Angus Wilson (CCY); (g): YouTube/Mike Korostelev (CCY); (h): treehugger.com (CCY).

entirely open sperm whale oral cavity (Figure 3f; Werth, 2004a). *Physeter* mandibles can be 5 m long, but the fused median symphysis, where all dental alveoli occur, occupies over half of this length. This means the sperm whale tongue, unlike other odontocete tongues, lies entirely caudal to the tooth rows and cannot touch teeth. (In all odontocetes the tongue lies caudal to the mandibular symphysis, but in all taxa except *Physeter* the tongue lies between tooth rows.) The physeterid tongue is short, wide, and firm, with a dorsum that is (for odontocetes, apart from kogiids) unusually rounded rather than flattened. It has a thick corium (heavily cornified epidermal layer, a small free tip, and extensive longitudinal folds or plicae along the lateral margins; Werth, 2004a). The tongue has few intrinsic muscle fibers (Werth, 2004a). Much of its body comprises hyoglossus fibers originating on the robust hyoid skeleton (Omura, 1964). The sperm whale tongue's unusual location and oral relations posterior to teeth mean that it cannot be used for prey prehension or transport (Table 1 #1, #2), as in some other odontocetes, but it is ideally situated for suction ingestion via rapid, piston-like retraction (Table 1 #6; Werth, 2004a), which accords with what is known of sperm whale foraging ecology and stomach contents (Werth, 2000b). A distinct sublingual space of loose connective tissue presumably facilitates retraction (Werth, 2007a). Although the tongue cannot easily reorient prey grasped by tooth rows (Table 1 #4), it could position items to be swallowed or sucked into the caudal-most portion of the open oral "cavity" or possibly even directly into the oropharyngeal opening (Table 1 #6; Werth, 2004a). This type of ingestion—sucking food items not into the oral cavity proper but instead directly into the oropharynx—is unlike the suction feeding commonly used by fishes, amphibians, and secondarily aquatic tetrapods, including many other odontocetes (Werth, 2006a) and pinnipeds (Marshall & Goldbogen, 2015). Without a proper oral cavity into which to suck prey, most suction-feeding cetaceans have external throat grooves (in thick blubber) reflecting the need to temporarily accommodate ingested prey or water in the pharynx (Werth, 2000b). In terms of mobility the sperm whale tongue is limited; it apparently cannot be moved much beyond powerful retraction (Werth, 2004a). There is considerable evidence that sperm whales prey on benthic items (and commonly ingest stones or other benthic debris), such that they could use tongue movements to produce jetting currents, like those used to expel ingested water (Table 1 #7), to locate or uncover prey in or under substrates (Hocking et al., 2013, 2014; Marshall et al., 2008, 2014, 2015).

An extensive fossil record reveals many diverse sperm whale relatives, including at least 10 extinct physeterid genera and about 15 other physeteroid genera of unknown phylogenetic position (Fordyce, 2018). Some of these taxa appear to have been similar to modern sperm whales, based on mandibles and large, conical teeth, and thus good candidates for teuthophagous (i.e., primarily squid-eating) suction feeding (Werth, Loch, et al., 2019). Many other archaic sperm whales had large, powerful jaws and probably tongues with disparate mobility and function (Lambert, Bianucci, & de Muizon, 2017). This includes the huge carnivorous Miocene *Livyatan melvillei*, one of several "hyper-predatory macro-raptorial" ancient sperm whales that probably fed, much like killer whales, *Orcinus orca*, on large sharks or whales (Lambert et al., 2010).

2.9 | Odontoceti, Kogiidae

Pygmy and dwarf sperm whales (*Kogia breviceps* and *K. sima*) have been documented, via experimental kinematic analysis (Bloodworth & Marshall, 2005, 2007), to ingest food with intraoral suction pressures generated by rapid hyolingual depression and retraction (Table 1 #6). Kogiids are closely related to *Physeter*; traditionally (until recently) *Kogia* was classified within Physeteridae (Miller, 1923). Just like the sperm whale, both *Kogia* species have a disproportionately large hyoid relative to other odontocetes (Omura, 1964) and robust hyoglossus muscle inserting on a firm, rounded muscular tongue with a small free tip (Bloodworth & Marshall, 2007). Like *Physeter*, *Kogia* has a small number of external throat grooves to accommodate temporarily ingested water (within the oropharynx and possibly esophagus), which, video-recorded experiments confirm, is then purged by being "squirted" from the mouth as the tongue returns to its normal position (Figure 3e; Bloodworth & Marshall, 2005).

Short, blunt, wide ("amblygnathous") heads contributing to a rounder mouth opening have been shown to correlate with suction feeding (Table 1 #6; Werth, 2006a, 2006b), and kogiids have the widest, bluntest heads of any odontocetes (Bloodworth & Marshall, 2005). Kogiids retain open gape but with (relative to most odontocetes) a rounder oral aperture based both on jaws as well as soft tissue "cheeks" (Figure 3h). Kogiids possess a long mandibular symphysis (not as long as in *Physeter*), but *Kogia* tongues appear, as in *Physeter*, to have little mobility, especially in limited protrusion. Like most odontocete suction feeders, kogiids are teuthophagous and have reduced dentition, particularly in the upper jaw (Werth, Loch, et al., 2019). The few lower teeth are fang-like (narrow and sharp; Bloodworth & Marshall, 2005, Werth, Loch, et al., 2019), apparently suited to retaining ingested squid (Werth, 2006a). Overall, the robust kogiid hyolingual apparatus appears strongly adapted to rapidly sucking in (Table 1 #6) and expelling (Table 1 #7) large volumes of water. The strongly vaulted palate and nearly circular oral aperture match well with the notably short, wide tongue, which is, as in sperm whales, rounded dorsally. As with physeterids, kogiids have a rich fossil history (Mchedlidze, 1984). All known genera exhibit wide, blunt rostra and jaws, such that suction feeding appears to have a long history in this clade (Marshall & Pyenson, 2019), with piston-like tongues consequently adapted to generating subambient pressures (Table 1 #6).

2.10 | Odontoceti, Ziphiidae

Beaked whales are, apart from oceanic dolphins (Delphinidae), the most diverse and speciose odontocetes, with 22 living species in six genera and at least 25 fossil genera that first appeared in the Miocene about 25 Ma (Bianucci et al., 2016). Despite their high diversity and large body size (4–13 m), ziphiids are among the least well-known of all mammals. Only three beaked whale species are well known; most are rarely seen alive and known only from skulls or rare strandings (Heyning & Mead, 1996). Beaked whales are found mainly in deep waters, often far from coastlines. They appear to have low abundance and live alone or in small groups. Despite their size they were rarely targeted for whaling and they have almost never been kept in captivity. For all these reasons, the anatomy of these cryptic species remains poorly understood. However, we know from several lines of anatomical and ecological evidence (e.g., stomach contents), as well as digital-tag biologging studies, that beaked whales are not only superb divers but also teuthophagous suction feeders specializing on deepwater squid (Rommel et al., 2006).

Except for one ziphiid species (*Tasmacetus shepherdi*) bearing 17–27 pairs of small, sharp upper and lower teeth, beaked whale dentition is greatly reduced (Werth, Loch, et al., 2019). In many species, especially of the genus *Mesoplodon*, there is only one pair of tusk-like lower teeth which often erupt only in males and protrude outside the oral cavity, likely for display or male–male fighting to establish dominance and battle for females (Heyning & Mead, 1996). Although teeth apparently play virtually no role in feeding, the prominent beaked whale tongue appears to be ideally suited for suction feeding (Table 1 #6). Unlike the short, wide tongues of *Physeter* and *Kogia*, all beaked whale tongues that have been studied are long, narrow, and flat (Werth, 2007a): a perfect hemicylindrical piston that readily and with little effort slides backwards and forwards in track-like fashion between the mandibles and oropharynx, activated via lingual retraction and gular depression (Heyning & Mead, 1996). All ziphiids' paired external throat grooves appear to be an adaptation (as in other large cetaceans, notably sperm and gray whales) for pharyngeal expansion, accommodating large volumes of engulfed water despite thick gular blubber (Werth, 2000b). Heyning and Mead (1996) reported prominent extrinsic (especially hyoglossus) muscles after examining five beaked whale species, with the most notable distinction involving very loose connective tissue surrounding the tongue, including a ventral sublingual space, that, in combination with robust musculature, apparently facilitates rapid lingual motion. Heyning and Mead (1996) described the typical ziphiid palate as rugose and heavily ribbed with transverse ridges, presumably to secure captured prey with the tongue (Table 1 #4). Tongues of newborn Stejneger's beaked whales (*Mesoplodon stejnegeri*) and some other ziphiids have marginal papillae that potentially create an effective oral seal (Shindo et al., 2008). Heyning and Mead (1996) described young captive beaked whales (three specimens of two species) strongly sucking on human fingers. For the most part ziphiids feed in deep, open ocean waters (Madsen et al., 2005), but there is limited evidence of feeding on benthic fish and crustaceans (Macleod & D'Amico, 2006) and possibly gouging the sea floor (Auster & Watling, 2010). Tongue use to locate and uncover benthic prey via hydraulic jetting (Table 1 #8) is therefore possible.

2.11 | Odontoceti, "river dolphins" (Platanistidae, Iniidae, Pontoporiidae, Lipotidae)

Several diverse dolphins occupy freshwater habitats in Asia and South America, including the blind, side-swimming susu of the Ganges and Brahmaputra Rivers and tributaries (*Platanista gangetica* subsp.); the Amazon, Bolivian, and Araguaian River dolphins and subspecies (*Inia* spp.); the baiji or Chinese whitefin dolphin (*Lipotes vexillifer*), recently declared functionally extinct; and the franciscana or La Plata river dolphin (*Pontoporia blainvillei*) of coastal Brazil, Uruguay, and Argentina (Berta et al., 2015). These four families also include many extinct genera and species (Hamilton et al., 2001). These small (~2 m) species were long classified in a single family, but are now recognized as convergent lineages of long-snouted, exclusively freshwater dolphins (Hamilton et al., 2001), with *Pontoporia*, which inhabits coastal marine and estuarine waters, the sole exception. All have numerous sharp teeth (about 25–60 in each row) with which they grasp fish or other prey (Werth, 2000b). Teeth are mostly conical, but posterior-most teeth of *Inia geoffrensis*, the boto or Amazon river dolphin, have a large, shelf-like medial cusp (Werth, Loch, et al., 2019). This is presumed to be an adaptation for crushing armored or spiny catfishes, turtles, and crustaceans. Extinct cetaceans (including all archaeocetes) had heterodont dentition (Massare, 1987; Uhen, 2010), but this is the sole instance within all of extant Cetacea of any dental cusp, the only case (along with triangular ziphiid and spatulate phocoenid teeth) of non-conical teeth, and the lone situation in which there is any cetacean dental/oral processing. The tooth count of *Pontoporia* (up to 244 teeth, nearly six times the normal eutherian maximum; Werth, Loch, et al., 2019) reflects both the extremely long jaws and rostra of river dolphins and their universal habit of biting, aided by unusually flexible necks and heightened tactile sensitivity (Layne, 1959; Werth, 2000b).

Accounts of river dolphin tongues (Arvy & Pilleri, 1972; Li, 1983; Yamasaki et al., 1976b), attest to tongues that are, as in most dolphins (Figure 3a) and typical mammals, robustly muscular and mobile, capable of anterior and lateral protrusion outside the oral cavity to aid in capturing and ingesting small fish or other prey items (Table 1 #1; Layne, 1959). There are superficial glands but no apparent gustatory papillae (Arvy & Pilleri, 1970). The tongue presumably also manipulates, carries, and holds prey against the palate and teeth (Table 1 #3, #4), and can roll longitudinally into a rough tubular shape (perhaps by simultaneous contraction of genioglossal and hyoglossal fibers; Reidenberg & Laitman, 1994). Intrinsic lingual musculature is more robust than in other cetaceans, but still less prominent than in typical terrestrial mammals, with fewer longitudinal fibers (Li, 1983). Tongue use in suction ingestion (Table 1 #6) is unlikely but possible, because tongue-generated suction is probably employed for effective water-borne prey transport (Table 1 #2) to the posterior of the mouth for easier swallowing (Werth, 2006b), as documented in gars and other long-snouted fishes (Werth, 2006a).

2.12 | Odontoceti, Monodontidae

The beluga whale (*Delphinapterus leucas*) is a documented suction feeder (Kane & Marshall, 2009). Ray (1966) described stationary captive belugas playfully sucking in (Table 1 #6) and squirting out (Table 1 #7) leaves and coins. The narwhal (*Monodon monoceros*) is similarly presumed to be a suction feeder based on morphology (e.g., absent dentition) and observed foraging (Best, 1981). *Delphinapterus* purses its mouth into a circular orifice (Figure 3d) by contracting facial muscles (orbicularis oris, buccinator, etc.), greatly aiding suction ingestion (Table 1 #6); it has 8–10 teeth in each row, but these are soft, with thin enamel, and easily wear into low stubs (Werth, Loch, et al., 2019). In all monodontids, teeth likely retain fish, squid or other sucked-up prey (Table 1 #4), but belugas can grasp and bite prey as well (Kleinenberg et al., 1969). One of the authors (A.J.W.) observed captive belugas (adult and subadult) moving and manipulating their tongues, which appear to change shape somewhat, although less than commonly seen in canids, felids, or bovids (Chibuzo, 1979). The tongue likely forms a strong oral seal for suction ingestion (Table 1 #1) and suction-based transport (Table 1 #2), and probably can manipulate (Table 1 #3) and hold (Table 1 #4) ingested prey. The presence of shallow-water benthic prey (including infaunal invertebrates) in stomach contents suggests a tongue role not only in suction ingestion (Table 1 #6) but also in hydraulic jetting (Table 1 #7), to disturb or uncover prey in, on, or under bottom deposits (Table 1 #8; Werth, 2000b). According to Kleinenberg et al. (1969), the beluga tongue is ideally suited to orienting ingested prey for better (e.g., headfirst fish) swallowing (Table 1 #5).

Monodontid tongues are like those of oceanic and river dolphins—not as short and wide as *Physeter* or *Kogia* tongues nor as long and hemicylindrical as ziphiid tongues—but are slightly larger, thicker, and more robust, with extensive extrinsic musculature and broad, thickened hyoid bones (Omura, 1964; Reidenberg & Laitman, 1994). The narwhal tongue has not been formally described but is known to be similar to the beluga tongue, which Kleinenberg et al. (1969) described as highly mobile and piston-like yet small relative to the size of the oral cavity. Kleinenberg et al. (1969) claims the smooth beluga tongue "maintain[s] a constant shape" due to its "marked density," its thick, inelastic, strongly keratinized epidermal corium, and its firm connection to continuous tissues lining the oral floor. Large stylo- and hyoglossus muscles retract and depress the tongue, whereas strong genioglossus and geniohyoid muscles readily protract the tongue to return it to its resting position, hold it against the palate, and expel water (Table 1 #7; Kleinenberg et al., 1969). As noted above, the extinct suction feeder *Odobenocetops* is probably allied with monodontids, and probably possessed a tongue with similar structure and function.

2.13 | Odontoceti, Phocoenidae

Porpoises (seven extant species in three genera) are small delphinoids, including the smallest cetacean, the vaquita (1.4 m, 54 kg), most closely related to monodontids (Figure 4), with rounded, beakless heads and spade-shaped teeth but some diversity in jaw shape (Racicot et al., 2014). Porpoises consume pelagic or benthic fish, cephalopods, and invertebrates. They generate substantial intraoral suction pressure (Table 1 #6) via hyolingual depression (Kastelein et al., 1997; Tomilin & Morozov, 1968). Tongues expel ingested water (Table 1 #7) and may be used for hydraulic jetting (Table 1 #8; Werth, 2006b). Dall's porpoises, *Phocoenoides dalli*, have ridged palates presumed to grasp slippery cephalopods with the tongue (Table 1 #4) as in ziphiids (Miller, 1929). Phocoenid tongues are similar to those of other delphinoids except shorter and with an anterior depression (Behrmann, 1988). Hyoid elements are proportionally thicker than in delphinids (Omura, 1964; Reidenberg & Laitman, 1994), suggesting tongue use in suction ingestion (Table 1 #6). Tongues of young phocoenids have numerous marginal papillae, but these are greatly reduced in older animals; Kastelein and Dubbeldam (1990) speculated that papillae create a better oral seal for suckling (Table 1 #14) and also aid in water expulsion (Table 1 #7). Sokolov and Volkova (1973) posited, with little evidence, that papillae are mechanosensory.

2.14 | Odontoceti, Delphinidae

The largest cetacean family comprises 30 extant species of oceanic dolphins (Fordyce, 2018) exhibiting a wide range of foraging and feeding habits (Kane & Marshall, 2009; Werth, 2000a). The abundant bottlenose dolphin, *Tursiops truncatus*, is the most commonly sighted cetacean in the wild and in captivity; it exemplifies the delphinid trait of being highly opportunistic, resourceful, and adaptive in its diet and tremendously varied means of acquiring food, from purposely beaching itself as it follows chased prey onto shore to begging scraps from fishing vessels and cooperatively aiding people trapping fish in nets (Werth, 2000b). Not only do delphinids pursue and capture prey in various ways, but feeding methods also vary (Figure 4). Long-snouted forms mostly bite (Boessenecker et al., 2020; McCurry et al., 2017; Taylor, 1987), whereas blunt-headed species with rounder mouths tend to use suction (Werth, 2006a), Many delphinids, including *Tursiops* and *Orcinus*, use sucking or biting depending on prey size and type, depth, etc.

As with river dolphins, oceanic dolphin tongues are mobile and can be protruded somewhat to contact prey or other items (Table 1 #1; Ferrando et al., 2010; Pfeiffer et al., 2001; Ping, 1927). However, delphinid tongues have limited protrusive ability (even if greater than that of most cetaceans; Donaldson, 1977); Donaldson (1977) ascribed this to the absence of a superior longitudinal intrinsic muscle (Sokoloff, 2000), and to a general lack of intrinsic fibers and of a small free tongue tip compared to dogs (Chibuzo, 1979; Gordon & Herring, 1987). Delphinid tongues can change shape, though considerably less than tongues of typical terrestrial mammals due to their generally thicker form and epidermal tunic (Iwasaki et al., 1987; Schwenk et al., 1989) and their greater proportion of extrinsic lingual musculature at the expense of intrinsic muscles (Lawrence

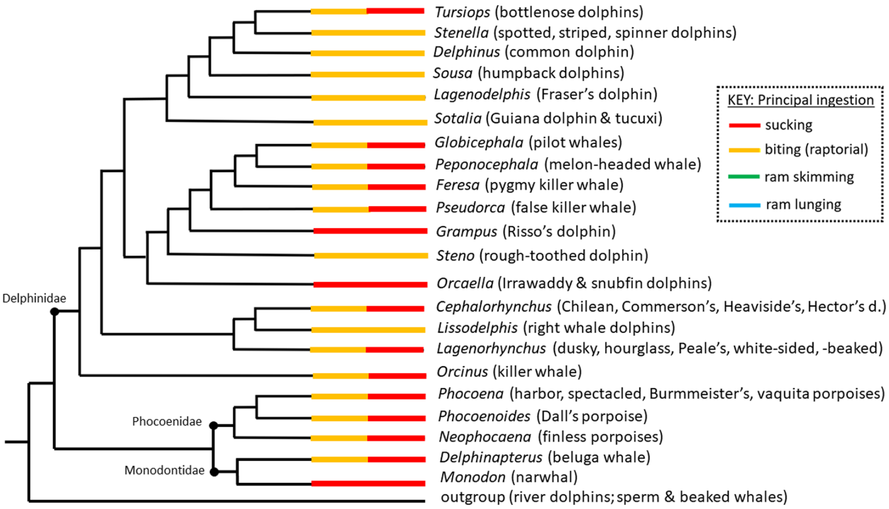

FIGURE 4 Phylogeny of extent delphinoid odontocete genera (based on McGowen et al., 2009) showing marked variation in principal feeding methods: some biting or suction feeders but many using both. There is similar diversity among outgroups (with sperm and beaked whale suction feeders and river dolphin raptorial feeders), making it difficult to determine which method, if either, was plesiomorphic for Odontoceti. It is equally likely that some combination of biting and sucking, and hence tongue use for (1) prehension/grasping (Table 1 #1), (2) suction (Table 1 #6), and (3) suction- or tongue-based oral transport (Table 1 #2), is not only widely used but the default, ancestral mode for Odontoceti.

& Schevill, 1956; Werth, 2000b). Delphinids have fewer intrinsic lingual fibers than river dolphins, but more than most cetaceans (Werth, 2007a). Delphinid tongues often have marginal papillae (Figure 3d), especially in young animals (Werth, 2000b). Juveniles are also more likely to have a shallow anterior spoon-shaped depression which, like papillae, may aid sucking (Werth, 2007a); adult tongues are mostly flat but can have a very shallow central furrow (Werth, 2007a). Relative to typical mammals, delphinid tongues have a smaller tip and frenum and stronger lateral connection to the oral floor (Werth, 2007a). Still, delphinid (and diverse river dolphin) tongues are clearly flexible and motile (Figure 3) and appear to be used in multiple ways (Table 3). Some reports (e.g., McBride, 2021) suggest killer whales use their tongues to remove and expel bones before swallowing fish.

2.15 | Neoceti baleen evolution

Baleen's origins remain a mystery (Berta et al., 2016; Deméré et al., 2008; Ekdale & Deméré, 2021; Fordyce, 1980; Fordyce & Barnes, 1994; Gatesy & O'Leary, 2001; Gingerich et al., 1983; Marx et al., 2017; Marx & Fordyce, 2015; McGowen et al., 2014; O'Leary & Uhen, 1999; Pyenson, 2017), but the tongue likely played a role in bulk filtration's evolution, enabling simultaneous ingestion of myriad prey items and calories, and hence leading to gigantism in Mysticeti (Fordyce & Marx, 2018; Goldbogen et al., 2007, 2010; Goldbogen, Calambokidis, Croll, et al., 2012; Goldbogen & Madsen, 2018; Potvin et al., 2012; Pyenson & Vermeij, 2016; Slater et al., 2017). Several studies suggest suction ingestion preceded baleen filtration (Fitzgerald, 2010; Geisler et al., 2017; Hocking, Marx, Fitzgerald, & Evans, 2017; Lambert, Martínez-Cáceres, et al., 2017; Marx, Lambert, & Uhen, 2016; Peredo et al., 2017), highlighting the tongue's importance in mysticete origins.

2.16 | Mysticeti, Balaenidae

Bowhead (*Balaena mysticetus*) and right whales (*Eubalaena* spp.) possess remarkably long (4+ m), finely fringed baleen to capture tiny zooplankton, mostly rice grain-sized copepods (Werth, 2012). Balaenids are often observed skimming through dense prey aggregations at the surface, but feed at all levels of the water column, even near the bottom as indicated by muddy, abraded snouts and sonar scans (Werth, 2004b). The balaenid feeding strategy involves slow, high-drag filtration using the world's largest biological filter (George et al., 2016; Werth & Potvin, 2016) in a huge head that occupies one-third of the body (Figures 5 and 6). Balaenids possess exceptionally large (up to 5 m long and 1 m high and wide) tongues—the largest muscular organs in the world (Werth & Sformo, 2020)—although not as large as they appear in some post-mortem photographs (Figure 5a) which depict distended tongues bloated from decomposition. Nonetheless, the massive, elevated tongue sits high in the mouth, between paired baleen racks (Figure 5a,c) when feeding at the surface or at depth (Table 1 #9 Werth, 1990).

Unlike other mysticetes, balaenids filter continuously (Werth, Rita, et al., 2020). Instead of separating prey from a single, discrete mouthful of engulfed prey-laden water, balaenids rely on a steady stream of incurrent water from which prey are removed, with filtered excurrent water likewise continually flowing (Simon et al., 2009; van der Hoop et al., 2019; Werth, 2004b, 2013). Flow is unidirectional, as in filtering fishes (from small anchovies and sardines to giant

TABLE 3 Tongue functions (following Table 1 # scheme) classified by extant cetacean families, indicating functions performed by any (not necessarily all) taxa within family.

Key

■ =known or documented (sources cited in text)

▨ =probable function

░ =possible function

[unshaded] = highly unlikely or impossible

Family	#1 Prey prehension	#2 Transport/ manipulate	#4 Hold prey	#5 Swallow	#6 Generate suction	#7 Expel water	#8 Hydraulic jetting	#9 Create flow regime	#10 Channel oral flow	#11 Fold into pouch	#12A Clean baleen by contact	#12B Clean baleen by backwash
Physeteridae		▨	░	■	■	■	▨					
Kogiidae		▨	▨	■	■	■	▨					
Ziphiidae		▨	▨	■	■	■	░					
Platanistidae	▨	■	▨	■								
Iniidae	▨	■	▨	■								
Pontoporiidae	▨	■	▨	■								
Lipotidae	▨	■	▨	■								
Monodontidae	▨	■	▨	■	■	■	▨					
Delphinidae	▨	■	■	■	■	■	▨					
Phocoenidae	▨	■	▨	■	■	■	░					
Balaenidae				■				■	■	■	■	■
Neobalaenidae				■				▨	▨		■	■
Eschrichtiidae		▨		■			▨				░	■
Balaenopteridae				■						■	░	■

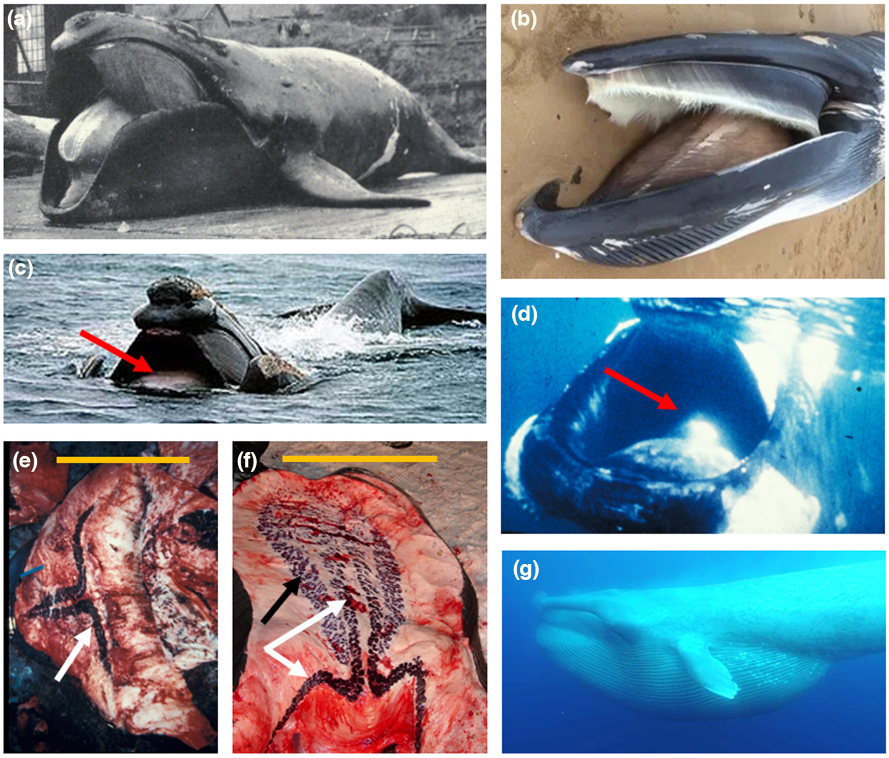

FIGURE 5 Tongue form, mobility, and function in balaenid and balaenopterid mysticetes. (a) Extremely large, firm, muscular tongue (here, exaggerated due to decomposition) of Southern right whale, *Eubalaena australis*. (b) Floppy, flaccid tongue of subadult fin whale, *Balaenoptera physalus*. (c) Surface skim feeding of North Atlantic right whale, *E. glacialis*, showing tongue (red arrow) aiding incurrent water flow (Table 1 #9). (d) Presumed underwater skim feeding behavior, in clear, non-feeding water, showing tongue (red arrow) channeling intraoral flow to baleen racks (Table 1 #10). (e, f) Transverse tongue sections of bowhead whale, *Balaena mysticetus*, showing huge adipose stores (Table 1 #23); (e) dorsal at left, white arrow shows genioglossus slip; (f) dorsal at top, black/white arrows show two genioglossus slips (gold scale bar = 1 m in both). (g) Video screen grab of blue whale, *Balaenoptera musculus*, underwater lunge feeding showing oral pouch inflated with ingested water as tongue invaginates into ventral cavity (Table 1 #11). Photo credits (a): reddit (CCY); (b, e, f): A.J. Werth; (c): M.J. Moore; (d): Des & Jen Bartlett; (g): BBC TV series "The Hunt" by Hugh Pearson, copyright Silverback Films/David Reichert, in collaboration with Cascadia Research Collective (permit #16111) and reproduced here with permission.

whale and basking sharks and manta rays), and evidence suggests that as in fishes there is cross-flow filtration, in which incurrent flow is along or tangential to the filter, rather than dead-end (through-put) filtration, with flow perpendicular to (i.e., straight into) the filter (Brainerd, 2001; Werth & Potvin, 2016; Potvin & Werth, 2017; Werth, Kosma, et al., 2019; Werth & Sformo, 2020). This precludes clogging and deposits a slurry of accumulated prey by the tongue root for easier swallowing.

Unlike fish, cetaceans have no opercular opening. Water exits the balaenid mouth through a jet-like port (Werth, 2004b) behind the semicircular lip by the posterior-end of the tongue and baleen racks. Underwater footage (Figure 5d) indicates the tongue slowly sweeps laterally, apparently channeling flow toward baleen (Table 1 #10) or altering the crucial distance between the tongue and baleen (Gaskin, 1982; Nemoto, 1959), as corroborated by mathematical and physical modeling (Werth, 2004b; Potvin & Werth, 2017) and flow tank experiments (Werth, Lillie, et al., 2018; Werth & Potvin, 2016). Lambertsen et al. (1989) posited that balaenid tongue size, shape, and location together create a Bernoulli effect along baleen's medial mat, which in turn (with continuous flow) creates a Venturi effect that slightly lowers pressure where water enters the mouth anteriorly, at the subrostral gap between baleen racks. This hypothesis was supported by experimentally obtained pressure measurements (Werth, 2004a; Werth & Potvin, 2016), demonstrating intraoral pressures lower than those just anterior to the mouth—likely insufficient to generate suction, but preventing a compressive bow wave that might disperse or warn tiny prey ahead of the mouth (Werth, 2012). These basic yet important hydrodynamic phenomena (Table 1 #9) depend upon the massive tongue's position, and the fluid effects change as the tongue moves even slightly, altering the crucial distance between the tongue and baleen (Potvin & Werth, 2017). These related yet distinct actions—first creating the initial Bernoulli + Venturi flow regime (Table 1 #9) and then altering cross-flow filtration (Table 1 #10) by minor lateral tongue movements—are simple yet highly effective balaenid adaptations. Both depend fundamentally on the tongue.

Open-gape skimming exposes the mouth to potentially frigid waters for extended periods. Balaenid tongues possess vascular adaptations (Ford et al., 2013; Ford & Kraus, 1992) to conserve or shed heat when necessary (Table 1 #21; important given the body's extraordinarily thick blubber). Bowhead tongues also include copious fat (Figure 5e,f) for insulation and nutritional storage (Table 1 #23; Werth & Sformo, 2020). Werth (2007b) showed a trend of increasing lingual

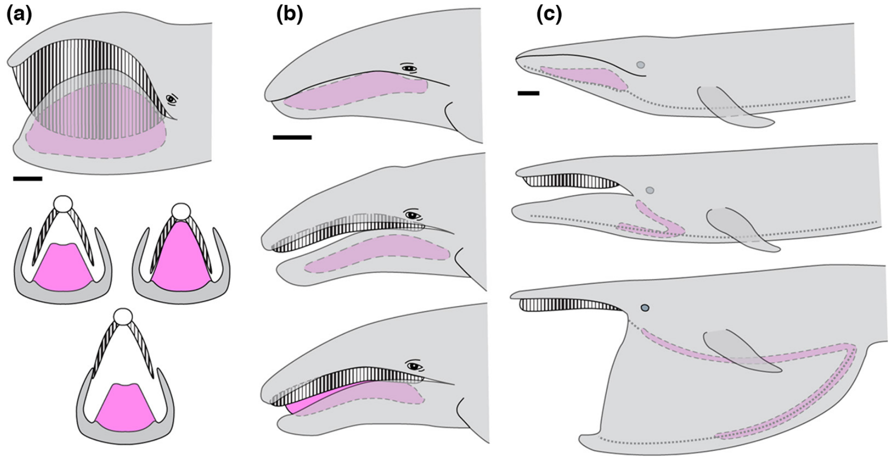

FIGURE 6 Schematic diagrams indicating relative tongue position, relations, and mobility in balaenid [bowhead, (a)], eschrichtiid [gray, (b)], and balaenopterid [fin, (c)] whales, all with tongue highlighted in pink and scale bar = 1 m. Top image in (a) series shows left lateral view of partially open gape, as during bowhead skim feeding, with extensive baleen rack partially obscured behind semicircular lower lip, and elevated, firm, highly muscular tongue; middle left (a) shows same scenario in transverse section. Middle right (a) shows transverse section of elevated tongue contacting baleen; bottom (a) image shows mouth and tongue moved to the left to differentially channel water flow to and around baleen (Table 1 #10; based on Werth 2004, Potvin & Werth, 2017). (b) Series shows gray whale tongue in left lateral view including normal position with closed gape (top), depressed tongue during suction generation (middle; Table 1 #6), and elevated position to potentially contact baleen (bottom; #12). (c) Series (based in part on Goldbogen, 2010) shows fin whale tongue with extent of ventral sublingual cavity (dotted line) during normal closed gape (top), partial inversion of the tongue as gape opens and water enters for lunge engulfment (middle), and complete tongue invagination into cavity during total engulfment (bottom; Table 1 #11). The full extent of tongue stretching is unclear; it may cover only the dorsal side of the inflated pouch's interior, or (instead of the expanded oral floor) also line the ventral pouch surface. The bottom image of (c) shows both possibilities.

adipose content, at the expense of muscle, in older balaenids. There is a similar ontogenetic trend of relatively fewer intrinsic lingual muscles as age increases (Werth, 2007b). This possibly relates to tongue use for milk ingestion in juveniles, but this is speculative.

2.17 | Mysticeti, baleen cleaning

A major benefit of balaenid cross-flow filtration is that filtered solids (retentate) flow primarily along rather than directly through the filter, keeping it clean (Potvin & Werth, 2017). This is of tremendous benefit when filtering dense swarms of tiny prey bristling with snagging appendages through a fibrous, hair-like mat. Copepods are almost never found trapped within the mesh-like free fringes (AKA baleen bristles or hairs) eroded from constituent hollow horn tubules (Werth & Potvin, 2016). Nonetheless, there has been considerable perennial speculation in both popular and scientific literature regarding the mysticete tongue's role in “cleaning” baleen of ensnared or embedded prey (Table 1 #12). Werth (2001) discussed this potential problem and outlined three ways whales might solve it: (1) through physical contact, by mechanically scraping baleen's medial surface with the tongue (Table 1 #12A); (2) by shaking the head to dislodge trapped prey (Table 1 #12A); and (3) by rapidly depressing the tongue to “pull” prey from the filter into the mouth's center via suction-generated backwash (Table 1 #12B). Although the first mechanism (direct tongue contact; Table 1 #12A) is frequently cited in popular accounts of whale feeding, and probably makes the most sense (especially when combined with lingual retraction to transport and swallow food), there is at present no way to reliably assess whether this actually occurs in balaenids or indeed any mysticetes. Scattered field accounts exist of brief, vigorous balaenid head shaking (Gaskin, 1982) and of head dipping which might coincide with backwash flow (Table 1 #12B; Mayo & Marx, 1990), but there are no observations suggesting obvious hyolingual motion. Skimming whales appear to pause, probably to swallow accumulated prey (Table 1 #5), at irregular intervals from 30 s to several minutes, perhaps depending on prey concentration (van der Hoop et al., 2019). Lab experiments to clean filters underwater (Werth, 2004b, 2013) suggest that direct tongue contact (Table 1 #12A) might exacerbate clogging, whereas suction-based backwash (Table 1 #12B) would prove most effective. Nonetheless it remains uncertain whether any sort of baleen cleansing is needed. Field necropsy observations and flow tank experiments suggest entrapped prey pose no problem, and that cleaning is thus largely unnecessary (Werth, Harriss, et al., 2016). However, it seems likely that the tongue would be involved to some extent and in some fashion, either by direct contact or backwash flow, in removing captured prey from the filter and transporting them (Table 1 #2) for swallowing (Table 1 #5). In sum, the tongue is essential for multiple aspects of balaenid feeding (Table 3).

2.18 | Mysticeti, Neobalaenidae

Pygmy right whales, *Caperea marginata*, are the smallest (6 m) mysticete (Kemper, 2017). Long classified as balaenids because of their resemblance to right whales due to the curved rostrum accommodating relatively long, finely-fringed baleen, *Caperea* is now classified as the sole neobalaenid, or by some researchers (Fordyce & Marx, 2013; Marx & Fordyce, 2016) as a remnant cetothere, the lone survivor of an otherwise extinct Oligocene-Pleistocene family (Gol'din & Startsev, 2017). *Caperea* is generally seen as closer to Balaenopteridae than Balaenidae (Figure 7), but is clearly intermediate (Székely et al., 2021).

Ecological (Sekiguchi et al., 1992) and morphological accounts (Werth, Potvin, et al., 2018) indicate that *Caperea* skims copepods and small krill, like balaenids. Due to this species' rarity, the pygmy right whale tongue has not yet been adequately described (Werth et al., in prep.), but is similar in general form to the balaenid tongue: large, firm, muscular, and elevated within the mouth. Unlike bowhead and right whale tongues, *Caperea*'s tongue includes no fat deposits (Table 1 #23), although it possesses thermoregulatory vascular specializations (Table 1 #21; Heyning, 1997) in addition to robust extrinsic and intrinsic lingual musculature (Werth et al., in prep.). Whether *Caperea* employs cross-flow filtration, as in balaenids, is unknown; however, the skim-feeding rorqual sei whale, *Balaenoptera borealis*, is probably a better analogue in both morphology and behavior (Brodie & Vikingsson, 2009; Segre et al., 2021). Pygmy right whales' sturdy tongues appear well-suited to cleaning baleen (Table 1 #12), though whether they are used for this purpose remains uncertain.

2.19 | Mysticeti, Eschrichtiidae

Gray whales, *Eschrichtius robustus*, are morphologically and ecologically distinct from other mysticetes and the sole member of a monotypic family. This coastal species is closely related to rorquals; molecular studies (McGowen et al., 2009) reveal *Eschrichtius* evolved within Balaenopteridae, as a sister group to fin (*Balaenoptera physalus*) and humpback (*Megaptera novaeangliae*) whales (Figure 7). Gray whales are intermediate between rotund balaenids and slender rorquals. They typically suction feed (Table 1 #6), engulfing benthic epifaunal and infaunal crustaceans, mostly mysids, amphipods, and isopods (Murison et al., 1984; Nerini & Oliver, 1983). They swim near the bottom and rotate (normally rightward; Kasuya & Rice, 1970; Woodward & Winn, 2006) along the body axis to locate the mouth above the seafloor (Shull, 2009), then rapidly expand the oral cavity via hyolingual depression and retraction, just as in odontocete suction (Table 1 #6; Nerini, 1984). Two to seven external throat grooves, as in sperm and beaked whales, facilitate buccal expansion to engulf prey-laden water (Ray & Schevill, 1974).

Because gray whales regularly ingest benthic zooplankton (and sediments) via powerful suction currents, they are most likely among mysticetes to contend with the problem of clogged baleen. However, they are also able to draw "clean" water through the coarse filter (Young et al., 2015), again via tongue-generated suction (Table 1 #12B), should clogging become problematic. The tongue could also scrape baleen clean (Table 1 #12A). Although gray whales are mainly suction feeders (Table 1 #6), their foraging is resourcefully diverse. They have been observed feeding in mid-water, both with slow, open-mouthed skimming like balaenids and with rapid lunges like balaenopterids (Sund, 1975), although gray whales lack rorquals' extensive throat pleats that allow for voluminous gular expansion. Gray whales have been observed with kelp in the mouth, perhaps to strip crustaceans clinging to algal blades (Werth, 2000b).

The neonate gray whale tongue was described in detail by Johnston et al. (2010) and Kienle et al. (2015) as unusually mobile and robust relative to other mysticetes, with well-defined muscles (apparently true in adults; Andrews, 1914). Kienle et al. (2015) described a prominent hyoglossus originating from a substantial hyoid, and a broad genioglossus with unique fiber orientation and extensive insertion within the tongue body. The tongue has a flaring tip, median furrow, and no fat. There are scattered yet indistinguishable "undifferentiated… crisscrossing" intrinsic fibers, suggesting mobile

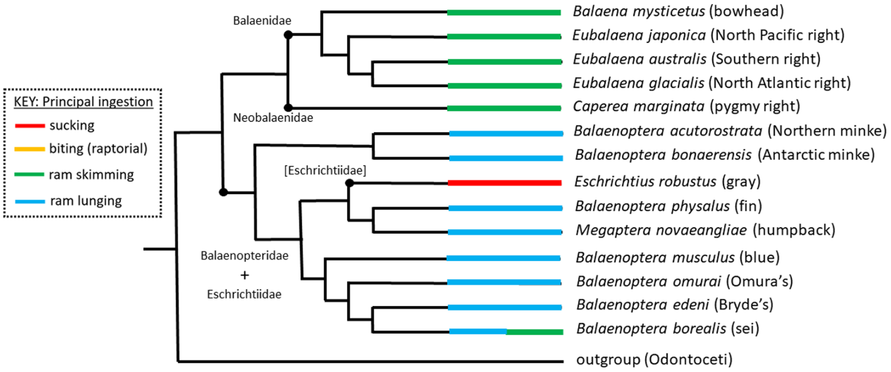

FIGURE 7 Phylogeny of extant mysticete species (from Székely et al., 2021; does not include newly described Rice's whale, *Balaenoptera ricei*) showing distribution of principal feeding methods. [There are no biting mysticetes.] Note that current phylogenies place the gray whale, *Eschrichtius*, within balaenopterids. Pre-filtration tongue-driven suction ingestion (Table 1 #6) is often presumed to be plesiomorphic for Mysticeti (Marx, Hocking, et al., 2016), but today occurs solely in *Eschrichtius*, revealing major tongue function changes in Mysticeti. Placement of pygmy right whale, *Caperea*, is uncertain; many recent phylogenies based on morphological and molecular data place it closer to and within Balaenopteroidea (rorquals + gray whale). Skim feeding is found in basal lineages (plus rorqual sei whale), but fossils indicate that tongue-driven skim and lunge feeding probably arose after suction as specialized derivations.

shape-changing ability (Kienle et al., 2015), potentially useful for neonatal suction (Table 1 #14) and possibly adult suction ingestion (Table 1 #6) and baleen cleansing (Table 1 #12). Kienle et al. (2015) also documented lingual fungiform papillae, possibly for chemoreception (Table 1 #15). Gray whale tongues have extensive lingual retia (Table 1 #21; Ekdale & Kienle, 2015; Heyning & Mead, 1997).

2.20 | Mysticeti, Balaenopteridae

Tongues of rorquals ("groove-throated whales," including blue, fin, humpback, and seven other whale species) are not only among the most interesting vertebrate tongues, but also the most dynamic of all biological structures. Rorqual tongues have yet to be described in anatomical detail, but invaginate by inflating with enormous volumes of prey-laden water (Table 1 #11; Pivorunas, 1979) engulfed during a ram-driven lunge (Figures 5g and 6c). The inverted, water-filled tongue then sinks into and fills a loose space, the *cavum ventrale* (ventral hollow) of the ventral oral floor, extending caudally from the mandibles to the umbilicus (Goldbogen, 2010; Kot, 2005; Schulte, 1916). The mechanism of invagination, in which the lingual epithelium becomes the cavity's lining (Table 1 #11; Figure 6c), was described by Lambertsen (1983). This capacious space lies just deep to the ventral groove blubber (Orton & Brodie, 1987; Shadwick et al., 2013), an extensive network of elastic throat pleats which expand in accordion-like fashion, akin to a pelican's pouch, to accommodate temporarily engulfed water (Werth & Ito, 2017). This briefly converts a normally sleek, streamlined balaenopterid into a swollen, tadpole-like form (Werth & Ito, 2017; Figures 5 and 6). The volume of engulfed water depends on the species; in large blue whales it has been estimated to be as large as 80,000–100,000 L or more (Goldbogen et al., 2017). Aerial photography (Werth, Kosma, et al., 2019) reveals the *cavum ventrale*'s patent opening as gape opens and water starts flowing from outside the mouth through the oral floor aperture to fill the cavity.

Adult rorqual tongues resemble flaccid, floppy waterbeds, not only after post-mortem removal from the oral floor but even in situ (Slijper, 1962). They lack substantial muscular firmness and are remarkably different from tongues of other mysticetes (Werth & Ito, 2017). A small tip can barely be observed, more so by the tongue's dorsum rather than from muscular insertion as revealed by dissection (Werth, Lillie, et al., 2018). In situ manipulation of deceased rorquals reveal that tongues cannot be protruded beyond the anterior tip of the mandibles or rostrum (Werth & Ito, 2017). However, tongues readily slide posteriorly during engulfment/invagination to contain the sudden influx of prey-laden water (Table 1 #11; Werth, Lillie, et al., 2018), which is subsequently filtered by the keratinous baleen (Goldbogen et al., 2017).

In fetal and newborn specimens, balaenopterid tongues are firm and muscular. In general appearance and myology these closely resemble other mysticete tongues, having not yet attained their unique and distinctive floppy adult form (Werth & Ito, 2017). When this transformation occurs is unknown, but necropsy of stranded specimens indicates that juvenile (yearling) rorqual tongues have already lost much of their typical muscular form and connection to the oral floor, and that this process is completed or nearly so in subadult whales (Werth, Lillie, et al., 2018). Manipulatory experiments confirm that fetal rorquals possess a ventral cavity into which fetal tongues readily slide and at least partially invaginate following water influx (Werth, 2007a). In fetal and neonatal specimens, genioglossus and hyoglossus muscles predominate, with smaller yet distinct styloglossus and palatoglossus fibers (Werth & Ito, 2017). In very young rorquals, a notable genioglossal tubercle near the mandibular symphysis is externally visible (Werth, 2007a). Rorqual fetal and neonate tongues contain little adipose or other connective tissue (Werth, Lillie, et al., 2018). Intrinsic lingual fibers are scattered and substantially less organized compared to typical mammals, but sparse perpendicular vertical and transverse fibers can be distinguished (Werth, 2007a). In contrast, it is difficult to detect obvious patterns of intrinsic lingual fiber orientation in adult rorquals; scattered fibers remain, but these are interspersed with stretchy connective tissue fibers: likely elastin, collagen, and perhaps some areolar and reticular fibers (Werth, Lillie, et al., 2018), although formal histological analysis has yet to be completed and described in published literature.

Typical mammal tongues are, like elephant trunks and octopus tentacles, muscular hydrostats (Kier & Smith, 1985). As constant volume structures (like water balloons), they extend along one axis as they shorten along another. This is not the case in balaenopterid whales. Tongues of rorquals, probably alone among mammals, do not exhibit conventional constant-volume relations. This stems from the lack of a firm external tunic and coherent muscular arrangement, and presence of a large sublingual cavity as well as other lingual spaces and clefts, mostly along fascial planes (Werth, Lillie, et al., 2018). When distorted to line the inflated oral pouch during engulfment (Table 1 #11; Figures 5g and 6c), the rorqual tongue's shape, dimensions, and position are determined less by its internal arrangement and volume than by the form of the two entities it lies stretched between: the engulfed water mass interiorly and expanded ventral groove blubber exteriorly.

The chief contributor to adult rorqual tongues is the genioglossus, which includes fibers that fan out through the tongue "body" (if such a limp, flabby structure can be characterized as such) in at least three slips (Werth & Ito, 2017). Inserting genioglossal slips range from firm, distinct fiber bundles anteriorly and ventrally, closer to the muscle's origin on the mandibular symphysis and rami and the more superficial geniohyoid and mylohoid muscles, as well as arrays of genioglossal fibers radiating posteriorly and to a lesser extent dorsally as they insert in internal lingual connective tissues (Werth, Lillie, et al., 2018). A distinct hyoglossus is evident but smaller; other tongue muscle bundles cannot reliably be identified (Werth, 2007a). The principal noteworthy feature of the adult rorqual tongue involves not musculature but several closely adherent layers of slick fascia (Werth, Lillie, et al., 2018) that evidently enable the inverting balaenopterid tongue to slide rapidly and readily, in track-like fashion, through an intermuscular cleft into the ventral cavity. During invagination (Table 1 #11), thousands of tiny (0.5–2 mm) folds of the oral floor along all sides of the tongue apparently stretch, in accordion fashion, to allow the now-inverted, balloon-like tongue to fill with tens of thousands of liters of engulfed seawater and, importantly, with fish or zooplankton included within the water (Werth, Kosma, et al., 2019). It is not entirely clear where the lingual dorsum resides when the tongue temporarily assumes this inverted form. Abundant accordion-like pleats and plicae in the oral floor anterior and lateral to the tongue, less abundant near the tongue root, suggest the invaginated tongue briefly becomes located on the cavity's dorsal aspect, near the oropharyngeal aperture (Figure 6; Werth & Ito, 2017). This hypothesis nonetheless requires further analysis and remains uncertain.

What appears more certain is that the adult rorqual tongue, although extraordinarily (and truly uniquely) mobile, is with one major exception largely unmovable on its own. The lunge-feeding water engulfment process is ram-driven by forward locomotion (Simon et al., 2012) and assisted by gape opening from mandibular depression and to a lesser extent cranial elevation (Kosma et al., 2019; Werth, Kosma, et al., 2019). Once the mouth opens, incurrent water quickly flows passively inward. Contraction of ventral groove musculature (Goldbogen et al., 2017; Shadwick et al., 2013), perhaps along with hydraulic rebound of ingested water (Potvin et al., 2009, 2020, 2021; Werth, Kosma, et al., 2019), forces engulfed water back out of the mouth, but now with narrowed gape, such that water flows through the curtain of paired baleen racks, trapping prey items along the eroded, fibrous medial surface (Table 1 #9; Werth, Straley, & Shadwick, 2016). The robust genioglossus muscle then presumably contracts, not to protrude the tongue outside the mouth as in many vertebrates, but instead simply to return the tongue to its resting position in the middle of the mouth (Werth & Ito, 2017), in preparation for gape closure (Werth, Ito, & Ueda, 2020; Werth, Rita, et al., 2018) and further lunges.

When engulfed water is expelled (Table 1 #7) back into the oral cavity and through baleen (Table 1 #9) by hyolingual elevation, faucial closure prevents water entry into the oropharynx. Only when accumulated prey are swallowed do the fauces relax, as tongue retraction moves food into the oropharynx (Table 1 #5). Gil et al. (2022) described a musculo-fatty soft palate oral plug that seals the oropharynx, but simple tongue elevation should expel water, push food toward the fauces, and create greater overlapping of the soft palate and epiglottis. This would tighten the laryngeal position and protect the respiratory tract as a slurry of prey flows around the interlocked larynx (Reidenberg & Laitman, 2007), following paired lateral channels of the piriform sinuses, as in most (non-human) mammals. The laryngeal aditus is shielded from food and water by its intranarial position, which remains unchanged during swallowing (German & Crompton, 1994; Laitman & Reidenberg, 1993).

Rorquals generally feed on small (3–8 cm) krill or 5–20 cm forage fish such as herring, anchovy, or sand lance (Goldbogen et al., 2017). These are unlikely to become entangled in coarse rorqual baleen and probably simply fall downward onto the tongue and oral floor, although the whale is by no means in dorsal-upright aspect during feeding lunges (Cade et al., 2016), and powerfully expelled excurrent water might ensnare prey in baleen. Tongue movements might therefore serve to cleanse baleen (Table 1 #12). Weak lingual retraction would suffice to swallow an accumulated bolus of prey (Table 1 #5).

Soft mysticete tongues are a favored food of transient killer whales, which often leave a baleen whale carcass undisturbed after eating only a rorqual (Silber et al., 1990) or gray whale tongue (Baldridge, 1972).

3 | NON-FEEDING FUNCTIONS OF CETACEAN AND GENERAL MAMMAL TONGUES

Typical mammalian tongues perform or assist numerous non-feeding functions, including drinking water or other fluids, suckling milk, respiration, vocalization, panting or other thermoregulation, and gustatory sensation (Herring, 1993; Hiiemae & Crompton, 1985). There is little evidence that the tongue is involved with these activities in any cetacean species (Werth, 2007a).

3.1 | Drinking/lapping fluids

Lingual protrusion and shape changes often collect and convey aliquots of water into the mouth during drinking, especially in ungulate and carnivoran taxa (Table 1 #13; Halpern, 1977). Mobile lips, when present, may be pursed to aid in sucking water, and when the mouth is submerged, lingual depression also pulls water into the mouth (German & Crompton, 1996). As commonly seen in cats and dogs (and occasionally cows or other large ungulates), the tongue alone is dipped into “lapped” water (Crompton & Musinsky, 2011). It initially appears as if a spoon-shaped tongue tip depression ladles water into the mouth with rapid serial movements, but high speed and X-ray videos confirm that a small volume of water adheres to the tongue with each lap (Crompton & Musinsky, 2011). The tongue is quickly appressed to the palate, where transverse ridges (Linton, 1905) hold water in place as sequential lingual motions convey the water to the fauces as additional cycles elevate new aliquots (Crompton & Musinsky, 2011). As is typical of many tongue functions, this process is (1) outwardly simple-looking yet deceptively complex, and (2) dependent upon a rhythmic series of sequential muscle contractions modulated by closely monitored sensory reception (Ewert et al., 1994).

Neither this lingual lapping nor any other drinking is found in any cetaceans, which drink no fresh or seawater (Reynolds & Rommel, 1999). Cetaceans instead subsist on water contained within food or on small volumes of metabolically-generated water (Slijper, 1962). Cetacean kidneys, unlike those of most terrestrial mammals, possess sufficient concentrating ability to gain a net osmotic benefit from incidentally ingested seawater and from food that is isotonic to seawater (Reynolds & Rommel, 1999). Most sources (Donaldson, 1977; Kleinenberg et al., 1969) argue that instead of drinking water, a more important role for cetacean tongues, especially in the absence of mobile lips, is expelling water from the mouth to prevent excess seawater from being swallowed (Table 1 #7; Figure 4).

3.2 | Suckling

Suckling of milk is a hallmark of newborn and juvenile mammals (Table 1 #14). This occurs by a different mechanism than tongue-based lapping or other drinking, although suckling too depends on a stereotypical sequence of rhythmic motions. Suckling involves creation of two oral seals by pressing the tongue against the (1) teat and (2) stiffened palate and then depressing the tongue, creating suction via pumping (Gordon & Herring, 1987). Suckling also typically involves release of stored milk via compression of the teat's mammary papilla by the tongue against the palate, and compressive action by the tongue or gums against the lactiferous sinuses (Arvy, 1974). Because cetacean tongues apparently do not create these paired oral seals or compressions, in contrast to other mammalian tongues, there is no true suckling, or at best only a greatly reduced version. Provision of milk in Cetacea is therefore properly termed nursing. The tongue plays at best a minor role in cetacean nursing (Arvy, 1974; Oftedal, 1997). Although cetacean lactation remains poorly understood, it appears that profuse, prominent smooth muscle fibers surrounding mammary glands and milk ducts forcefully expel dense, semisolid milk into the angle of the mouth of young cetaceans (Ratsimbazafindranahaka et al., 2022). There are at least five reasons for this peculiar departure from typical mammalian nursing.

First, all cetacean nursing occurs underwater (Slijper, 1962), and thus must involve brief interruptions in which the infant rises regularly to the surface to breathe. Unlike pinnipeds, cetaceans spend their entire lives away from land. Second, cetacean milk is notoriously thick, with a fat content of 35%–50% and semisolid consistency more like that of whipped cream or toothpaste than liquid (Slijper, 1962), such that smooth muscle aids in pushing milk through ducts (Arvy, 1974). Exceptionally fatty milk guarantees that young cetaceans acquire calories needed for rapid growth, ensuring easier locomotion, protection from predators, and thermoregulation by diminishing the neonate's surface to volume ratio (Reynolds & Rommel, 1999). Third, in the largest cetaceans huge volumes of milk must be quickly produced and pumped to neonates. It has been estimated, based on growth rates, that a newborn blue whale consumes 500–600 L of milk per day (Arvy, 1974). Fourth, cetacean mammary glands and milk ducts are internal and covered by a thick layer of abdominal blubber, with paired mammary slits through which milk is ejected (Drinna & Sadleir, 1981). Fifth, the size, shape, and structural arrangement of the infant's head, with a "notched" gape open at the sides of long jaws, precludes optimal presentation of an oral opening into which milk can be sucked or squirted (Werth, 2000b). Observational evidence from multiple cetacean species ranging from small porpoises to giant mysticetes, in the wild and captivity, indicates that breath-holding young rapidly approach the mother's flank and position themselves under her abdomen with the mammary slit, through which teats extrude during nursing, adjacent to the angle (corner) of the mouth. Although this arrangement is not optimal for nursing, the calf uses its curled tongue, as much as possible, to grasp the extruded teat and channel milk to the fauces for swallowing (Ratsimbazafindranahaka et al., 2022; Figure 3). Each bout of milk ingestion typically occurs within 5–10 s, followed by a break from the mother's abdomen and ascent so that the young can exchange air in its lungs (Johnson et al., 2010). There is no evidence for hypothesized "nasal suckling" (milk ingestion through the nares) in Cetacea, although nasal rubbing may stimulate the "let down" reflex, including nipple erection and extrusion (Gero & Whitehead, 2007). There is limited and equivocal evidence hinting at weak, brief hyolingual depression in neonate cetaceans, but this alone is insufficient to account for milk ingestion in all instances (Werth, 2007a). The presence of small marginal papillae on tips of neonatal but not adult odontocete tongues provides additional circumstantial evidence for some oral seal (Kastelein & Dubbeldam, 1990; Kobayashi, 1992; Yamasaki et al., 1976a, 1978a; Yoshimura et al., 2009; Yoshimura & Kobayashi, 1997). The ability of some young odontocetes to curl tongues longitudinally suggests a means to improve milk ingestion or limit its escape from the mouth (Ratsimbazafindranahaka et al., 2022; Shindo et al., 2007, 2008). Still, it is likely that ejecting large volumes of extraordinarily thick milk depends to a considerable extent on forceful smooth muscle contraction. It remains the case that from a generic mammalian perspective, lingual function during nursing is markedly atypical in cetaceans and does not involve the typical eutherian suckling mechanism (Table 1 #14).

3.3 | Taste reception

Chemosensory abilities have long been thought to be severely limited or absent altogether in Cetacea (Table 1 #15; Feng et al., 2014; Slijper, 1962; Zhu et al., 2014). With regard to olfactory reception, this is due to minimized olfactory lobes/tracts and an ethmoid cribriform plate that is considerably or entirely non-perforated, particularly in Odontoceti (Berta et al., 2014; Ichishima, 2016). The trend toward cribriform plate closure apparently began early in cetacean evolution, during the Eocene (Kishida et al., 2015). Nonetheless some baleen whales retain partial "smelling" sensation by olfactory bulbs of the forebrain (Kishida et al., 2015). Likewise there are few lingual papillae or obvious gustatory receptors, and no reliable field or experimental evidence of chemosensation. Thus the cetacean tongue, unlike typical mammal tongues (Yamasaki et al., 1980), is presumed to play no or virtually no role in gustation. There is speculation that marine mammals might locate prey by detecting dimethyl sulfide (Owen et al., 2021), although evidence for even weak chemosensory abilities in Cetacea is equivocal (Zhu et al., 2014). It remains likely, however, that cetacean tongues retain tactile abilities via mechanoreception and proprioception. As Sonntag (1922) reported, cetacean tongues differ from typical mammal tongues in their dearth of surface papillae (Komatsu & Yamasaki, 1980). Even where few fungiform and filiform papillae are present in baleen whales (Kienle et al., 2015) and toothed whales (Suchoskaja, 1972), these papillae may be vestigial or wholly tactile in sensory ability (Yamasaki et al., 1978b). However, recent findings (Keenan et al., 2022) suggest that lingual vallate papillae in four odontocete species may bear functional taste buds. Although evidence for cetacean taste reception is equivocal, the tongue is innervated as in other mammals (Marshall et al., 2007), with motor innervation mainly from the hypoglossal (XII) nerve, plus a nucleus and branch of the vagus (X) to the palatoglossus muscle. Trigeminal (V), facial (VII), and glossopharyngeal (IX) cranial nerves receive the tongue's sensory information (Werth, 2007a), including any possible chemoreception.

3.4 | Respiration

Another non-feeding tongue function in most mammals involves respiratory gas exchange and maintenance of open airways (Table 1 #16; Sokoloff & Burkholder, 2012). However, the tongue plays no respiratory role in any cetacean due to the obligate intranarial position of the larynx. The extended tubular larynx protrudes directly through the oropharynx, with its dorsal tip completely and tightly bound by the encircling palatopharyngeal sphincter anterior to the atlas (Reidenberg & Laitman, 1987). This completely separates digestive and respiratory pathways, ensuring whales cannot breathe through the mouth. However, whales can (and occasionally do) asphyxiate if large prey, most often cephalopods with mobile arms bearing adhesive suckers, pull or otherwise dislodge the larynx and block the respiratory pathway (Mignucci-Giannoni et al., 2009). Nonetheless, the intranarial laryngeal position common to all cetaceans precludes any respiratory function by the tongue, or any other oral or digestive structure. This prevents oral suction creation via pulmonary aspiration (i.e., ingressive flow), as occurs when humans suck through straws or whistle (Harrison et al., 1967).

Because of the palatopharyngeal sphincter, there is no free soft palate per se (*palatal velum*) in any cetacean (Jacob, 1835). There are strong pharyngeal constrictors and palatoglossus, palatopharyngeus, and hyopharyngeus muscles (Reidenberg & Laitman, 2007), and a small pterygoid hamulus, but no obviously distinct tensor or levator veli palatini muscles (Lawrence & Schevill, 1956). Swallowing therefore differs in Cetacea relative to other mammals. Palatoglossal contraction presumably elevates the tongue against the hard palate and palatopharyngeal sphincter (which serves as a sort of soft palate), closing the fauces so that further retraction or depression of the tongue root would initiate swallowing (Lawrence & Schevill, 1956).

In most mammals, the fauces serve as a muscular sphincter (bounded by the soft palate, tongue, and "arches" or "pillars" of palatoglossal fibers) separating the oral cavity from the oropharynx (Herring, 1993). In terrestrial mammals, this opening is closed during swallowing by contraction of palatoglossus and intrinsic lingual muscles, forcing the tongue posteriodorsally against the tensed soft palate (German et al., 1992). In cetaceans, however, the palatoglossus simply forces the tongue against the hard secondary palate (Werth, 2007a). This not only leads to a different swallowing mechanism, but also relates to enclosure of engulfed and expelled water during mysticete lunge feeding (described in Section 2.17). It is important to recognize that cetaceans do not possess a proper oral cavity, as they lack true lips and cheeks and possess rudimentary orbicularis oris and buccinator muscles (Werth, 2000a). Whereas suction feeding fishes and tetrapods typically suck prey into the oral cavity, it is possible, even likely, that sperm whales and other species suck prey directly through the fauces into the oropharynx (Werth, 2004a), and in this way they not only eliminate a grasp-and-transport stage but may also combine ingestion with swallowing (Werth, 2006a).

3.5 | Vocalization

Similarly, the complete separation of all digestive structures from cetacean airways prevents the tongue from playing any part in vocalization (Table 1 #17). Some controversy remains as to the potential role of laryngeal structures in cetacean sound generation, but a wealth of diverse and compelling evidence (Cranford et al., 1996; Pilleri, 1990) strongly suggests that at least in odontocetes, most sounds are generated via air passage through reverberating folds in nasal passages; in mysticetes, sounds may be produced by reverberations of laryngeal folds (Reidenberg & Laitman, 1988, 2007). Vocalization is undoubtedly an essential aspect of toothed and baleen whale behavioral ecology, with remarkable sonic production from extremely low (≤1 Hz) frequency pulses potentially conveying messages across entire oceans, to trains of ultra-high frequency clicks and whistles for communication and sensitive echolocation (Pilleri, 1990). Regardless of whether air flow generates vocalizations in nasal or laryngeal pathways, the fact remains that unlike typical mammals, which produce a broad range of sounds aided by lingual movements, the tongue can play no role whatsoever in cetacean vocalization.

3.6 | Coughing, vomiting

Tongue movements are involved in non-feeding activities related to passage of air or digesta through the pharyngeal chiasm in humans, due to the low laryngeal position and anterior pharyngeal wall being partly formed by the posterior third of the tongue (Levy, 1990). These activities include coughing, sneezing, and vomiting or emesis (Table 1 #18, 19). However, the tongue likely plays little or no role in these activities in typical (non-human) mammals because of the closely apposed larynx and nasal passages. Due to the cetacean larynx's permanent intranarial position and subsequent patent airway (Figure 2) only through the blowhole (single in odontocetes, paired in mysticetes), air cannot be coughed or sneezed into or through the cetacean mouth: the tongue can play no role in these activities. Vomiting of partially or fully digested stomach or intestinal contents (e.g., ambergris), and of recently swallowed and therefore undigested stomach contents, occurs in stressed cetaceans (Gaskin, 1982), as noted by whalers (Slijper, 1962). The extent to which the cetacean tongue is involved in vomiting is unknown; there is no known gag reflex. It appears likely that involuntary regurgitation via retrograde flow of stomach contents occurs by reverse peristalsis, initiated by contracting longitudinal and concentric smooth muscle fibers of the gastrointestinal (GI) tract, along with relaxing pharyngeal, cardiac/esophageal, and other GI sphincters, so that cetacean tongues play little or no role in activating or aiding regurgitation of gut contents (Tarpley, 1985).

3.7 | Thermoregulatory panting

The tongue is used for thermoregulatory panting in many mammals, most familiarly carnivorans and some ungulates (Table 1 #20; Chibuzo, 1979). Mammals generally have far fewer sweat glands than humans and so depend on evaporative respiratory water loss for cooling. This can occur by many oral structures, but the mobile tetrapod tongue is ideally suited for this role, similar to the gular fluttering used by some birds and reptiles to lower body temperature. There is no evidence for thermoregulatory panting in Cetacea.

3.8 | Vascular thermoregulation

Although cetaceans do not pant, large whales surely use tongues for thermoregulation via specialized vascular adaptations, notably extensive networks of classic perarterial venous retia (Table 1 #21; Ekdale & Kienle, 2015; Ford et al., 2013; Heath, 1998; Heyning, 1997, 2001; Heyning et al., 1993; Heyning & Mead, 1996, 1997). Such vascular formations are found throughout the tongue of bowhead, right, and gray whales (Werth, 2007a) and may also be present, if less plentiful, in rorqual mysticetes (Heyning, 1997). These blood vessels alternately conserve or radiate excess heat. Balaenid tongues also possess numerous large veins just below the tongue's lateral surface (Werth, 2007a). Thick blubber stores, especially of polar bowhead whales (which like right whales lack a typical dorsal fin with thin blubber and high surface area to shed body heat), present a challenge for cooling off, especially during migrations or long bouts of fluke-driven, high drag skim feeding, both of which probably raise body temperature (Werth & Sformo, 2020). Even when not feeding, opening the mouth to allow warm blood to flow near cold water adjacent to the tongue provides a simple, effective means to radiate heat rapidly; infrared imaging confirms this (Ford et al., 2013; Heyning & Mead, 1997). Control of lingual vasculature prevents unwanted oral heat loss, particularly in mysticetes feeding for extended periods in frigid waters (Heyning, 2001). Lingual specializations for thermoregulation have not been found in odontocetes, likely because odontocetes tend to be smaller or use locomotor surfaces instead (Werth, 2007a).

3.9 | Palatal thermoregulation

A separate means of oral thermoregulation in bowhead and right whales, and perhaps other mysticetes, indirectly relates to the tongue. It involves flow of water contiguous to a highly vascularized palatal rete (Table 1 #22; Ford et al., 2013; Ford & Kraus, 1992). Like tongue vasculature, palatal vasculature is extensive, holds much blood, and is situated directly in the path of cold flowing seawater, especially because balaenids feed via continuous filtration during which gape remains open for extended periods (Werth & Potvin, 2016). The palatal organ's capacity to conserve or shed excess heat depends on the extent to which this organ is alternately exposed or covered by the large, well-insulated adjacent tongue. The tongue possesses a median central furrow suitably paralleling the apposite palatal organ (Werth, 2007a).

3.10 | Nutritional storage

Mysticetes are largely seasonal feeders, feeding at high latitudes during summer and fasting at low-latitude winter breeding and calving grounds (Berta et al., 2015). Just as blubber stores accumulate during summer, the tongue too serves as a valuable seasonal store of rich adipose tissue (Table 1 #23), especially along the lingual dorsum and sides in bowhead whales (Howell, 1930; Tarpley, 1985; Werth, 2007a). Subdermal and interior tongue fat can, in late summer, comprise well over half of the tongue's mass (Werth & Sformo, 2020). Even where balaenid tongues have large muscle contributions, adipose stores intermingle between scattered fibers of intrinsic and extrinsic lingual musculature (Werth, 2007a). Extensive adipose deposits not only store calories but also insulate lingual muscles, vessels, and nerves (Werth & Sformo, 2020). They create a larger, firmer tongue to alter intraoral flow relative to the baleen filter, as described previously in Section 2.16.

3.11 | Summary

Cetaceans diverged sufficiently from terrestrial ancestors in anatomy, physiology, and ecology/habitat that their tongues no longer (like typical mammal tongues) play substantive roles in numerous varied activities unrelated to solid food consumption, namely drinking water, suckling milk, breathing air, producing vocal sounds, providing gustatory sensation, and panting.

4 | CONCLUSION: HOW CETACEAN TONGUES EVOLVED

Cetacean bodies depart from mammalian norms in many ways, such as locomoting with limbless spinal flexion. Their tongues, unsurprisingly, pose no exception. Tongues were valuable for ingesting and swallowing food in reptilian ancestors (Schwenk, 2000) but take on indispensable functions for suckling milk and masticating food into small pieces with high surface area (Crompton, 1971), both crucial for fueling the mammalian endothermic lifestyle (Hiiemae, 2000). Tongues are essential for mammalian gustation, and commonly play major roles in breathing, panting, vocalizing, lapping water, and other important activities (Schwenk, 2000; Table 1).

As cetacean tongues took on new roles in feeding and other activities, they diverged from the standard eutherian model (Table 3; Iwasaki, 2002). Absent typical roles in mastication, suckling, or other mammalian tongue functions (taste, vocalization, drinking, breathing, etc.), cetacean tongues were freed to undertake markedly novel functions (Table 1 #8 expelling water to uncover prey, Table 1 #10 redirecting water flow, Table 1 #12 cleaning baleen, etc.), and in some cases evolved strikingly divergent anatomy (Heyning & Mead, 1996). This has culminated in the truly bizarre, aberrant tongues of balaenopterid (rorqual) whales, which lack the normal constant-volume relationships of muscular hydrostats (Werth & Ito, 2017).

Cetacean lingual function evolved in concert with dental changes (Werth, Loch, et al., 2019), including losing complex cusps, shearing surfaces, and an entire generation of deciduous teeth; gain of tooth numbers (polydonty); in some cases thickened and complexly structured enamel; increasing dental roles in sexual display/combat; and replacement of teeth with filtering baleen (Werth, Potvin, et al., 2018). But shifts to homodonty and baleen are only two of many evolutionary modifications that dramatically altered cetacean tongues (Werth, 2000b). Near-uniform loss of cheeks and mobile lips led to a largely open oral cavity and “notched” gape, altering water flow and feeding methods (Werth, 2006b). Palatal changes included retention of only a negligible pterygoid hamulus, and loss of a standard soft palate and its replacement by a strong palatopharyngeal sphincter and permanent intranarial larynx (Reidenberg & Laitman, 1987). This led to total structural and functional separation of digestive and respiratory pathways (Reidenberg & Laitman, 1994), which in turn altered tongue function. Cetacean tongues no longer needed to redirect and transport food during chewing, to pump milk during suckling, to taste food, or to channel air flow for breathing, panting, or vocalization. Instead, cetacean tongues became in some ways more like the non-muscular tongues of fishes (Konow et al., 2011), as piston-like structures moved to generate intraoral suction or as blocks used to temporarily secure soft, elusive prey against the palate (Werth, 2006b).

The story of cetacean tongue evolution is of marked loss of intrinsic musculature (Figure 2) and simplification of extrinsic lingual musculature (Werth, 2007b). Most cetacean tongue functions can be achieved with positional rather than shape change, and substantial shape change (as in rorquals) occurs passively via water influx rather than active muscular contraction (Werth, 2007a). Relative to other cetaceans, river and oceanic dolphins retained the most typical mammalian feeding functions; their tongues depart the least from ancestral conditions (Table 3). Of all cetacean tongues, dolphin tongues are the most capable of protrusion, lateral excursion, rolling, and active shape change (Donaldson, 1977; Figure 3). Tellingly, river and dolphin tongues are also the most muscular of all cetacean tongues (Yoshimura & Kobayashi, 1997), with the greatest contribution of intrinsic fibers; however, they have fewer longitudinal and other intrinsic fibers than most terrestrial mammals (Donaldson, 1977; Figure 2). Other alterations from ancestral tongue conditions include more collagen and other connective tissue fibers and prominent lingual adipose storage (Werth & Sformo, 2020). The sublingual space expanded as intralingual gaps and clefts appeared. The frenum is lost in most cetacean tongues, which have a closer connection to the oral floor. Numerous ribbed plicae containing many elastic and reticular fibers (Werth, 2007a) and slick underlying fascial layers (Werth, Lillie, et al., 2018) together aid positional tongue movements. The external tunic became thinner in some cetacean lineages (Yoshimura & Kobayashi, 1997), and papillae (dorsal and marginal) are lost in almost all lineages (Werth, 2000b). Innervation has not changed, but vasculature has, with prominent periarterial venous retia and other countercurrent exchangers (Werth, 2007a).

Cetacean tongues remain involved in crucial aspects of feeding, albeit in different ways than terrestrial forebears, by adapting to a fully aquatic existence (Howell, 1930; Kellogg, 1928). Whereas terrestrial mammal tongues are often flattened, curled, or protruded to bring food into the mouth via muscular contraction or salivary adhesion, then transformed in shape and position to carry food within the mouth, keep food in contact with dental cutting/crushing/shearing surfaces, and position food for swallowing (Hiiemae, 2000), cetacean tongues evolved different feeding-related functions (Table 3). Many odontocetes retain, at least for some situations and foods, tooth-based seizing or biting; others adopted the reliable aquatic solution of suction feeding (Lauder, 1985; Schwenk, 2000), swiftly drawing prey into the mouth with a volume of ingested water that in the absence of separate pharyngeal openings is expelled back through the mouth (Werth, 2006b). Although suction feeding occurs within all odontocete families except river dolphins (Figure 1), and in mysticete gray whales, morphological (Werth, 2006a) and functional evidence (Werth, 2006b) suggests this represents not plesiomorphic retention but a secondary adaptation to aquatic life that arose independently and convergently in many lineages (Werth, 2006a; Figure 1). Even biting taxa use suction to transport food intraorally (Werth, 2006a), unlike terrestrial mammals that often transport food using gravity or inertial head or jaw movements (Herring, 1993). Some odontocetes likely use expelled water to locate, uncover, or guide benthic prey items during foraging. Tongues position food for swallowing and propel it into the oropharynx (Smith, 1992).

In Mysticeti, tongues also generate intraoral suction (in gray whales) but take on novel feeding functions (Goldbogen et al., 2017). In bowhead and right whales (Balaenidae), the tongue's size, shape, and elevated position between baleen racks aids formation of hydrodynamic Bernoulli and Venturi effects that facilitate continuous skimming (Werth, 2004b). The tongue channels water to and through baleen for efficient cross-flow filtration, and if needed it can (by diverse means) clean the filter of trapped prey, either by physical contact or generating a cleansing backflow via rapid lingual depression (Werth, 2001). In rorquals (Balaenopteridae), the loose, flaccid tongue acts as a hollow saccular organ that invaginates into a hollow space in the ventral oral floor and expands tremendously, in balloon-like fashion, as a massive volume of prey-laden water rapidly flows into the distended mouth (Werth & Ito, 2017).

Cetacean tongues include the world's largest muscular organs. These multipurpose tools are among the most spectacularly dynamic, powerful, and innovative structures in nature. The tongues that cetaceans inherited from long-ago terrestrial ancestors have, during their long evolutionary journey toward fully aquatic life, lost or heavily modified much of the mobility and traditional functions of generic mammal tongues. At the same time, cetacean tongues have taken on noteworthy morphological changes as they evolved to accomplish extraordinary new tasks.

AUTHOR CONTRIBUTIONS

Alexander J. Werth wrote the first draft and prepared figures and tables. Both Alexander J. Werth and A. W. Crompton edited and reviewed all later versions.

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CONFLICT OF INTEREST STATEMENT

On behalf of all authors, the corresponding author states that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

N/A.

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