Chapter 19
Feeding in Aquatic Mammals: An Evolutionary and Functional Approach

Christopher D. Marshall and Nicholas D. Pyenson

Abstract The evolutionary history of aquatic mammals reveals numerous evolutionary experiments in feeding phenotypes and performance in response to changing environmental conditions. In many respects, aquatic mammals have departed from using ancestral terrestrial feeding mechanisms and adopted novel ways of feeding that are influenced by both phylogeny and ecology. Here we highlight feeding strategies as diverse as aquatic herbivory, raptorial biting, and suction to filter feeding, each of which has evolved in numerous mammalian lineages.

19.1 Introduction

Aquatically feeding mammals show extensive innovations for feeding that have been shaped by natural selection. Among the many aquatic mammals alive today, marine mammals, such as cetaceans (whales and dolphins) and sirenians (sea cows) best illustrate the power of selection to modify body plans for aquatic life. Today's marine mammals are just the most recent species-rich example of vertebrate lineages that underwent an evolutionary transition from land to sea. During the Mesozoic era (240–66 Ma), many other extinct reptile lineages (e.g., ichthyosaurs and mosasaurs) evolved convergent body plans, along with aquatic feeding systems (Kelly and Pyenson 2015). Marine mammals are arguably the most evolutionarily successful assemblage of aquatic mammals. The ancestors of both cetaceans and sirenians were the first marine mammals to reinvade aquatic and marine ecosystems in the Eocene (~50 Ma), followed by the ancestors of today's pinnipeds (walruses, sea lions, fur seals, and true seals) during the late Oligocene (~26–23 Ma). Other more recent invasions into the aquatic environment include sea otters. The fossil record preserves

C. D. Marshall (✉)
Department of Marine Biology and Department of Wildlife & Fisheries Sciences,
Texas A&M University, Galveston, USA
e-mail: marshalc@tamug.edu

N. D. Pyenson
Department of Paleobiology, National Museum of Natural History,
Smithsonian Institution, Washington, D.C., USA

many extinct groups of marine mammals that have left no descendants, such as the herbivorous desmostylians from the North Pacific Ocean and aquatic sloths from the western coast of South America (Domning 2001a).

There are also numerous other nonmarine mammals with semiaquatic lifestyles that feed within aquatic systems (e.g., tenrecs, shrews, moles, rodents, and some bats). The assemblage of mammal lineages and the timing of their transition to a fully aquatic or semiaquatic life history results in a diversity of feeding mechanisms that we are only now beginning to explore and appreciate.

Aquatic mammal feeding strategies span all trophic levels from algae and zooplankton to other aquatic tetrapods (Marshall and Goldbogen 2015). This prey range is made possible through the evolution of new innovations of feeding mechanisms. Ideally, the investigation of feeding mechanisms is best conducted as an integrative and comparative endeavor that incorporates a well-established phylogeny. Advances in new technologies are beginning to allow researchers to conduct more experimental and quantitative studies to demonstrate functional relationships among morphology, performance, and ecology, rather than inference alone. New phylogenetic tools are advancing investigations on how feeding evolved as animals made the transition from land to sea.

19.2   What Are Aquatic Feeding Mammals?

Investigations of aquatic feeding among mammals typically focus on marine mammals. Their extensive adaptations for life in water and evolutionary history warrant this emphasis. This focus is particularly true for cetaceans, which are held as a model for macroevolution (Gould 1994; Thewissen 1998; Marx and Uhen 2010). However, many mammalian lineages feed aquatically. We define aquatic feeding as any taxon that spends considerable time feeding and capturing their prey within aquatic habitats. Not all mammals that spend considerable time in aquatic environments are aquatic feeders. Likewise, some species that do not spend much time within aquatic habitats do feed aquatically. Marine mammals are often defined as those mammals that depend upon the marine habitat for survival (Rice 1998). Several taxa within this group are not necessarily aquatic feeders per se (e.g., Arctic foxes [*Vulpes lagopus*], polar bears [*Ursus maritimus*]) and many mammals including some species of tenrecs, shrews, rodents, and moles do apprehend prey within freshwater aquatic environments.

How does aquatic feeding differ from terrestrial feeding? The physical forces experienced within an aquatic environment impart strong selection pressures upon all vertebrates, especially on the evolution of feeding mechanisms. Perhaps the single most important change in the feeding strategies of marine mammals is the loss of mastication (in most lineages). Mastication is a hallmark of terrestrial mammalian feeding (Herring 1993; Weijs 1994; Hiiemae 2000). Thus, there is value in summarizing our knowledge of terrestrial feeding function as a comparative basis for

aquatic feeding. A more complete and detailed summary of terrestrial mammalian feeding mechanisms is provided in this volume (Williams, Chap. 20).

19.3 Terrestrial Feeding

Mammals arose from an insectivorous ancestor in the Jurassic (~160 Ma) that then diverged as mammals radiated and specialized in the late Cretaceous and especially in the Cenozoic (Weijs 1994; Hiiemae 2000; Luo et al. 2011). The "process model" (sensu Hiiemae 2000) characterizes terrestrial feeding as follows: ingestion (acquisition of food), stage I transport (to teeth), food processing (mastication), stage II transport (to the oropharynx) and swallowing (deglutition). Terrestrial innovations that define therian mammalian feeding include the expansion of the dentary to a single mandibular bone with an ultimate squamosal-dentary or temporal-mandibular joint (TMJ); changes in the shape of upper and lower jaws that allowed unilateral occlusion of teeth (one side of the jaw at a time); rearrangement of jaw adductors (Lautenschlager et al. 2016), and changes in the morphology of the craniodental joint to allow lateromedial and anteroposterior movement as part of the overall dorsoventral movement of the lower jaw against the upper jaw (Crompton and Hiiemae 1970). These changes also resulted in increased mechanical advantage and increased bite force.

Ancestral terrestrial mastication involved a unilateral, rhythmic cyclic movement of the mandible and jaws bearing heterodont dentition. Tribosphenic molars occlude precisely with each other due to their complex cusps and basins during occlusion (Crompton and Hiiemae 1970; Crompton 1971; Bown and Kraus 1979). It is likely that mutations of genes involved in the development of tooth shape resulted in multicuspid teeth and therefore precise occlusion (Ohazama et al. 2010). During jaw closure, the mandible moved dorsally, medially, and anteriorly in an orbital working loop. This process resulted in the precise placement of individual cutting edges on the lower molars onto the upper molars to allow shearing, which has been described as the tribosphenic chewing stroke (Crompton and Hiiemae 1970). Additional mammalian feeding innovations include the hard upper palate and the soft palate, which separates the airway from the oral cavity (Hiiemae 2000). The placement and movement of the tongue against the hard palate is also involved in the processing of soft food and influences the timing of the masticatory cycle (Hiiemae and Palmer 2003). Tongue movement is an important component of the feeding cycle in marine mammals. In terrestrial mammals, effective suction and suckling is a result of the hyolingual apparatus pulling the tongue caudoventrally to rapidly increase intraoral cavity volume (German et al. 1992; Thexton et al. 1998, German and Crompton 1996; Thexton et al. 2004), a mechanism modified and used by marine mammals extensively.

Mastication has two distinct components. The first, as food is acquired, is "chopping" (Ahlgren 1966) or "puncture-crushing" (Hiiemae and Crompton 1971) and should not be confused with "pierce biting" (e.g., raptorial biting that is used to apprehend prey). This "chopping" stage is followed by the rhythmic mastication

cycle that is most commonly associated with "chewing." Chopping functions to reduce the size of food for proper mastication and is widespread among vertebrates. During chopping, the teeth are not in occlusion; food may be chopped or crushed by either teeth or the hard palate and tongue. During chopping, the material property of food is compromised to allow its reduction to sizable portions for further manipulation or swallowing. Chopping can be an important component of aquatic feeding.

The point of the feeding apparatus is to increase the surface area of food for greater digestion efficiency. This function is not unique to mammals, just the mechanism in which it is accomplished. Modern birds use gizzards to mill down ingested food, and many reptiles use teeth or keratinous beaks and plates for oral processing (Reilly et al. 2001). Forms of chewing are observed in fossil synapsids, living reptiles (Reilly et al. 2001) and even bony fishes (Kolmann et al. 2016). Although the traditional paradigm is now being questioned (e.g., Reilly et al. 2001; Kolman et al. 2016), the functional precision of mastication occurs only among mammals. Although future data may change our perspective, currently no other vertebrate group, with the exception of birds, matches the decrease in particle size produced by mastication as observed in mammals. In this light, why most marine mammals have secondarily lost mastication and related craniodental innovations remains a question of interest.

19.4   Sensorimotor Integration and Feedback

Activation and motor control of masticatory muscles are produced by a masticatory central pattern generator (CPG; Lund et al. 1998; Lund and Kolta 2006) within the pons and medulla of the brainstem. Motor patterns (electromyograms or EMGs) determined by the CPG are governed by peripheral feedback from sensory receptors in the TMJ and periodontal receptors, which are sensitive to the magnitude and direction of bite force per tooth (Lund and Kolta 2006; Ross et al. 2007). Muscle spindles, heterogeneously distributed throughout the feeding apparatus musculature (Weijs 1994; Lund and Kolta 2006), also provide sensory feedback. Information from these peripheral structures is hypothesized to regulate the duration and force of muscle activation and perhaps even from fiber groups within individual muscles (Vinyard et al. 2011). As food breaks down during bolus formation, the CPG motor program continually adapts to changes in consistency and food particle size (Thexton et al. 1980; Lund and Kolta 2006). Although most aquatic mammals have secondarily lost mastication (and perhaps a CPG), sensory-motor feedback is still important for prey acquisition.

Feeding involves motoneuronal activity of the orofacial and jaw musculature. Therefore, much work has focused on the neural control of feeding by the trigeminal (V), facial (VII) glossopharyngeal (IX), and hypoglossal (XII) nerves and areas adjacent to the medial reticular formation (Rossignol et al. 1988; Ewert et al. 1994). In both terrestrial and aquatic feeding, motor control of the lips and tongue is critical to acquisition of food; stage I and II transport of the bolus (if present) may be mediated

by the facial nerve and nucleus. Motor neurons that supply CN VII and innervate the orofacial muscles are located within the brainstem's Facial Motor Nucleus (FMN; Marshall et al. 2005). Subnuclear organization of the FMN, as well as the trigeminal nucleus, such as number of subnuclei, consistency of subnuclear boundaries, and size and distribution of neuronal pools, varies and reflects differences in functional importance. Motor innervation of the tongue is controlled mainly by the hypoglossal nerve and nucleus and a branch of the Vagus nerve to the palatoglossus muscle. Studies in marine mammals show that these neural structures and their organization for motor control are similar to those of terrestrial mammals (Marshall 2007; Werth 2007).

Functional divisions of orofacial musculature for feeding are well known among terrestrial herbivorous mammals. Among marine mammals, sirenians possess functional division of their lips (Marshall et al. 1998b). The motor control of these muscles is of interest to determine if they diverge from terrestrial analogs. Direct experimental evidence is available from pigs (*Sus scrofa*) in which the upper lip (*M. orbicularis oris*) is divided anatomically, neuroanatomically, and functionally (Marshall et al. 2005). The motor neurons segregate into rostral and caudal neuronal pools that correspond with the anatomical and functional separation of the upper lip into rostral and caudal components. Furthermore, the motor neuron pools of all facial muscles are well organized and displayed a somatotopic organization within the facial motor nucleus. The segregation and somatotopy of motor neuron pools innervating orofacial muscles indicate functional independence and importance. Such functional data has been used to infer a similar function in marine mammals. The facial motor nucleus of Florida manatees (*Trichechus manatus latirostris*) also exhibits distinct subnuclei that are somatotopically arranged (Marshall et al. 2007). This suggests precise control over orofacial musculature for feeding. Furthermore, using functional and comparative inference, it is likely that the motor neurons that innervate the orofacial muscles of bearded seals (*Erignathus barbatus*) and walruses (*Odobenus rosmarus*) display similar neuronal organization.

19.5 Aquatic Feeding, Craniodental Morphology, Feeding Process, and Mode

Modern aquatic mammal feeding has diverged in significant ways from terrestrial feeding. This disparity includes substantial changes to the "process model" of mammalian feeding. Among cetaceans and pinnipeds, the major evolutionary changes include the loss of mastication, simplification of teeth, and consumption of prey whole. This emphasis on food acquisition is manifested as several feeding modes that have captured the attention of functional morphologists and biomechanists. Typical feeding modes include: raptorial biting (often referred to as pierce biting or simply biting), grip-and-tear, suction feeding, hydraulic jetting, and filter feeding (Marshall

and Goldbogen 2015). Such distinct feeding modes were originally designated for pinnipeds (Adam and Berta 2002), as an extension of previous work on Mesozoic marine reptiles (Massare 1987), but with the addition of mastication, they are applicable to all aquatically feeding mammals. Since new feeding performance, kinematics, and behavior data have come to light, it is clear that aquatically feeding mammals are flexible and opportunistic in their acquisition strategy using any feeding mode that works (Marshall and Goldbogen 2015).

19.6 Feeding Mechanisms of Marine Mammals

Understanding the evolutionary history of marine mammals is informative with respect to the diversity of extant innovations for feeding and how feeding mechanisms evolved in crown groups. Cetaceans are descended from artiodactyls (even-toed ungulates) over 55 Ma ago (Thewissen et al. 2007). The earliest known whales date to back to the early Eocene ~53.5 Ma from the Indo-Pakistan region (Bajpai and Gingerich 1998). These quadruped mammals were semiaquatic, spending time wading and swimming in shallow fluvial environments and coastal embayments (Roe et al. 1998; Clementz et al. 2006). Their heterodont dentition was derived from the primitive tribosphenic-like molars (O'Leary 1998), and they possessed shearing blades and molars with reentrant grooves on the anterior margins (O'Leary and Uhen 1999). Presumably, they retained the terrestrial ancestral raptorial biting feeding mode but facets indicated an arcilineal (orthal) motion with minimal translational motion typical of tribosphenic chewing (O'Leary, 1998).

Various stem lineages of cetaceans, sometimes termed "archaeocetes," represent early branches of cetacean evolution that include semiaquatic and fully aquatic members (Uhen 2010). The middle–late Eocene record of pakicetids, ambulocetids, and remingtonocetids all represent separate stem cetacean lineages with heterodont dentition, including the presence of molars with a protocone and wear facets on the cheek-teeth, implying a basic level of chewing (Thewissen et al. 2011; Fahlke 2012). Basilosaurids were the first demonstrably fully aquatic stem cetaceans that inhabited offshore regions and had a global distribution. Basilosaurids such as *Dorudon* and *Basilosaurus* still retained a heterodont (and diphyodont) dentition, but their premolars and molars were extensively labial–lingually flattened with series of numerous small cusps or denticles (Uhen 2004, 2010). Mastication was lost in cetaceans at some point in their evolutionary history. *Dorudon* is hypothesized to have masticated (Uhen 2004) based on cheek-teeth wear facets. Alternatively, this tooth wear can be attributed to premasticatory chopping behavior that helped to dispatch prey and reduced prey size. If true, then mastication was likely lost once whales became fully aquatic and developed the ability to dive in offshore habitats.

Crown group cetaceans share a common ancestor with the extinct stem group basilosaurids to form a clade termed Pelagiceti (Uhen 2010). Crown cetaceans (or Neoceti) include the common ancestor of all modern baleen and toothed whales, and their descendants. This clade, which likely originated near the Eocene/Oligocene

boundary (Geisler and Sanders 2003; Uhen 2004, 2010), includes the full diversity of the most species-rich group of marine mammals of all-time. The ancestors of modern mysticetes possessed heterodont teeth with multiple accessory denticles on their cheek-teeth. Some stem mysticetes possessed small, triangular teeth spaced far apart; some researchers, based on indirect evidence, have suggested that some stem mysticetes possessed proto-baleen (Deméré and Berta 2008; Deméré et al. 2008). Recently described fossil mysticetes from this time period suggest that baleen may have already replaced teeth completely in some taxa (Peredo and Uhen 2016), and new evidence suggests fossil mysticetes went through a transitional suction feeding stage in which tooth loss preceded the acquisition of baleen (Peredo et al. 2018).

The oldest odontocetes date from early Oligocene rocks. They differed greatly from their basilosaurid ancestors and possessed many of the diagnostic characters of modern toothed whales (Fordyce 2008; Uhen 2010). These early odontocetes still possessed a heterodont and polydont dentition; most of the odontocetes, by the start of the Neogene, exhibited homodonty and increased the degree of polydonty (Uhen 2010). It is assumed that Oligocene odontocetes consumed prey by raptorial biting (Bianucci 2005). Anatomical evidence from all fossil odontocetes suggests that prey were detected using echolocation; all fossil odontocetes possess cochlear structures that are associated with high-frequency hearing in modern species (Park et al. 2016; Churchill et al. 2016). If mastication was retained within archaeocetes, then its loss was surely complete within early odontocetes.

19.7 Cetacean Feeding Mechanics

Extant cetaceans are solely represented by Odontoceti and Mysticeti and these two lineages have diverged in their feeding mechanisms. Odontocete skulls exhibit innovations for the integrated dual functions of prey capture and echolocation to target single prey items, whereas baleen whale skulls are modified and arched to support baleen, a filtering innovation that allows them to feed in bulk on aggregations of small prey (Goldbogen et al. 2006; Simon et al. 2009, 2012). Both echolocation and bulk filter feeding represent major evolutionary innovations that underlie the ecological success of these marine mammals.

19.7.1 Raptorial Biting in Odontoceti

Toothed whales primarily use raptorial biting and suction to acquire prey. A ram component is often involved in feeding events. Ram refers to a predator's ability to overtake the targeted prey using speed and agility (Weihs and Webb 1984; Werth 2000; Bloodworth and Marshall 2005). In contrast, suction is an equally important feeding mode in many odontocetes as demonstrated by their well-developed tongue musculature, increased surface area of the hyoid (Werth 2007), and orofacial

morphology (Bloodworth and Marshall 2007). Odontocetes are multimodal in their feeding strategies. Feeding ranges from pure ram feeding to ram with raptorial biting, ram with raptorial biting with suction, to ram with suction or pure suction feeding (Bloodworth and Marshall 2005; Werth 2006b).

The skulls of odontocetes are characterized by overlapping and telescoping of facial bones over the neurocranium and the elongation of the rostrum and mandible (Rommel 1990). The ratio of neurocranial-to-facial length varies greatly among odontocetes resulting in spectrum of species from blunt, wide heads (e.g., *Delphinapterus and Kogia*) to long narrow rostra (e.g., *Lagenorhynchus* and *Platanista*; Werth 2006a; Fig. 19.1). This spectrum is correlated with a dichotomy of feeding mechanics and diet. The short blunt rostra and jaws of toothed whales with reduced or complete loss of dentition are correlated with suction feeding, teuthophagy (squid-eating), and deep diving in many species (Werth 2006a; Slater et al. 2010). In contrast, piscivory is associated with long narrow rostra and mandibles, and jaws filled with numerous teeth. There is a mechanical trade-off in any lever system that allows for either maximal force or velocity, but not both simultaneously (Westneat 1994). The longirostral phenotype conveys high velocity at the jaw tips at the expense of forceful jaw closing (bite force) due to a decreased mechanical advantage of the mandible. This trade-off is advantageous for capturing small elusive prey. Rapid snapping of the jaws as the rostrum is swept side-to-side is likely successful due to hundreds of small, conical, homodont teeth. This phenotype and the associated feeding mechanics have evolved independently numerous times among aquatic vertebrates (Kelly and Motani 2015; McCurry et al. 2017a, b). The evolution and development of this dental battery provide an illustration for linking genotypic and phenotypic changes with better-known mechanisms. Early tooth differentiation (and type of tooth) during development involves the expression of *Bmp4* in the rostral (mesial, anterior) domain of the jaw, and *Fgf8* caudally (distal, posterior; Armfield et al. 2013). *Bmp4* (bone morphogenetic protein) is involved in the formation of simple, single-cusped incisors (Vainio et al. 1993; Neubuser et al. 1997; Tucker et al. 1998) whereas Fgf8 (fibroblast growth factor) is involved in the formation of multicuspid molars in the caudal region (Sharpe 1995; Tucker and Sharpe 2004; Mitsiadis and Smith 2006). This is considered the plesiomorphic condition in mammals. In contrast, pantropical spotted dolphin (*Stenella attenuata*) embryos either have lost, modified, or do not express the regional differences in tooth morphology (i.e., they have a homodont phenotype) expressed by the *Fgf8* gene. Instead, the *Bmp4* gene domain extends into the caudal region of the developing dolphin jaw. This suggests that homodonty is related to the expansion of the *Bmp4* gene domain. It is hypothesized that the functional constraints underlying mammalian occlusion have been released in cetaceans, which has modified genetic control of early dental development. Major developmental changes in the dental arcade are correlated with major shifts in diet and food processing during cetacean evolution (Armfield et al. 2013).
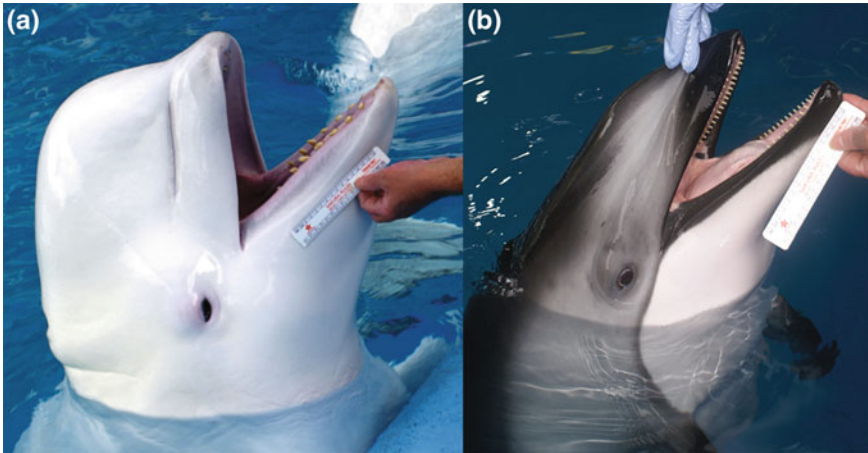
Fig. 19.1 Odontocete feeding dichotomy exemplified by two species **a** Belugas (and *Kogia sp*—see Fig. 19.2a) possess a short broad rostrum with relatively few teeth vs. **b** Pacific white-sided dolphin with longer, narrower rostrum and numerous smaller teeth (Kane and Marshall 2009)

19.7.2   Suction Feeding

Suction in marine mammals is generated by the rapid depression and retraction of the tongue (but in some cases by the addition of fast jaw opening velocities), which results in a rapid increase in buccal volume and a concomitant decrease in pressure (Marshall and Goldbogen 2015). This "gular depression" during feeding has been experimentally demonstrated in odontocete cadavers (Werth 2006a) of varying head shape and bluntness of the rostrum. Gular depression as a mechanism to produce subambient pressure has been empirically demonstrated in several living toothed whale species (pygmy and dwarf sperm whales (*Kogia* spp.; Bloodworth and Marshall 2005), harbor porpoises (*Phocoena phocoena*; Kastelein et al. 1997), long-finned pilot whales (*Globicephala melas*; Werth 2000), and belugas (*Delphinapterus leucas*; Kane and Marshall 2009)).

It is thought that the muscles associated with the enlarged basihyoid bone of the hyoid apparatus (Reidenberg and Laitman 1994; Heyning and Mead 1996; Werth 2007) results in a greater force of lingual depression and presumably an increase in subambient pressure. A kinematic study and functional model incorporating vector analyses of hyolingual musculature of kogiids versus bottlenose dolphins (*Tursiops truncatus*), which assessed differences in maximum theoretical muscle tensions of hyolingual complexes, did not find significant differences within or between species (Bloodworth and Marshall 2005, 2007). In addition to blunt rostra and wide jaws, some odontocetes produce a circular mouth aperture to enhance suction performance (Bloodworth and Marshall 2005, Kane and Marshall 2009). This shape can be accomplished in numerous and different ways, as exemplified by belugas and kogiids (Figs. 19.1a and 19.2). These morphologies function to occlude lateral
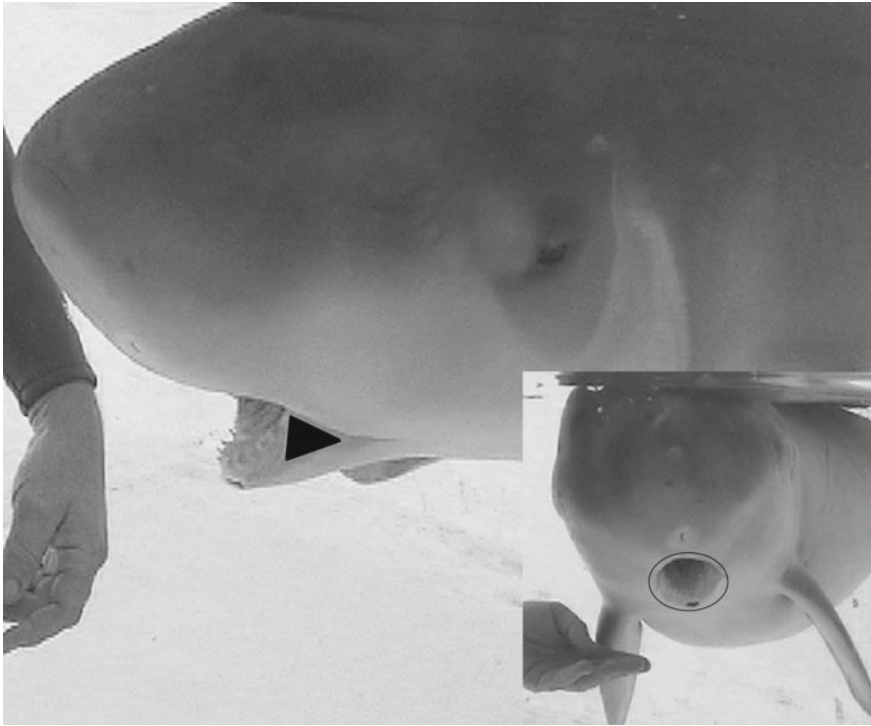
Fig. 19.2 Orofacial feeding innovations. The mandible of *Kogia sp.* is short with lateral flaps (black triangle) that blocks lateral gape. At full open gape the short jaw creates a circular aperture similar to a pipette (see inset) that maintains intraoral sub- and superambient pressures generated for suction and hydraulic jetting feeding modes (Bloodworth and Marshall et al. 2007)

gape and direct subambient pressure anteriorly in front of the mouth. Thus, associated orofacial morphology greatly influences suction performance in odontocetes and is likely just as important as hyolingual musculature mass. These solutions are convergent with more basal vertebrates (Lauder and Shaffer 1993; Deban and Wake 2000; Lemell et al. 2002; Wilga et al. 2007); such traits and correlated performance measures are well known for teleost fish (Wainwright et al. 2007).

19.7.3   Mysticeti Feeding Mechanics

All extant baleen whales engulf, or skim, a volume of prey-laden water that is subsequently filtered out of the mouth. The ancestors of baleen whales possessed teeth that were eventually replaced by baleen (Fig. 19.3). Modern mysticetes are edentulous, but possess racks of flexible baleen (Werth 2016a) of various lengths, numbers, and function. Baleen hangs from the roof of the mouth in two racks of vertically oriented
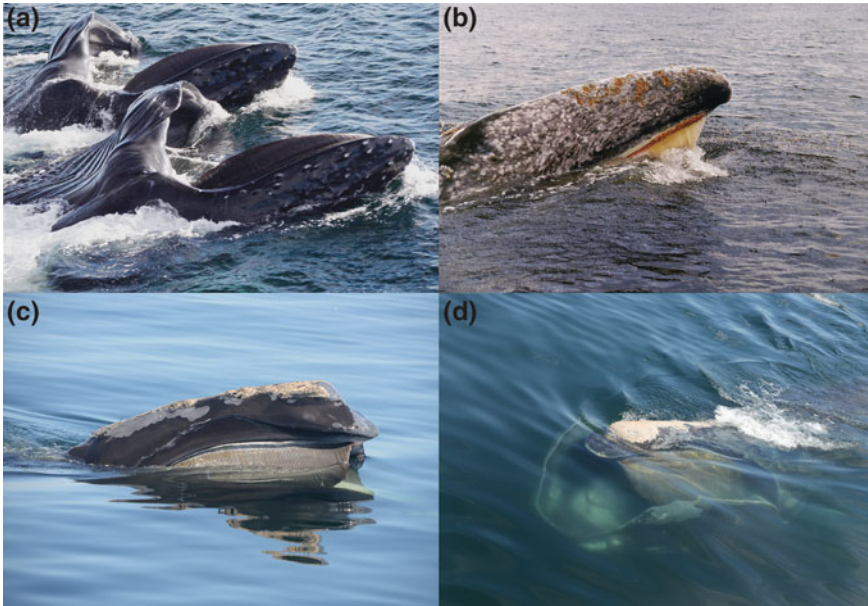
Fig. 19.3 Mysticete feeding modes. **a** Humpback whale lunge feeding mode (*Photo Credit* Jeremy Goldbogen). **b** Skim feeding by a gray whale (Pyenson and Lindberg 2011). Gray whales can skin, lunge or use a suction benthic feeding mode. **c**, **d** North Atlantic right whale skimming behavior which is representative of balaenid filter feeding. *Photo Credit*: Amy Knowlton, New England Aquarium, NOAA Permit Number 15415. Note the variation in the baleen morphology of each mysticete group

plates (Fig. 19.3); in some species, the racks unite anteriorly to form a continuous arcade, whereas in other species they are completely bilaterally separated (Pinto and Shadwick 2013). Each individual baleen plate consists of a series of tubules that are imbedded in a calcified, alpha-keratin matrix (Fudge et al. 2009; Szewciw et al. 2010). As these tubules become exposed they create fringes on the lingual side that connect adjacent plates and collectively form a fibrous mat on the lingual side of the rack. It is this fibrous mat that filters prey from seawater.

Balaenids (bowhead and right whales) and balaenopterids (rorquals) differ from each other in their body morphology, their feeding apparatus and the hydrodynamic mechanisms employed to capture and filter prey from seawater. Balaenids have a rotund body compared to balaenopterids and swim at slow, steady speeds (<1 m/s) with their mouths agape to continuously drive water into the mouth (Simon et al. 2009; Fig. 19.3c, d). In bowhead whales, selection for head growth and a large filtering apparatus during ontogeny is sustained at the expense of growth in the rest of the body (George et al. 2016). Their tongues are large and stiff and have been hypothesized to direct a continuous flow of prey-laden water past the long baleen plates. Recent evidence shows that wear on baleen is due to water flow and not necessarily tongue movement against baleen (Werth et al. 2016b).

New information regarding the fluid dynamics through balaenid baleen is challenging the traditional view of mysticete feeding. It was thought that prey-laden water enters into the mouth and flows through the baleen plates, where plankton are separated, and out of the back of the mouth. This process is known as throughput filtration (TPF). Now, experimental evidence suggests that cross-flow filtration involving the formation of vortices may be the actual filter feeding mechanism of baleen (Werth and Potvin 2016). The cross-flow filtration model depicts a more dynamic system compared to the static throughput filtration particle sieving system. In the cross-flow filtration model, water flow can be anterior-to-posterior, dorsal-to-ventral, and interbaleen. It appears that fewer particles actually flow through the baleen rack and that most particles flow directly to the back of mouth on the lingual side of the baleen, and accumulate on the posterior baleen fringes to be ingested. Particles captured on these posterior baleen fringes tended to be captured at the ventral margin indicating dorsal–ventral flow. These are still needed for empirically studies that test functional hypotheses.

Despite their enormous size, rorquals are more slender and faster than balaenids. They feed by rapidly accelerating to lunge feed (Goldbogen et al. 2006, Simon et al. 2012). The forward momentum and the sudden increase of inertial drag as the jaws open cause wide gapes and the distention of the gular region (or pouch) ventral to the mouth and body (Figs. 19.3a and 19.4). Numerous throat grooves expand to allow the engulfment of enormous quantity of water. Throat grooves are pleats of blubber that undergo large-scale deformation (Vogl et al. 2015; Shadwick et al. 2013). The cavity created (cavum ventrale) can expand to as much as four times its resting length circumferentially, and up to 1.5 times its resting length longitudinally in fin whales (Orton and Brodie 1987), and is commensurate with the species of whale's body size (Goldbogen et al. 2007). Their tongues are largely flaccid and adapted for inversion into the cavum ventrale (Werth 2007). After engulfment, water is filtered through the relatively shorter, wider, and fewer plates of baleen. Water flow is driven past the baleen plates by the elastic recoil and contraction of the expanded ventral pouch musculature (Shadwick et al. 2013). Lunge feeding is shared by numerous species of varying sizes. The mechanical advantage of the mandible is greater in smaller sized rorquals and this is likely related to and ameliorated by the relatively longer time scale of lunge feeding events in larger rorquals (Pyenson et al. 2013). The scaling of pouch allometry has important consequences for rorqual diving physiology, feeding performance, and ecological niches (Goldbogen et al. 2012). Interestingly, the engulfment apparatus scales with significant positive allometry whereas the caudal peduncles scale with significant negative allometry. Balaenopterids, like balaenids, invest in growth of the filtering apparatus at the expense of the posterior part of the body (Goldbogen et al. 2010; George et al. 2016).

Gray whales (Eschrichtiidae) are generalist filter feeders that are able to use engulfment and skimming (Fig. 19.3b) in combination with suction (Nerini 1984). Gray whales have well-developed hyolingual musculature and ventral grooves that facilitate the production of subambient pressure (Werth 2007). Despite several observational and anatomical studies, the filter-feeding mechanisms in gray whales remain poorly understood. Just as interesting are pygmy right whales (*Caperea marginata*;
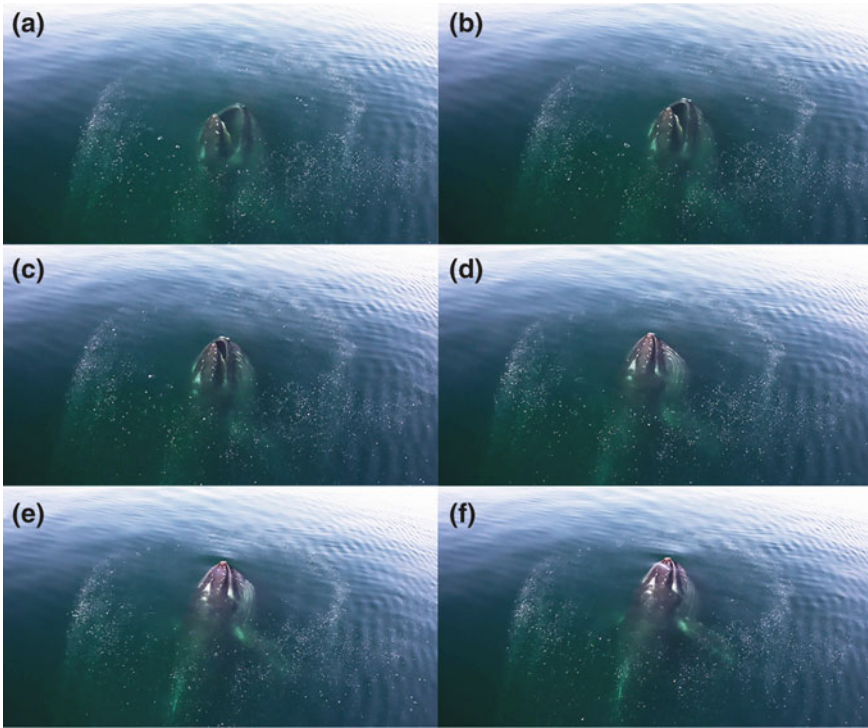
Fig. 19.4 A sequence of photos (**a**–**f**) demonstrating a humpback whale lunge feeding. Note the circle of bubbles that humpbacks use during cooperative feeding and herding of prey. *Photo Credit* Jeremy Goldbogen

Neobalaenidae), which share many morphological characters with bowhead and right whales (balaenids) but may also use methods similar to rorqual whales (Fordyce and Marx 2012). The functional morphology and ecology of pygmy right whales are essentially unknown.

Mysticetes are among the most specialized mammals in terms of feeding mechanics. In terms of the "process model" of feeding, food acquisition involves swimming into patches of food. Stage I transport involves hydrodynamic flow of prey to the baleen, which filters in lieu of teeth. The role of the tongue during stage I transport is unclear and may not be involved in balaenopterids. Recent cross-filtration flow data suggests that prey accumulates near the oropharyngeal arch for deglutition; these hydrodynamic patterns would effectively function as stage II transport. Whether the tongue functions to either alter flow or physically remove prey from the baleen for stage II transport is unknown.

19.8   Pinniped Evolutionary History

Pinnipeds are a monophyletic lineage whose shared common ancestry is supported by both morphological and molecular data (Berta et al. 2015). Molecular data, as well as combined data analyses, support an otariid and walrus alliance (Otaroidea), although there is still debate on the alternate hypothesis of a phocid–walrus alliance (Phocoidea). The oldest pinnipeds are represented by *Enaliarctos* and *Pteronarctos* (Mitchell and Tedford 1973; Berta et al. 1989; Berta 1991). These stem pinnipeds are found in the late Oligocene to early Miocene deposits of the eastern North Pacific Ocean (Berta 1991, 1994). *Enaliarctos* fossils date from 27–25 Ma and *Pteronarctos* from 19–15 Ma. Together, *Enaliarctos*, *Pteronarctos,* and Pinnipedia define Pinnipedimorpha (Berta 1994; Berta and Wyss 1994). The terrestrial origins of Pinnipedimorpha are unresolved, but they most likely arose from an arctoid carnivoran ancestry, with relationships to either musteloid or ursoid carnivorans (Berta et al. 2015). The recently discovered freshwater carnivore *Puijila darwini* from Neogene rocks of the Canadian Arctic (Rybczynski et al. 2009) has been proposed as a near relative to *Enaliarctos*, a pinnipedimorph, or an early arctoid. Its affinity relative to the ancestry of pinnipeds remains unresolved until a full description is published, but it may represent a relictual or ghost lineage of basal pinnipedimorph that persisted until the Miocene (Kelly and Pyenson 2015).

Otariids (fur seals and sea lions) are crown pinnipeds (Churchill et al. 2014). The fossils *Pithanotaria starri* from ~11 Ma in the late Miocene and *Thalassoleon* from 8–6 Ma also from the late Miocene are the oldest stem otariids (Berta and Wyss 1994; Deméré and Berta 2005; Churchill et al. 2014). Crown Otariidae likely includes the fossil *Hydrarctos* and all extant otariids; *Hydrarctos* is known from the Pliocene—Pleistocene of Peru (Berta et al. 2015). More recently extinct fur seals (*Callorhinus gilmorei and C. sp.*; Berta and Deméré 1986; Boessenecker 2011) emerged 5–2.7 Ma in the late Pliocene–early Pleistocene. This lineage continues as extant northern fur seals (*C. ursinus*). Northern fur seals are the basal-most branching lineage of extant otariids Berta and Churchill (2012). Sea lions are represented in the fossil record by *Proterozetes ulysses* from the late Pliocene of Oregon (Barnes and Koretsky 2006).

The fossil record of true seals (Phocidae) is sparse and the relationships of stem phocids are unclear. Phocid fossils are known from the middle Miocene 15 Ma. By the late Miocene, the two major subfamilies of phocids, Phocinae (including Northern Hemisphere seals) and Monachinae (monk, elephant, and Southern Hemisphere seals) were established (Koretsky and Domning 2014). Fossil pinnipeds such as *Allodesmus* and *Desmatophoca* were thought to be closer to otariids and walruses (Barnes 1989), but more recent phylogenetic analyses show that this group, called Desmatophocidae, forms an extinct clade that is sister to crown phocids (Berta and Wyss 1994).

Modern walruses (*Odobenus rosmarus*) are representative of a group whose richness is mostly extinct. The earliest known walrus fossils (*Prototaria* and *Proneotherium*) are from the early middle Miocene of Japan and Oregon, respectively (Kohno et al. 1994; Kohno 2006). These stem walruses were smaller, similar in

appearance to stem pinnipedimorphs and extant sea lions, possessing large canines rather than tusks (Mitchell and Tedford 1973; Kohno et al. 1994; Boessenecker and Churchill 2013). Trends in walrus evolution include increases in body size, simplification and reduction of teeth, the development of short tusks in some groups (Dusignathinae), and tusklessness. In other groups (Odobeninae), there was fusion and ankylosis of the mandibular symphysis in later species, and the retention of a piscivorous diet (Boessenecker and Churchill 2013). The large distinctive tusks of today's walruses do not appear in any other extinct odobenidae species with an exception of *Valenictus*, which is the sister taxon to *Odobenus*. Similarly, suction feeding and molluskivory did not evolve until very recently in walrus evolution; evidence for such feeding behavior is inferred from craniodental morphology of more recent walruses such as *Ontocetus*, *Valenictus* (Deméré 1994a, b), and known for *Odobenus* (Fay 1982; Kastelein and Mosterd 1989; Kastelein et al. 1994). The oldest fossils of *Odobenus* are ~600,000 years old (Berta et al. 2015).

19.9 Pinniped Feeding Mechanisms

The major evolutionary trend of pinnipedimorph feeding is the accumulation of aquatic characters of the teeth and jaws over time (Boessenecker 2011). These are exemplified by *Enaliarctos* and stem pinnipeds. In short, there was an increase in labial–lingual compression of cheek-teeth, a more anterior–posterior alignment of tooth cusps, reduction and loss of tooth cusps, reduction in the number of tooth roots, and presumable loss of shearing function, decrease in tooth size, increase in tooth spacing, eventual homodonty of cheek-teeth, and the loss of mastication (Berta 1991; Churchill and Clementz 2015).

19.9.1 Raptorial Biting

The craniodental morphology of stem pinnipeds is remarkably similar to arctoid carnivores. *Enaliarctos* possessed nearly homodont cheek-teeth with sheering blades on the upper cheek-teeth. The mandibular (glenoid) fossa of *Enaliarctos* and other stem pinnipeds have extensive pre- and postglenoid processes. Such an arrangement greatly constrains the mandible to a primarily arcilineal motion with minimal-to-no translational movement. The restricted jaw movement and simplification of dentition suggests that stem pinnipedimorphs employed a raptorial biting mode that was similar to arctoid carnivores.

Support for a biting feeding mode comes from feeding performance data of northern fur seals. Despite the near-universal prevalence of suction-feeding capability to acquire prey among aquatic vertebrates (Lauder and Shaffer 1993; Deban and Wake 2000; Wainwright et al. 2007; Wilga et al. 2007), *Callorhinus ursinus* did not produce any measurable subambient pressures related to capturing food (Marshall et al. 2015).
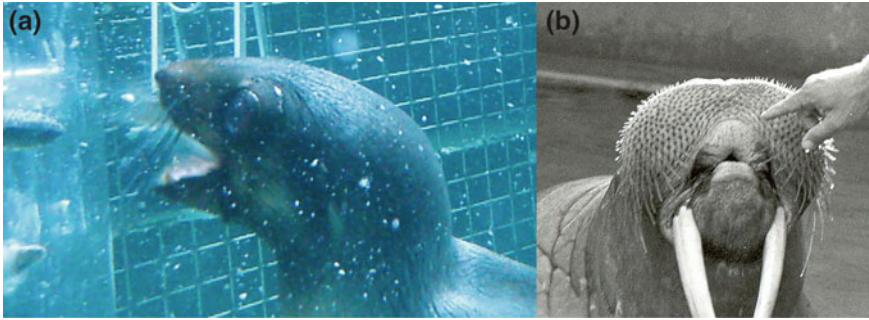
Fig. 19.5 a Northern fur seals exemplify raptorial biting as shown in this feeding performance test. **b** Suction feeding often involves hypertrophied facial and lip muscles that are used to purse the rostral lips to form a circular aperture, which function to project a steep subambient pressure gradients rostral to the lips for prey acquisition. Lateral lip musculature is used to occlude lateral gape and maintain subambient pressures in the oral cavity

Instead, they used a stereotypical raptorial biting feeding mode that was characterized by wide gape, lack of lateral gape occlusion, an aquatic form of inertial transport of food to the oropharynx and the fastest maximum gape angle opening velocity (GAOV = $622.3 \pm 214.12°\,s^{-1}$) reported for any marine mammal (Fig. 19.5a). During these trials, biting by northern fur seals (and Steller sea lions) was used to either remove fish from the feeding apparatus or to cleanly sever a piece of fish with a fast, single arcilineal biting motion (Marshall et al. 2015). The morphology of *Callorhinus ursinus* is part of a craniodental morphological continuum of the *Callorhinus* lineage, with few functional differences between extinct and extant species (*C. gilmorei* + *C.* sp. + *C. ursinus*; Boessenecker 2011). Therefore, it would be expected that feeding behavior of northern fur seals would not differ significantly from their ancestors and that feeding performance can be inferred back to their extinct relatives. Northern fur seals appear to feed with the ancestral feeding mode of the *Callorhinus* lineage (Marshall et al. 2015). It is probable that the feeding kinematics and performance of northern fur seals are indicative of the ancestral raptorial biting feeding mode of all stem pinnipeds. The trends in craniodental morphology also point to the loss of mastication early in their evolution, likely within stem pinnipeds, but after *Enaliarctos* and *Pteronarctos*. Although a grip-and-tear feeding mode is supported morphologically (Jones et al. 2013; Kienle and Berta 2016), it is likely this is a modification of raptorial biting for larger prey. While leopard seals (*Hydrurga leptonyx*) are on the only pinniped to use this feeding mode, it may have been an important feeding mode among stem pinnipeds.

Loss of mastication is associated with swallowing prey whole in both pinnipeds and cetaceans. In terms of the "process model", the emphasis is on prey acquisition at the expense of stage I transport and processing (mastication). In northern fur seals, and perhaps other pinnipeds, stage II transport (to the oropharynx) is accomplished via suction generated by the rapid opening of the oropharynx (Marshall et al. 2015). This is similar to the functional hypothesis of suction feeding by sperm whales (*Phy-*

seter macrocephalus) proposed by Werth (2004). Northern fur seals also used inertial transport for stage II transport, but it is not clear how widespread this phenomenon is. Although pinnipeds usually consume prey whole, they also consume prey that are too large to be swallowed whole. Some otariids "chew" on large fish and swing them with the head (at the water's surface) thereby breaking the prey into small parts that are then consumed whole (Hocking 2016). Such behavior falls within the chopping premastication behavior described above for terrestrial feeding behavior (Ahlgren 1966) and should not be conflated with mastication. Chopping compromises the structural integrity of large prey that allows breakage when momentum is applied via shaking (Hocking 2016). This behavior is also similar to grip-and-tear but on a smaller scale and is likely a form of raptorial biting.

19.9.2   Suction and Hydraulic Jetting

A small group of pinnipeds are suction specialists. The best known are walruses and bearded seals. Walruses target bivalves and other infaunal invertebrates but will occasionally consume marine birds and other marine mammals. Large bivalves are excavated from the sea floor by alternating suction with hydraulic jetting (Kastelein and Mosterd 1989). Hydraulic jetting is used to excavate bivalves by forcefully removing the sediment around their prey. Walrus skulls are distinctive in their size and proportions, relative to other pinnipeds. The flat and frontal orientation of the premaxilla broadens and shortens the rostrum, which is advantageous for benthic feeding. The dominant tusks of walruses are not used for feeding (Fig. 19.6a). The craniodental and orofacial morphology (Marshall 2016), feeding performance (suction and hydraulic jetting; Marshall et al. 2008), and trophic ecology of bearded seals converge with walruses. They both possess a suite of innovations to increase the change in intraoral volume that results in greater subambient pressure values. One such advantage is a vaulted palate that simply increases intraoral volume and therefore allows greater changes in intraoral volume. Walruses, bearded seals, Southern sea lions (*Otaria byronia*) and others (Kienle and Berta 2016) possess vaulted palates, and this feature is often used to infer a suction-feeding mode to fossil forms. Bearded seals employ a preparatory phase in which the tongue is raised against the hard palate just prior to hyolingual depression (Marshall et al. 2008). This functions to ensure maximal intraoral volume change. Additionally, they use fast opening of the lower jaw to generate additional subambient pressure. Bearded seals are capable of generating up to 91.2 kPa of subambient pressure whereas walruses can generate 108 kPa of subambient pressure, just greater than 1 atmosphere (Kastelein et al. 1994).

Orofacial muscles are important to all pinnipeds (and many odontocetes) when employing either a suction-feeding mode or hydraulic jetting. However, these muscles are hypertrophied in suction specialists, such as walruses and bearded seals (Kastelein et al. 1991; Marshall 2016). The hypertrophy of these muscles, three-dimensionality of the entire muscular array, soft tissue insertions, and constant vol-
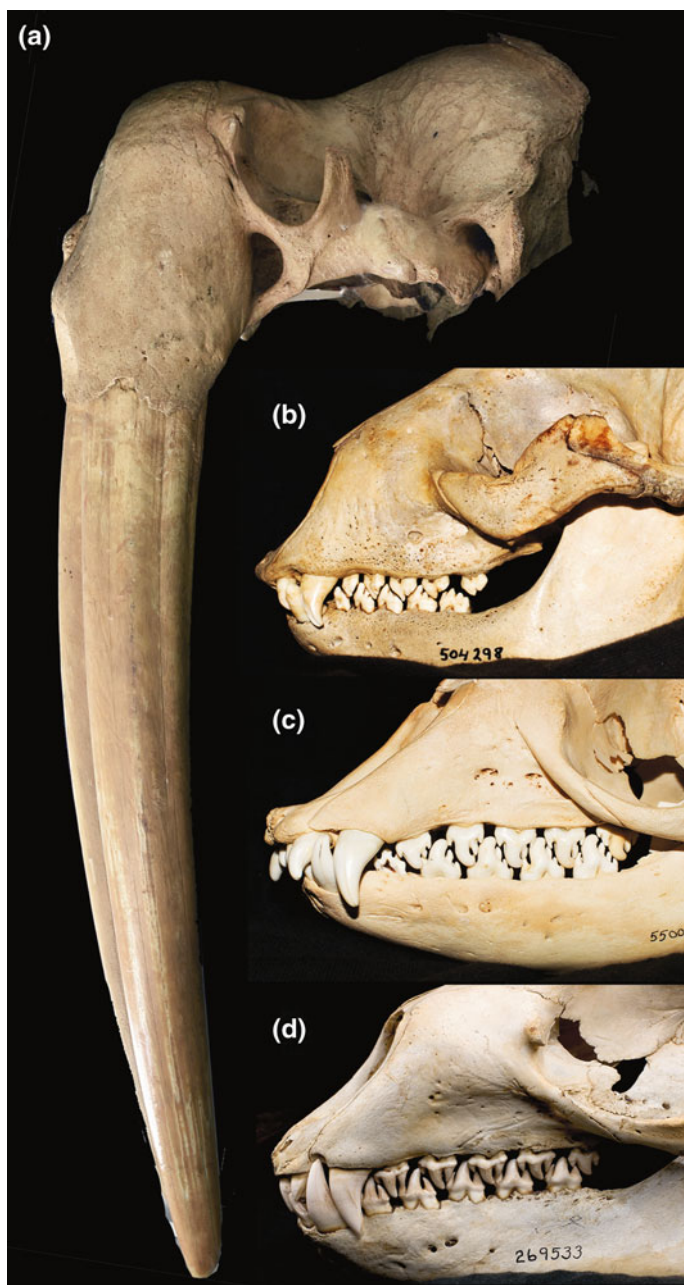
Fig. 19.6 Examples of pinniped dental innovations. **a** Large canines of modern walruses are not used for feeding, but for hauling out on ice (USNM 248161). **b** Generalized phocid dentition exemplified by a harbor seal (USNM 504298). **c** Lophed cheek teeth of crabeater seals (USNM 550078) presumably used for filter feeding. **d** Lophed cheek teeth of leopard seals (USNM 269533) differ from crabeater seals but are still presumed to be used for a filter feeding mode. Images not to scale

ume fit the model of a muscular hydrostat (Kier and Smith 1985) and explains the detailed, varied, and increased mobility of their snout. The robust lateral lip complex functions to occlude lateral gape during subambient pressure generation. The rostral portion of the superficial muscle group functions to purse the rostral lips to form a circular aperture (Fig. 19.5b) important for projecting steep subambient pressure gradients rostral to the lips for prey acquisition, particularly in bearded seals and walruses (Marshall 1997, 2016; Marshall et al. 2008). Such traits and correlated performance measures are well known for teleost fish (Wainwright et al. 2007). Feeding performance data of pinnipeds and cetaceans demonstrates that even among non-suction specialists, suction is the preferred feeding mode. While pinniped suction-feeding specialists are able to generate up to an atmosphere or more of subambient pressure, generalist pinniped foragers can also produce substantial subambient pressures during feeding.

19.9.3   Multimodal Use of Feeding Modes

Harbor seals (*Phoca vitulina*) and Steller sea lions (*Eumetopias jubatus*) are ideal species to discuss a more integrative perspective of aquatic feeding mechanisms. Harbor seals are the ultimate pinniped generalists. They are the most widely distributed pinniped species (Burns 2009), are found in a wide range of habitats and exhibit an opportunistic and generalized feeding ecology. Prey are consumed opportunistically and the type of prey varies seasonally, in accordance to prey abundance and availability over their geographic range. Animal-borne cameras attached to harbor seals provide evidence that prey capture is multimodal; both suction and biting are used (Bowen et al. 2002). A feeding performance study of harbor seals report that they prefer a suction-feeding mode (84% of all feeding events; Marshall et al. 2014) but a raptorial biting mode is also important (in 16% of feeding events; Marshall et al. 2014). While their suction-feeding performance is not on par with suction-feeding specialists, they can produce nearly ½ atmosphere of subambient pressure (48.6 kPa; Marshall et al. 2014). Harbor seals also use hydraulic jetting as needed and can produce about ½ atmosphere of positive (suprambient) pressure (53.9 kPa).

Among all marine mammal performance studies to date, raptorial biting is kinematically distinct from suction feeding. Suction feeding is characterized by a significantly smaller gape and gape angle, pursing of the lateral lips to occlude lateral gape, pursing of the rostral lips to form a circular aperture and marked gular depression. Raptorial biting is characterized by a large gape and gape angle, lack of lateral gape occlusion, often lip curling to expose teeth and a lack of gular depression. Processing of prey by teeth (mastication) is secondarily lost. Stage II transport is difficult to observe in harbor seals but may involve oropharyngeal suction as reported for northern fur seals (Marshall et al. 2015). Water (with bubbles) is commonly observed being expelled at the corner of the mouth, and this may be related to stage two transport. This appears to be a modification of hydraulic jetting. Inertial transport of food has not been observed in harbor seals.

Among otariids, Steller sea lions are also generalist foragers and can be used to test the hypothesis that harbor seal feeding mechanics is characteristic of all generalist pinnipeds. Steller sea lions feed on both small schooling fishes (e.g., herring) as well as larger demersal fishes (e.g., rockfishes; Pauly et al. 1998). Additionally, Steller sea lions will occasionally prey upon the pups of northern fur seals, harbor seals, and sea otters (Pauly et al. 1998). They also prefer a suction-feeding mode (87% of all feeding events) but will also use a raptorial feeding mode (12% of all feeding events). The maximum subambient and maximum suprambient pressures (hydraulic jetting) generated were similar in magnitude to those of harbor seals (45 kPa, respectively). Animal-borne cameras attached to Steller sea lions confirm their multimodal prey-capture modes. They have been observed to use raptorial biting, suction, and hydraulic jetting while foraging over benthic, rocky habitat (Olivier 2015). Hydraulic jetting is used to flush fish out from under or between rocks that are then captured by biting or suction-feeding modes. The feeding kinematics and performance of Steller sea lions are similar to harbor seals (Marshall et al. 2014, 2015). Where Steller sea lions likely differ, is in the magnitude of their bite force, which has not been directly measured, but can be inferred. A large bite force would enable individuals (likely males) to consume the pups of other marine mammals. Constraints of gape and bite force likely limit their ability to prey on other marine mammals to only pups. Maximum gape and bite force are most likely sexually dimorphic and related to male–male aggression. Male–male combat and the influence of mating strategies appear to act as a strong evolutionary driver in pinniped mandibular function (Jones et al. 2013). Both harbor seals and Steller's sea lions display a wide repertoire of behaviorally flexible feeding strategies in which prey acquisition was multimodal. Multimodal feeding and behavioral flexibility when foraging likely form the basis of the opportunistic, generalized feeding ecology and concomitant breadth of diet in the majority of pinnipeds.

19.9.4   Filter Feeding and Hydraulic Jetting

Phocid teeth are generalized for piscivory and teuthophagy, but outstanding exceptions for filter feeding exist (Fig. 19.6). Two species, crabeater seals (*Lobodon carcinophaga*) and leopard seals possess intricate lophs of their cheek-teeth that are hypothesized to assist in filter feeding (Fig. 19.6c, d). The lophs of the distinctive postcanine teeth of crabeater seals possess three long cusps. Observations of captive crabeater seals show that they ingest krill using a suction-feeding mode, followed by the expulsion of water through their elaborately lophed postcanine teeth effectively filtering krill from seawater (Ross et al. 1976, Klages and Cockcroft 1990). The expulsion of water for filtering is likely a form of hydraulic jetting (Marshall et al. 2008, 2014, 2015) in which the hyolingual apparatus is raised to the roof the oral cavity, as in the preparatory phase of bearded seals, but the posterior lateral lip margins at the corner of the mouth are relaxed instead of the anterior lips. Although leopard seals are known to feed on large vertebrates (penguins and other seals) using

a grip-and-tear feeding mode, they also have pronounced lophs on their postcanine teeth. This lophed phenotype is hypothesized to be as effective for filtering as in crabeater seals (Øritsland 1977; Hocking 2013). Behavioral data demonstrates that they use suction when feeding (Hocking et al. 2013). Although the magnitude of this pressure remains unknown, a reinvestigation of the leopard teeth morphology in conjunction with a feeding study supports the hypothesis that they use their postcanine teeth to filter feed (King 1983; Klages and Cockcroft 1990; Hocking et al. 2013) and expel water from the oral cavity as described above. Thus, filter feeding is the most derived form of pinniped feeding behavior, employing suction to ingest prey-laden water, and hydraulic jetting to filter out prey with specialized dentition. Another filter feeder, Antarctic fur seals (*Arctocephalus gazella*), feed heavily on krill, but without a lophed dental phenotype. Instead, their postcanine teeth are among the smallest of any fur seal, and the narrow spacing is thought to be a modification for straining krill (Bonner 1968; Repenning et al. 1971; King 1983).

19.10   Sirenian Evolutionary History

Sirenians are herbivorous marine mammals that possess innovations for grasping, excavating, and processing aquatic plants. Their evolutionary history is as long as cetaceans. Sirenians transitioned independently to aquatic environments about the same time as cetaceans ~50 Ma (Domning 2001b; Velez-Juarbe et al. 2012). Like cetaceans, sirenians underwent a parallel series of morphological transformations in their early evolutionary history as successive lineages adapted to obligate aquatic life. The earliest sirenians were quadrupedal and waded in marine coastal waters to feed upon aquatic vegetation (Domning 2001b). All evidence suggests that sirenians began their evolution in estuarine marine systems but many lineages radiated into freshwater systems (Clementz et al. 2006). Sirenians arose from a clade called Tethytheria (Sirenia, Proboscidea, and Desmostylia) in the early to middle Eocene (Domning 2001b; Savage et al. 1994).

Sirenians are comprised of four families. The earliest were the now extinct Prorastomidae and Protosirenidae. Modern sirenian assemblage includes two families, the Trichechidae and the Dugongidae. Trichechids comprise three manatee species: West Indian manatees (*Trichechus manatus*), West African manatees (*T. senegalensis*) Amazonian manatees (*T. inunguis*). Modern dugongids comprise two species, dugongs (*Dugong dugon*) and the recently extinct Steller's sea cow (*Hydrodamalis gigas*). The lineages leading to dugongs and manatees first appeared in the middle Eocene and Oligocene, respectively. *Prorastomus sirenoides* is the earliest known sirenian and is known from the Middle Eocene of Jamaica (Domning 1982), and likely represents a close relative to crown Sirenia (i.e., the common ancestor of manatees and dugongs, and all of their descendants). *Prorastomus* and another stem sirenian, *Pezosiren portelli* (Domning 2001b), were terrestrial quadrupeds that fed on seagrasses in marine coastal habitats (Clementz et al. 2006, 2009).

Dugongids first appear in the middle Eocene. They were a diverse family that radiated into three subfamilies (Halitherinae, Hydrodamalinae, and Dugonginae) but only *Dugong dugon* survives today. The earliest dugongids (e.g., *Eosiren*, *Halitherium,* and *Metaxytherium*) had strongly downturned rostra and possessed small tusks that were semiconical in shape and thought to be used to feed on seagrasses leaves and their rhizomes (Clementz et al. 2009). Hydrodamalines evolved in the North Pacific during the Neogene, ending with the recently extinct Steller sea cow (*Hydrodamalis gigas*). These dugongids were unusual in that they invaded northern cold-water habitats, grew to large sizes, and specialized on kelp rather than seagrasses (Domning 1978a). The lineage shows a reduction, followed by a complete loss of dentition, which was replaced by keratinized, horny, and rugose palatal pads to process marine macroalgae. The dugongines are characterized by a diversity of blade-like tusks, downturned rostra, and a preference for consuming the leaves and rhizomes of larger seagrass species (Domning 2001b; Domning and Beatty 2007). The fossil record leading to modern dugongs is limited, but modern dugongs are thought to have descended from relatives of halitheriines in the Oligocene. The *Dugong* lineage differs from other dugongines in their dentition. Extant dugongs evolved open-rooted, ever-growing cheek-teeth, and root hypsodonty. Their tusks are not used for feeding, which is in contrast to the feeding mechanisms of their ancestors (Doming and Beatty 2007). The feeding mechanism of modern dugongs is not representative of the former diversity.

Modern trichechids arose from close relatives of either protosirenids (Domning 1982; Sagne 2001) or halitheriine dugongids in the late Eocene to early Oligocene (Domning 1994). The radiation resulted in two subfamilies, the Miosireninae (*Anomotherium langewiesche* and *Miosiren kocki*), which are noted for their thick palatal regions and possible molluskivory (Domning 2001b; Diedrich 2008; Clementz et al. 2009), and the Trichechinae, which gave rise to our modern manatee radiation. Domning (1982) provided the first evolutionary hypotheses regarding the origin of Trichechidae, suggesting that ancestral Early or Middle Eocene protosirenids reached South America by waif (wandering) dispersal. These protosirenids became cut off genetically from their pan-Tethyan Sea parent group and gave rise to Trichechidae. The earliest known trichechid is *Potamosiren magdalensis*. It is distinguished by the indeterminate replacement of molars, similar to modern *Trichechus*. *Potamosiren* was followed by another early trichechid from South America, *Ribodon limbatus* (~6–5 Ma). *Ribodon* possessed continually erupting supernumerary molars and likely represents a close relative in the lineage leading to *Trichechus*. The apparently unlimited, continual eruption, and forward migration of cheek-teeth are unique to trichechids and are an adaptive response to an abrasive grass diet and increased tooth wear.

Modern *Trichechus* appears in the Pliocene–Pleistocene in western Amazonia (Domning 1982). The geological events during this time in South America shaped trichechid evolution. Before the Andean uplift in the Neogene, the river drainage basins in present-day Amazonia drained into the Pacific as well as the Caribbean and Atlantic. These rivers were nutrient poor with little vegetation. Early trichechids, such as *Ribodon*, the first trichechid with supernumerary teeth, entered these basins

and rivers from coastal marine waters. Uplift of the Andean mountain chain in the Miocene shut off Amazonian drainage to all but the Atlantic (Hoorn et al. 2010), creating higher erosion and siltation rates in Amazonian rivers, which, along with the rise of abundant and diverse grasses spreading to the Neotropical aquatic ecosystems, filled floodplain lakes and whitewater rivers of the Amazon Basin with luxuriant aquatic vegetation (Domning 1982). The increase in aquatic vegetation biomass was likely exploited by early trichechids. Direct ingestion of silt and the high content of abrasives, such as silicon in grasses drove the evolution of craniodental innovations to resist excessive tooth wear. Subsequent to Andean uplift, trichechids become isolated from coastal populations; there was sufficient time for trichechids to become genetically isolated and diverge, leading to the origin of *T. inunguis*. The coastal populations in the Atlantic and Caribbean extended its range in the Pliocene to North America but remained relatively unchanged to this day as *T. manatus*. Domning (1982) argues that some of these wandering manatees may have made their way to Africa by major ocean currents. Today, *T. senegalensis* inhabits the west coast of Africa.

19.11 Sirenian Feeding Mechanics

Sirenians possess a series of highly derived morphological and masticatory innovations to acquire and process vegetation. Dugongs and manatees are quite different in their trophic ecology and feeding mechanisms. Dugongs are benthic specialists whereas manatees are generalists. There are several trends in sirenian feeding mechanisms that reflect their foraging ecology. These include the degree of rostral deflection, tooth replacement, tusk size, tusk morphology, and the vibrissal-muscular complex. Rostral deflection varies among all sirenians and is indicative of their preferred feeding location within the water column (Domning 1980; Velez-Juarbe et al. 2012). Amazonian manatees possess the least deflection rostra among modern sirenians. They feed primarily at the surface upon natant vegetation (Poaceae formally Gramineae; Best 1981; Rosas 1994). West African manatees also primarily consume natant vegetation but more recently it has been discovered that they also consume fish and freshwater mollusks (Keith Diagne 2014), a behavior that first appeared in the early miosirenines. Both Amazonian and West African manatees inhabit turbid habitats where submerged aquatic plants are not widely supported (Best 1981). Correspondingly, these trichechids possess the least deflected snouts (~25–42° and 15–40°, respectively). Dugongs possess the most extreme rostral deflection of modern sirenians (70°). This deflection corresponds to their benthic foraging niche (Domning 2001b). Both above- and below-ground biomasses are consumed. The target of the below-ground biomass is rhizomes, which are a rich source of carbohydrates. Rhizophory has been a part of sirenian trophic ecology throughout their evolution. West Indian manatees inhabit a broad range of habitats from coastal marine, estuarine, and freshwater ecosystems. They consume 60+ species of aquatic vegetation that are found across these habitats (Hartman 1979). Although they primarily consume

Fig. 19.7 Close up of a Florida manatee orofacial region depicting the use of the upper bristle group (U2 bristles) for grasping and manipulating food and objects in their environment

seagrasses, brackish, and freshwater submerged aquatic vegetation, many terrestrial grasses are also consumed (Hartman 1979). Their generalized rostral deflection (29°–52°) enables West Indian manatees to feed anywhere in the water column (benthic, mid-water, natant, emergent, and terrestrial; Domning 1980).

The acquisition of plant material by sirenians is unique among mammals. The orofacial muscles of all sirenians are hypertrophied (Domning 1978b; Marshall et al. 1998a) and form a muscular hydrostat (Kier and Smith 1985). These muscles enclose modified vibrissae for manipulating vegetation. Sirenian vibrissae, or bristles, are short, thick, and organized in a series of six fields located on both the broad and expanded upper and lower lip margins (Reep et al. 1998, 2001; Marshall et al. 2003; Fig. 19.7). This muscular-vibrissal complex is an effective and forceful plant gathering apparatus. Bristles are used to crop or clip the blades of aquatic vegetation. The bristles of dugongs can excavate the root system (below-ground biomass), with rhizomes, from the benthic substrate. This action leaves a signature "feeding trail" on the sea floor (Anderson and Birtles 1978).

Unlike many marine mammals, sirenians masticate their food. Plant matter is processed using teeth and/or cornified palatal pads to reduce particle size, increase surface area, and rupture the tough plant cell walls. Trichechids differ from dugongs in their mechanism to resist tooth wear. Manatees have a mechanism in which six to eight erupted and functional cheek-teeth migrate horizontally from the posterior region of the tooth-row to the anterior region as they wear (Domning and Hayek 1984). By the time cheek-teeth reach the anterior-most location, little to no crown remains. The roots of these now nonfunctional teeth are reabsorbed and the tooth falls out. New molars erupt at the posterior tooth-row and migrate anteriorly as replacements. The number of replacement teeth is indeterminate.

Dugongs do not possess such a conveyor belt mechanism to resist an abrasive diet. This may have put them at a competitive disadvantage compared to trichechids historically when consuming grasses (Domning 1982). Dugongs possess open-rooted, simple peg-like molars that consist of dentin covered by cementum. These molars erupt slowly over their lifetime, a process called molar progression (Lanyon and Sanson 2006a, b) and is a mechanism to resist tooth wear. They have a finite number of molars (six). Evidence suggests that dugongid cheek-teeth are not functional (Lanyon and Sanson 2006a, b). Processing of seagrasses is instead transferred to the enlarged, heavily cornified, and rugose palatal pads. It is clear that these pads do assist in processing seagrass if not completely take over the function of molars. In addition, simple orthal movements of these palatal pads can transport seagrasses into the buccal cavity. Although trichechids also possess cornified palatal pads, those of dugongs are much more robust and cover a larger surface area (Marsh et al. 1999; Lanyon and Sanson 2006a, b). In terms of the "process model" of feeding, sirenians' have not altered this mechanism substantially. The method of food acquisition and stage I transport (to the teeth) is unique among mammals. For manatees, tough plant material is masticated (processing), a bolus is formed, and the bolus is moved to the palatoglossal arch (stage II transport) and swallowed (deglutition). Dugongs have a similar method of gathering seagrass compared to manatees, but stage II transport is combined with processing by the rugose palatal pads (Marsh et al. 1999). If mastication does occur, food processing is divided into two discrete regions of the feeding apparatus (teeth and palatal pads). A bolus is presumably formed within the buccal cavity and transported for swallowing as in manatees (stage II transport).

19.12 Evolutionary History and Feeding Mechanics of Other Aquatic Herbivores

The extinct Desmostylians were large marine herbivores that lived in coastal environments exclusively along the North Pacific Rim between the late Oligocene and late Miocene. They were quadrupedal, with elongated, cropping rostra, and columnar cheek-teeth without analog among any other mammal, living or extinct (Domning 2001b; Beatty 2009). Their specific sister group remains unclear, but they are closely

related to Sirenia, and consistently group within Tethytheria. Desmostylians preceded the presence of sirenians in the North Pacific and then overlapped in sympatry with them throughout the Miocene (Pyenson and Vermeij 2016). It is likely desmostylians were kelp specialists, but they also consumed seagrasses and may have competed with sirenians for this resource (Clementz et al. 2003). Along with elongated skulls and broad rosta, desmostylians possessed procumbent incisors and tusk-like canines. In many of the later diverging lineages, the premolars and molars consisted of packed bundles of columns, reflecting a degree of hypsodonty that was likely an herbivorous adaptation for resisting tooth wear (Inuzuka et al. 1994). Desmostylia are now extinct.

In the Southern Hemisphere, a notable group of extinct marine mammal herbivores were aquatic sloths, which were closely related to today's xenarthran mammals that live in Neotropical forests. Five species of the Nothrotheriidae *Thalassocnus* lived from the late Miocene through the late Pliocene (~11–2.5 Ma) exclusively on the west coast of South America. The gradual and progressive adaptive trends in *Thalassocnus* qualifies as an example of anagenesis (i.e., evolutionary change within a single, unbranching lineage), with increasing pachyosteosclerosis in their limb bones (Amson et al. 2014), and expansion of the premaxillary and osteological proxies for large manipulative lips and orofacial morphology in each successive species (Muizon et al. 2003, 2004). Their extinction in the late Pliocene is likely related to the closure of the Panamanian isthmus that resulted in decreased water temperatures (O'Dea et al. 2016) and coincided with the disappearance of seagrass communities along nearly the entire length of the western coast of South America. Competition with dugongids may also have been a contributing factor (Domning 2001a; Muizon et al. 2003, 2004; Amson et al. 2014).

19.13   Sea Otter Evolutionary History

Sea otters (*Enhydra lutris*) are among the most recent groups of marine mammals to return to marine habitats. They arose ~3–1 Ma in the North Pacific during the late Pliocene and Pleistocene (Repenning 1976; Boessenecker 2016), and belong to Mustelidae (weasels, otters, and badgers), the most diverse family of Carnivora.

Two subfamilies are recognized, the Mustelinae (terrestrial mustelids such as fishers, martens, and wolverines) and the Lutrinae (all otters). As with pinnipeds, the fossil record for sea otters is sparse. Otters diverged from stem mustelids during the early Miocene (Koepfli and Wayne 1998). The genus *Mionictus* is the oldest known otter fossil and dates back to ~20 Ma (Koepfli and Wayne 1998). An extensive Bayesian molecular phylogeny of lutrines resolved three monophyletic lineages (Koepfli et al. 2008). The first lineage comprises Old World river otters and sea otters (clawless otters (*Aonyx capensis*), Asian small-clawed otters (*Aonyx cinereus)*, smooth-coated otter (*Lutrogale perspicillata*), Eurasian otters (*Lutra lutra*), hairy-nosed otter (*Lutra sumatrana*), and spotted-necked otters (*Hydrictis maculicollis*).

The second lineage includes New World otters (North American river otters (*Lontra canadensis*), marine otters (*Lontra felina*), and Neotropical river otters (*Lontra longicaudis*)). The third lineage consists of giant otters (*Pteronura brasiliensis*).

Sea otters were the earliest lineage to diverge from Old World otters (Koepfli and Wayne 1998). The genus *Enhydra* diverged from the basal lutrinae species during the Miocene (~20–5 Ma), (Berta and Morgan 1985). According to molecular (Masuda and Yoshida 1994) and morphological (Berta and Morgan 1985) data, *Lutra* is the closest extant relative of sea otters. There are two lineages of fossil sea otters (Berta and Morgan 1985; Lambert 1997). One led to the extinct *Enhydriodon* and a second led to the giant, now extinct, *Enhydritherium* and extant sea otters. *Enhydritherium* appeared in the fossil record during the late Miocene–Pliocene of Florida and California and inhabited coastal marine environments and inland habitats (Lambert 1997). *Enhydritherium* and *Enhydra* share specific traits with extant sea otters. The craniodental morphology of *Enhydritherium* is consistent with a durophagous trophic niche as observed in *Enhydra*. A congener of modern sea otters, *Enhydra macrodonta* from the late Pleistocene of California, is now extinct (Kilmer 1972) but resembled *E. lutris* closely. *E. macrodonta* possessed a more robust horizontal mandibular ramus, larger molars with increased occlusal surface area and an extended tooth-row indicating a strong durophagous niche.

19.14 Sea Otter Feeding Mechanics

Sea otter trophic ecology varies substantially among subspecies (northern sea otters, *Enhydra lutris kenyoni*; southern sea otters, *Enhydra lutris nereis*; and Russian sea otters *Enhydra lutris lutris*) and among discrete populations. In general, shellfish and urchins comprise a large portion of the diet. Clams and other invertebrates are excavated using the hands. Urchins and shellfish are often pried from the rocky substrate. Fish, when consumed, are pursued underwater. All prey are consumed at the surface. Fish are normally killed by a strong bite to the head. Shellfish are commonly pounded open using a rock, or another tool, carried in a flap of skin in the axilla region or crushed with bunodont cheek-teeth. Urchins and crabs are dispatched with a bite; urchin spines are bitten off and the urchin shell is crushed with cheek-teeth. Crab shells are opened with incisors, canines, and hands. The material inside the shell is scooped out by dragging the shell, held by the forepaws, over the lower incisors and canines. Sea otter cheek-teeth have secondarily lost the shearing cusps of the carnassial teeth (Kenyon 1969). Their cheek-teeth are broad, flat, and covered with an enamel that is thicker than in other carnivores (Kenyon 1969) and more resilient in its structure (Chai et al. 2009). As a result, it is 2.5 stronger than human enamel (Ziscovici et al. 2014). In terms of the "process model", sea otters have behaviorally separated food acquisition, which occurs at depth, from food processing. Therefore, while food acquisition is aquatic, food processing is still very terrestrial in its mechanism.

Sea otters differ from other otters in that their craniodental morphology is correlated with durophagy, which is enhanced by an extremely blunt and wide skull and mandible, large occlusal surface area relative to body size, and the use of hands (vs. mouth) to acquire prey (Timm 2013; Timm-Davis et al. 2015, 2017). Sea otters exhibit taller and wider mandibular rami, and shorter, blunter skulls, and a greater cross-sectional area of the masseter and temporalis muscles than other otters (Timm 2013; Timm-Davis et al. 2015), which is consistent with increased bite force at the carnassials of other mammals (Sacco and Van Valkenburgh 2004, Nogueira et al. 2009). In fact, the skulls of sea otters are among the most blunt for mammals and are wider than they are long (Timm 2013; Timm-Davis et al. 2015). Among otters, sea otters possess a relatively high masseteric mechanical advantage, which increases the force at the most posterior molars as an adaptation for durophagy (Timm 2013). Kinematic investigations of captive and wild sea otter biting demonstrate that they possess innovative adaptations to produce powerful bites at wide gapes (Timm 2017). These physiological innovations for increased bite force performance are supported in southern sea otters (Law and Mehta 2016).

19.15 Feeding Mechanisms of Other Otters and Carnivorans

Prey acquisition by otters is categorized as either mouth-oriented piscivory or hand-oriented invertebrate specialists (Timm-Davis et al. 2015). These categories are similar to the "fishotters" and the "crabotters" described by Pohl (1919, p. 201). Mouth-oriented feeding is considered the basal feeding mode (Berta and Morgan 1985). These behavioral categories for both feeding strategies are not this simplistic. Some Asian small-clawed otters will incorporate fish into their diets and some populations of sea otters will consume fish and occasionally sea birds (Riedman and Estes 1988). Morphometric analyses and kinematic deductions of otter feeding mechanisms support strong divergent craniodental patterns concomitant with mouth-oriented versus hand-oriented foraging (Timm-Davis et al. 2015). These divergent food acquisition strategies involve, on one extreme, mechanisms to capture elusive, open-water organisms that do not require crushing (e.g., fish), and at another extreme relatively non-elusive, benthic hard-bodied organisms (e.g., crustaceans, mollusks). Those species that primarily use mouth-oriented prey-capture mechanisms possess long mandibles, long rostra, long and gracile pterygoid hamuli, and shearing blades on carnassial teeth. Their feeding mode follows a basic biomechanical trade-off of force and velocity. Long narrow skulls and mandibles sacrifice bite force to maximize jaw velocity, an important adaptation for capturing elusive fish. In these species, the adductor mechanical advantage is greatest for the temporalis muscle, which focuses force anteriorly at the incisors and canines. In contrast, hand-oriented predators possess blunt mandibles and rostra, and flat bunodont teeth (sometimes with increased occlusal surface area) that have secondarily lost the shearing blades on carnassial

teeth. Their skulls and mandibles maximize bite force at the expense of jaw velocity. Hypertrophic jaw adductors and an increased masseteric mechanical advantage add to the suite of characteristics for durophagy. The evolution of the functional divergence of these feeding modes among otters appears to have occurred early in lutrine history resulting from a single, deeply rooted evolutionary transition in foraging mode and concomitant shift in morphology and biomechanics (Timm-Davis et al. 2015).

Extinct marine carnivorans unrelated to sea otters likely converged on similar functional solutions to durophagy. The extinct walrus relative *Gomphotaria pugnax*, from the late Miocene of California, has been proposed as durophage, based on the highly broken and worn cheek-teeth in the only known specimen (Barnes and Raschke 1991). Recently, Tseng et al. (2016) examined the feeding morphology of the enigmatic arctoid carnivoran *Kolponomos*, an extinct Miocene bear-like marine mammal known only from a few specimens that exhibit laterally expanded molars most similar in morphology to a sea otter. Using biomechanical simulations and comparative shape analysis, Tseng et al. (2016) argued that *Kolponomos* possessed a largely non-analogous masticatory system that showed mandibular shape and function similarities with *Smilodon* (saber-toothed cat), while also exhibiting a crushing bite most similar to extant sea otters.

19.16   Other Aquatically Feeding Mammals

Outside of marine mammals there is a less known, but a surprisingly diverse, assemblage of semiaquatic mammals. These mammals are found on most continents and multiple mammalian orders have semiaquatic representatives (Veron et al. 2008). As with marine mammals, semiaquaticness does not confer aquatic feeding capabilities. Many species that spend time in aquatic habitats actually feed in terrestrial environments, others will feed in both terrestrial and aquatic environments, while fewer feed primarily in aquatic environments. The majority of nonmarine mammals that are aquatic feeders do so in freshwater habitats such as small mountainous streams, ponds, lakes, and rivers (Veron et al. 2008). As with (sea) otters, the common pattern is that prey is acquired aquatically but is processed either at the surface (as in lutrines) or complete out-of-water.

Two extant marsupials are semiaquatic. Among the best known are platypuses (*Ornithorhynchus anatinus*). They have extensive adaptations for an aquatic lifestyle and are commonly found in the freshwater streams, lagoons, and lake of eastern Australia and Tasmania (Pasitschniak-Arts and Marinelli 1998). The majority of the scientific interest regarding feeding has focused on understanding their electroreceptive bill. This aquatic sense allows these animals to find benthic macroinvertebrates among the detritus in these freshwater habitats. Once prey is captured, it brought to the surface for processing and swallowing. Adult platypuses are edentulous and possess keratinous grinding plates with shearing ridges. Cursory inspection of footage of platypus feeding clearly shows translational movements of the mandible, presum-

ably to grind macroinvertebrates against these plates, but no detailed reports of its mechanisms are available. This is apparently a derived state since some fossil platy-puses (e.g., *Obdurodon*) appear to possess teeth (Pasitschniak-Arts and Marinelli 1998).

Water opossums (*Chironectes minimus*) are semiaquatic marsupials with a dense pelage, streamlined body and webbed feet (Rosenthal 1975; Fish, 1993) and range from southern Mexico to northeast Argentina. They are always found near freshwater aquatic habitats, swimming and wading in shallows to feed on crayfish, shrimp, and fish (Marshall 1978; Fish 1993). Although no detailed analyses are available regarding their feeding, they are reported to grasp prey in the water with their mouths (open gape) then process and consume prey out of the water. The prey is held down with the forefeet while eating (Rosenthal 1975).

Most mammals discussed so far acquire prey and food within aquatic habitats either by mouth or by hand. Certain bats possess innovations of their hind limbs to capture fish. Specifically, the greater bulldog bat (*Noctilio leporinus*; Bloedel 1955) and several evening bats (Verspertilionidae) of the genus *Myotis* (Alterbach 1989; Ma et al. 2003) are known fishing bats. These bats inhabit tropical lowlands and forage over streams and lagoons. Fish residing just below the water's surface are detected by echolocation (Schnitzler et al. 1994). The digits of the hind feet are elongated, ending with hook-like claws; these claws are rotated 180 degrees so that their tips are directed forward. The digits and claws are laterally compressed (Fish et al. 1991). These bats "fish" by flying low over the water with hind legs and feet held straight down, "raking" the water in an effort to gaff fish with the forward-facing claws (Bloedel 1955). Prey capture is synchronized with the power stroke of the wing beat. The modifications of the hind limbs, pes, and claws function to reduce drag and any loss of momentum while "raking" (Fish et al. 1991). Once a fish is caught, the bat rises in the air and transfers the prey to the mouth and then roosts to process the meal (Alterbach 1989). The feeding apparatus of bats is generalized and mastication is considered to be similar to marsupials and insectivores (Weijs 1994). The diversity of bat feeding mechanisms is reviewed by Dumont (2007).

Strict semiaquatic carnivory has evolved numerous times among tenrecs, shrews, moles, and rodents. Among rodents, semiaquatic carnivory has evolved in at least eight families (Veron et al. 2008). Radiations of semiaquatic foraging behavior are most notable in New Guinea (Olsen 2008), Africa (Peterhans and Patterson 1995) and South America (Voss 1988). While each group has its specific natural history traits, the common pattern in all these groups is the possession of specific aquatic traits that include: webbed feet (in many), elongation of metatarsals, increased density of body hair, reduced pinnae, and stiff mystacial whiskers (Voss 1988; Veron et al. 2008). These animals are accomplished swimmers and divers considering their body size. Prey include small fish and small benthic invertebrates (Sorenson 1962; Stone 1985, 1987a, b; Voss 1988; Veron et al. 2008; Benstead et al. 2001; Catania et al. 2008; Olsen 2008; Rowe 2014). Prey detection is through contact with whiskers and subsequent grasping of prey with the mouth (raptorial biting; Catania et al. 2008). Few data are available regarding specifically how prey is captured.

A few studies on a limited number of species may provide a template that can be widely applied to these aquatic feeding mammals. *Limnogale mergulus* (web-footed tenrecs) spends substantial time foraging in water by swimming and diving for prey (Benstead et al. 2001). Dives last for 10–15 s and prey are detected by sweeping motions of the head and contact of prey with vibrissae. Prey are seized by the mouth and always brought to the surface and consumed while holding prey in its forefeet (Malzy 1965). Water shrews (*Sorex palustris*) are the smallest mammalian diver, diving to the bottom of streams and ponds to consume both insects and small fish (Sorenson 1962 Catania et al. 2008). In captivity, fish <6-inches long fish are acquired using an open gape to grasp the prey with a bite directly behind the head (Sorenson 1962 Catania et al. 2008; Fig. 19.8). After capture, prey were torn by holding it down by the forefeet, biting it and pulling up with the head (Sorenson 1962). Pyrenean desmans (*Galemys pyrenaicus*) and Russian desmans (*Desmana moschata*), members of the mole family (Talpidae), possess similar adaptations for semiaquatic carnivory. Movement and foraging patterns of Pyrenean desmans are similar to those reported for web-footed tenrecs (Stone 1985; 1987a, b; Benstead et al. 2001). Although not specifically discussed, it is probable that prey acquisition is similar to that reported for water shrews (Sorenson 1962; Catania et al. 2008). Similar acquisition for prey is reported for semiaquatic murine rodents such as Sulawesi water rat*s* (*Waiomys mamasae*; Rowe et al. 2014) and ichthyomyine rodents (Voss 1988). While no specific study of feeding mechanisms exists for aquatic tenrecs, shrews, moles, and rodents, once prey are acquired, the feeding mechanisms most likely follow that for their terrestrial counterparts. For example, in tenrecs jaw opening is accompanied by jaw protrusion followed by jaw closing with retrusion (Weijs 1994). Rodents have a more specialized feeding mechanism due to their elongated incisors and gnawing behavior (Turnball 1970; Weijs 1994), but raptorial feeding most likely involves propalineal movement of the mandible to increase gape.

19.17 Conclusion

The feeding mechanisms of aquatic mammals provide insights to the evolution of mammalian feeding. Aquatic feeding adaptations show a broad diversity of evolutionary innovations, ranging from bony to soft tissues structures that acquire and process prey. Their evolutionary history also shows a loss of diversity in feeding mechanisms as exemplified by walruses, dugongids, desmostylians, and aquatic sloths. The relative evolutionary newcomers to aquatic habitats (otters, tenrecs, shrews, moles, and rodents) have separated food acquisition, which occurs in water, from food processing behavior that occurs either at the water's surface or on land.

Most aquatic mammals are multimodal trophic opportunists that have made substantial departures from the classic terrestrial process model of feeding. Major departures from the process model have focused on food acquisition, and for most, the loss of mastication and intraoral transport to teeth, homodonty, and even the total loss of teeth in some lineages.

Fig. 19.8 a–d Sequence of video frames of a water shrew feeding on fish using raptorial biting (Catania et al. 2008)

Advances in our understanding of aquatic feeding innovations have occurred when workers employ experimental and quantitative methodologies using new technological scientific tools both in the field and in the laboratory. New directions for the field include embracing such new technologies and using experimental methodologies. Nevertheless, the most pressing need is the collection of comparative data. Even basic biomechanical measures such as mechanical advantage of jaws on comparative basis are lacking. Addition comparative data are needed regarding brain–behavior relationships. Currently, relatively much more is known regarding mammalian sensory systems and behavior and much less regarding neuromuscular and sensorimotor control of feeding behavior in a comparative context. Exciting discoveries of new fossils and the development of new phylogenetic tools will allow scientists to further clarify functional transitions from land to sea and provide new perspectives on the evolution of mammalian feeding.

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