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Convergent and Alternative Designs for Vertebrate Suspension Feeding

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THE SKULL

VOLUME

3

Functional and Evolutionary Mechanisms

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Convergent and Alternative Designs for Vertebrate Suspension Feeding

S. Laurie Sanderson and Richard Wassersug

INTRODUCTION

SUSPENSION-FEEDING AQUATIC ANIMALS capture planktonic prey as water flows past the feeding apparatus. Vertebrate suspension feeders include species of fishes, tadpoles, whales, and birds and are of evolutionary, ecological, and economic importance. Ancestral vertebrates are thought to have been suspension feeders as larvae (Jollie 1982; Northcutt and Gans 1983) or as adults (Mallatt 1985). Suspension feeding appears to have evolved independently multiple times in teleost fishes and in elasmobranchs (Moss 1977, 1981; Cavender 1970). By consuming phytoplankton, zooplankton, and/or detritus, suspension feeders obtain their energy at a relatively low level in the trophic pyramid and may attain large standing stocks (e.g., herrings and sardines) or large body size (e.g., whales and whale sharks).

The morphology and physiology of a large number of invertebrate suspension-feeding species have been described (reviews in Wallace and Merritt 1980; Jørgensen 1966, 1975; Vanderploeg 1990; Wotton 1990). The physical mechanisms operating in trophic fluid transport systems and in biological filters have been examined through the application of theoretical fluid mechanics to invertebrate suspension feeding (Shimeta and Jumars 1991; LaBarbera 1990, 1984; Jørgensen 1983; Rubenstein and Koehl 1977). The hydrodynamics of feeding in aquatic vertebrates have only recently received attention (Sanderson et al. 1991; Lauder and Shaffer 1986; Muller and Osse 1984; Lauder 1980; Weihs 1980), and the mechanics of vertebrate suspension feeding remain an open field for research. Ecological information on vertebrate suspension feeding far exceeds our understanding of the functional morphology involved. For example, functional morphological studies are needed to establish the structure of the prey-capturing surfaces. But more important, the pattern and velocity of water flow within the oral and (in fishes) opercular cavities must be deter-

Order of authorship is alphabetical.

mined. Without these data, the physical mechanism(s) used by vertebrates during suspension feeding cannot be fully understood.

In this chapter, we (1) provide an extensive list of vertebrate species that are known to suspension feed, (2) summarize the mechanistic components of vertebrate suspension feeding, (3) examine morphological and ecological patterns relating to convergent and alternative designs for vertebrate suspension feeding, and (4) identify potential research topics in this area.

Definitions of Suspension Feeding

Suspension feeding, as we use the term, involves both microphagy and planktivory. Microphagy is the consumption of prey too small to be sensed and engulfed as individual particles (Jørgensen 1966). Thus, more than one prey item is typically engulfed during each feeding bout, and some degree of nonselectivity is implied. Planktivory is the separation of particles from ambient water only. We exclude from consideration those animals that "bottom feed" by separating food from surrounding inorganic material and other nonfood particles at the sediment-water interface or that "deposit feed" by directly consuming particulate matter on or in the bottom (e.g., Hlohowskyj et al. 1989; Robotham 1982; Jørgensen 1966). Our definition, however, does not exclude feeding on material from the bottom that is brought into suspension by the activity of the animal. In this situation, inorganic material and other nonfood particles are often swallowed with the food rather than separated from the food in the oral cavity.

Jørgensen (1966) considered suspension feeders to be "typically nonselective feeders, which clear the surrounding water of particles at rates that are independent of the concentration of the particles below certain levels and of their value as food, and which feed continuously when undisturbed" (Jørgensen 1966, 134). As our knowledge of suspension-feeding organisms has grown, it has become clear that this definition may apply to a limited number of sessile invertebrate suspension feeders, but suspension-feeding activity in many other species is constantly regulated in a dynamic fashion. Vertebrates that suspension feed generally (1) respond to a reduction in the concentration of particles below a certain level by ceasing to suspension feed, (2) adjust their suspension-feeding rates in response to characteristics of the particles, and (3) do not suspension feed continuously when undisturbed (see, e.g., Runge et al. 1987; Gibson and Ezzi 1985; Durbin and Durbin 1975; O'Connell and Zweifel 1972; Seale et al. 1982; Viertel 1990). Jørgensen (1983, 89) offered a less restrictive definition that applies equally well to vertebrate and invertebrate suspension feeders, namely "aquatic animals that have evolved special structures to process

the surrounding water and to retain small suspended particles, including food particles such as phytoplankton." It is, of course, those "special structures" that are our primary concern here.

Mechanistic Components of Vertebrate Suspension Feeding

In this chapter, we examine three mechanistic components of vertebrate suspension feeding: transport of water into the mouth, transport of water past entrapment surfaces and out of the mouth, and separation of particles from the water. Two additional components are transport of captured food from the oropharyngeal feeding structures to the esophagus, and deglutition (Zweers et al. 1977). The least amount of information is available regarding these latter two processes and they are beyond the scope of this review (but see Zweers et al. 1977; Kooloos et al. 1989; Friedland 1985; Bertmar et al. 1969; Nelson 1967a).

Many invertebrate suspension feeders have entrapping surfaces located external to the mouth and rely on ambient currents to transport water to them (Vogel 1981). Consequently, authors analyzing invertebrate suspension feeding have not always included transport of water into the mouth as one of the stages in suspension feeding (e.g., Jørgensen 1983; LaBarbera 1984). For some vertebrates, notably those that lack gill slits, transport of water into the mouth is a process distinct from transport of water past the suspension-feeding structures, with the direction of flow differing between the two processes by as much as 180°.

TRANSPORT OF WATER INTO THE MOUTH

To fill the mouth with water, animals can use their own forward velocity, generate suction within the oral cavity, or use a combination of the two (Alexander 1967). We identify four categories of vertebrate suspension feeders, based on the methods used to transport water into the mouth (Sanderson and Wassersug 1990): (1) continuous ram feeders, (2) intermittent ram feeders, (3) continuous suction feeders, and (4) intermittent suction feeders (table 2.1). In the first two categories, extracranial body movements alone deliver water into the mouth. In the latter two, specializations of the jaws and pharyngeal structures produce pulses of negative pressure to suck in water.

Ecological Patterns

Continuous Ram Feeders. Ram feeders engulf a volume of water by swimming forward with an open mouth (figs. 2.1, 2.2). Continuous ram feeders allow water to escape posteriorly from the mouth as they swim, maintain-

TABLE 2.1 Characteristics of the four categories of vertebrate suspension feeders, with a listing of previous authors' terms

	Ram feeders		Suction Feeders	
	Continuous	Intermittent	Continuous	Intermittent
Other terms in the literature[1]:	Skimmers (Nemoto 1970)	Swallowers (Nemoto 1970)		Gulpers (Janssen 1976)
	Tow-net filter feeders (Lazzaro 1987)	Gulpers, gulping, engulfment (Matthews 1978; Pivorunas 1979)		Pump filter feeders (Drenner, O'Brien et al. 1982)
	Continuous (Krushinskaya 1986)	Pulse (Krushinskaya 1986)		
Some general characteristics:				
	Prey small, nonevasive	Prey larger, more mobile	Prey small, nonevasive	Prey small, nonevasive
	Uses forward body velocity to overtake prey	Uses forward body velocity to overtake prey	No forward body movement, uses suction to engulf prey	Limited forward velocity, uses suction to engulf prey
	Forward body velocity causes water to exit	Muscular contraction and elastic recoil force water to exit	Muscular contraction forces water to exit	Muscular contraction forces water to exit
	Body size moderate to large	Body size large	Body size small to moderate	Body size moderate to large
Examples:				
	Whale shark, menhaden, anchovy, right whale	Rorqual whales	Ammocoete larvae, tadpoles, flamingos, mallard	Tilapia, gizzard shad, cisco, megamouth shark

[1] Citations do not necessarily indicate the first or only use of that term.

Fig. 2.1. Basking shark, *Cetorhinus maximus* (8 m total length), continuous ram feeding in Carmel Bay, California. The ventral portions of the gill arches are visible inside the mouth, which is about 1 m wide. (From Hallacher 1977)

ing an open mouth for sustained periods of time. The mouth may remain fully open for half a second to several minutes (Runge et al. 1987; Batty et al. 1986; Hallacher 1977; Colin 1976; O'Connell and Zweifel 1972). The mysticete whales that Nemoto (1970) referred to as "skimmers," the right and bowhead, are continuous ram feeders (table 2.2). The fishes described by Lazzaro (1987) as "tow-net filter feeders" are also included in this category.

Table 2.2 lists vertebrates that have been observed to feed in this manner or that are inferred to be continuous ram feeders on the basis of di-

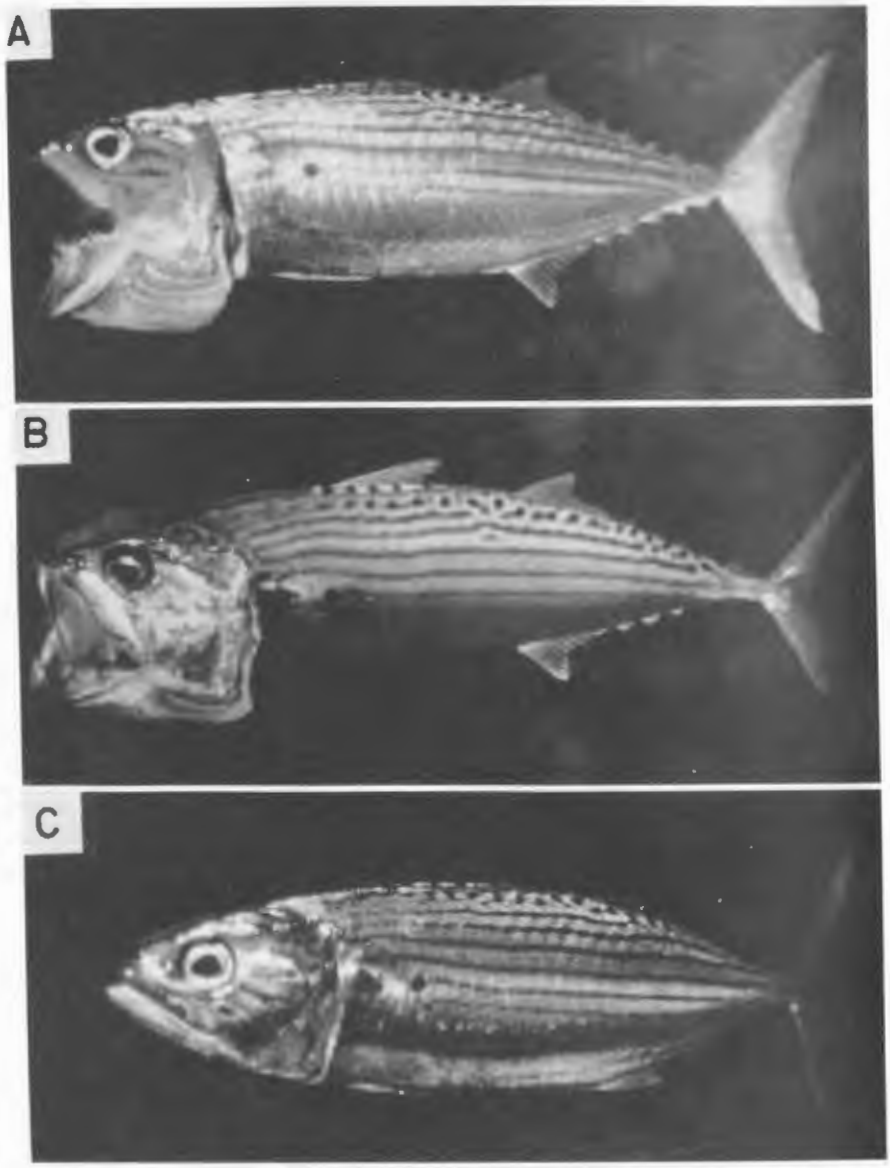

Fig. 2.2. Indian mackerel, *Rastrelliger kanagurta* (20–30 cm standard length), continuous ram feeding off Mbengga Island, Fiji (A, B) and swimming with mouth closed (C). (From Colin 1976)

gestive tract contents and the morphological features that are described below. Fishes that have a diet of phytoplankton, or that consume plankton species relatively nonselectively in the approximate proportions present in the environment, are suspension feeders by definition. Species listed in table 2.2 that have not been observed while feeding may be continuous ram feeders and/or intermittent suction feeders. With the possible exception of the basking shark, the fish species listed in table 2.2 are likely to be facultative suspension feeders. Most appear to be able to select individual food items from the water or off the bottom, in addition to continuous ram feeding (see references in table 2.2).

The whales that are continuous ram feeders consume smaller and less evasive prey relative to their intermittent ram-feeding relatives; i.e., they are microplanktophagous as opposed to macroplanktophagous, in the terminology of Tomilin (1967). The feeding structures inside their mouths present a high resistance to water flow and the resulting large pressure drag retards acceleration when the mouth is open. Continuous ram feeders are unable to capture large evasive prey that swim out of the open mouth's path (Tomilin 1967).

Intermittent Ram Feeders. Intermittent ram feeders use their forward velocity to force their mouths open widely (fig. 2.3) and fill their buccal cavity in a single pulse (Lambertsen 1983; Orton and Brodie 1987). As a feeding strategy, intermittent ram feeding is limited to the largest of all animals, the rorqual whales (table 2.3), swimming at a high (approximately 10^6) Reynolds number. No teleost fish or shark is known to feed in this manner.

In order for intermittent ram feeding to work, the inertial forces must be very high and the buccal floor compliant, otherwise the pressure head anterior to the animal would push water and food away. The rorqual whales direct their attacks on schools of fishes or local concentrations of krill. Complex herding behaviors may be used to further concentrate prey in front of the whales before they open their mouths (Hain et al. 1982; Watkins and Schevill 1979; Jurasz and Jurasz 1979).

Continuous Suction Feeders. An odd collection of animals comes under this heading: ammocoetes, tadpoles, certain ducks, and flamingos (table 2.4). What these organisms share is a dependence on an oscillating buccopharyngeal pump to generate feeding currents. Continuous suction feeders remain relatively stationary when feeding and thus, unlike most other suspension feeders, their locomotor capability is not directly linked to their feeding morphology. For continuous suction feeders with gill slits, the pharyngeal arches and associated musculature form the piston for the pump. For those that lack gill slits, the tongue and hyoid make up the pump.

TABLE 2.2 Continuous ram feeders

Family, species	Body length[1]	Prey[2]	Reference
Cetorhinidae			
Cetorhinus maximus[3] (basking shark)	> 6–10 m	Z	Hallacher 1977
Clupeidae[4]			
Alosa aestivalis (blueback herring)	7.2–29.0 cm FL	Z, D, B	Stone and Daborn 1987
Alosa pseudoharengus[3] (alewife)	5.0–33.8 cm FL	Z, P, D, B	Janssen 1976, 1978; Stone and Daborn 1987
Brevoortia tyrannus[3] (menhaden)	> 4 cm FL	Z, P, D, B (> 13–16 μm)	Durbin and Durbin 1975; Edgar and Hoff 1976; Friedland et al. 1989
Clupea harengus[3] (herring)	5–34 cm	Z, fish eggs, small fishes	Last 1989; Gibson and Ezzi 1990
Ethmalosa fimbriata (shad)	5.3–30.4 cm	Z, P, D, S	Blay and Eyeson 1982; Fagade and Olaniyan 1972
Gilchristella aestuarius (round-herring)		Z, P, B, S	White and Bruton 1983
Hilsa kelee (shad)	3–16 cm SL	Z, P	Blaber 1979
Sardinops caeruleus (Pacific sardine)	11.0–28.5 cm SL	Z, P	Hand and Berner 1959
Sardinops ocellatus (pilchard)	2–22 cm SL	Z, P	King and Macleod 1976
Sardinella longiceps (Indian oil sardine)	13.0–19.9 cm TL	Z, P	Bensam 1964
Engraulidae[5]			
Cetengraulis mysticetus[3] (anchoveta)	3–15 cm	Z, P, S	Bayliff 1963; Hobson 1963
Engraulis anchoita (Argentine anchovy)	0.3–9.0 cm	Z, P, B, S (> 100 μm)	Ciechomski 1967
Engraulis capensis[3] (Cape anchovy)	2–16 cm SL	Z, P, B, S (≈100 μm–2 cm)	King and Macleod 1976; James 1987; James and Findlay 1989
Engraulis encrasicholus maeoticus (Azov anchovy)	2.0–5.0 cm	Z, P, B	Mikhman and Tomanovich 1977
Engraulis mordax[3] (northern anchovy)	4.0–21.5 cm SL	Z, P, B, S (> 40 μm)	Leong and O'Connell 1969; Loukashkin 1970; Hunter and Dorr 1982
Mobulidae[6]			
Mobula hypostoma (devil ray)	< 1.3 m breadth	Z, S, small fishes	Radcliffe 1914; Coles 1916
Mobula thurstoni (devil ray)	0.6–2.3 m breadth	Z	MacGinitie 1947; Notarbartolo-di-Sciara 1988
Manta birostris (manta ray)		Z?, small fishes	Bigelow and Schroeder 1953
Polyodontidae			
Polyodon spathula[3] (paddlefish)	> 12 cm TL	fish (5–10 cm), Z, S	Fitz 1966; Michaletz et al. 1982; Rosen and Hales 1981; Weed 1925
Rhiniodontidae			
Rhiniodon typus[3] (whale shark)	14 m	Z, squid, small fishes	Gudger 1941b
Scombridae			
Rastrelliger kanagurta[3] (Indian mackerel)	5.5–30.0 cm TL	Z, P, fish eggs	Bhimachar and George 1952; Colin 1976; Rao and Rao 1957
Scomber japonicus[3] (Pacific mackerel)	20–25 cm SL	Z	O'Connell and Zweifel 1972
Scomber scombrus[3] (Atlantic mackerel)	adult	Z	Runge et al. 1987; Pepin et al. 1988
Balaenidae[7]			
Balaena mysticetus[3] (bowhead whale, Greenland right whale)	14–18 m TL	Z (3–4 mm copepods predominantly, euphausiacean krill), B (gammarid amphipods), S (pebbles)	Tomilin 1967; Nemoto 1970; Würsig et al. 1985; Reeves and Leatherwood 1985
Eubalaena glacialis[3] (right whale)	10–17 m TL	Z (3–4 mm copepods predominantly)	Tomilin 1967; Nemoto 1970

[1] TL = total length from tip of snout to end of caudal fin rays; SL = standard length from tip of snout to start of caudal fin rays; FL = fork length from tip of snout to start of fork in caudal fin rays; breadth = breadth of body from wing tip to wing tip.

[2] Z = zooplankton; P = phytoplankton; D = detritus; B = benthic organisms; S = sediment.

[3] Direct observations of feeding made in field or laboratory. Species that have not been observed while feeding may be continuous ram feeders and/or intermittent suction feeders, but have been placed in this table on the basis of morphological features.

[4] Additional clupeid species reviewed in James 1988.

[5] Additional engraulid species reviewed in James 1988.

[6] Additional mobulid species discussed in Notarbartolo-di-Sciara 1988.

[7] On morphological grounds the pygmy right whale could be added to this list, but it is not included because its diet and behavior are so poorly known (Baker 1985).

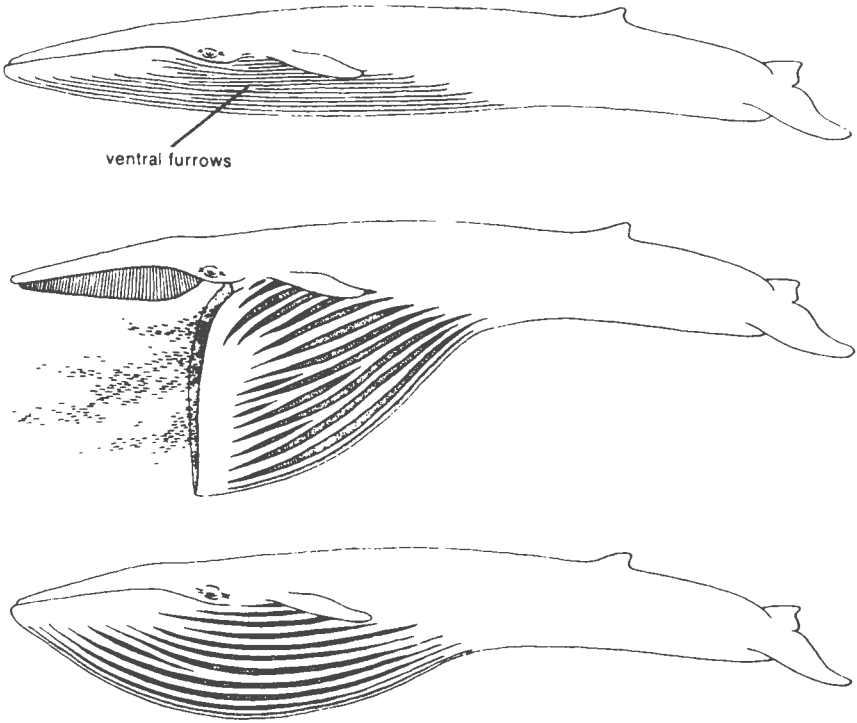

Fig. 2.3. Intermittent ram feeders, the rorqual whales, use their forward motion to fill their buccal cavity during feeding. The ventral furrows and compliant tissue of the buccal floor facilitate this expansion (Orton and Brodie 1987). Observations of whales feeding in the wild (e.g., Watkins and Schevill 1979) indicate that, while on the surface at least, whales rarely swim in a straight path as they open their mouths. Pitching and rolling motions that bring the baleen on one side and the rostrum upward are common. These motions may facilitate the closing of the mouth and the draining of water through the baleen. (From Pivorunas 1979)

Continuous suction feeders, of course, do not feed *all* of the time, but when they are feeding the pump oscillates continuously at a rather high frequency to maintain the flow of water and food to surfaces on which food particles are captured. These vertebrates feed on very small particles compared to their own size. Certain tadpoles, for example, can grow to metamorphosis on single-celled phytoplankton and bacteria < 10 μm in diameter. Since continuous suction feeders are often either within (e.g., ammocoetes) or on (e.g., tadpoles, flamingos) the bottom when they feed, they can resuspend bottom material when feeding (Seale and Wassersug 1979; Chapman 1905) and, depending on the species, detritus may form an important part of their diet.

There appear to be two groups of continuous suction feeders. Mem-

TABLE 2.3 Intermittent ram feeders

Family, species	Body length	Prey[1]	Reference
Balaenopteridae			All data from Tomilin 1967; Nemoto 1970; Ridgway and Harrison 1985; or cited therein
Balaenoptera musculus (blue whale)	22–27 m	Euphausiacean krill (2–7 cm)	
Balaenoptera physalus (fin whale)	18–24 m	Euphausiacean krill (3–6 cm), large swarming copepods, schooling fishes, squid	
Balaenoptera edeni (Bryde's whale)	13–15 m	Pelagic fishes (e.g., pilchard, mackerel, herring), euphausiacean krill, copepods	
Balaenoptera borealis[2] (sei whale)	12–20 m	Copepods principally; also amphipods, euphausiacean krill and small schooling fishes (e.g., anchovies) occasionally	
Balaenoptera acutorostrata (minke whale)	6–10 m	Schooling fishes, euphausiacean krill	
Megaptera novaeangliae (humpback whale)	12–14 m	Euphausiacean krill, schooling fishes (e.g., mackerel, herring, capelin); benthic organisms occasionally	

[1]Prey are given in approximate order of preference from Nemoto (1970).

[2]Of all of the balaenopterid whales, the sei consistently feeds on the smallest prey and can capture some food by continuous ram feeding at the surface as well as intermittent ram feeding (Nemoto 1970; Mitchell 1974; Gaskin 1976; Krushinskaya 1986). It is included in this table rather than the previous one on taxonomic grounds.

bers of the first group, ammocoetes and tadpoles, are small benthic or midwater forms for which mucus entrapment and ciliary transport are essential components of their suspension-feeding mechanism. They all have gill slits with internal entrapment surfaces that are part of their gill system. For these organisms, feeding and respiration are tightly linked (Feder et al. 1984; Wassersug and Murphy 1987). The second group, containing suspension-feeding birds, is made up of air breathers that are restricted to feeding in either shallow water or at the water's surface. They

TABLE 2.4 Continuous suction feeders

Family, genera	Body length	Prey	Reference
Petromyzonidae, Geotriidae and Mordaciidae ammocoetes (lamprey larvae)	10–20 cm	Diatoms, desmids, protozoa, rotifers, detritus	Hardisty and Potter 1971; Mallatt 1981, 1982; Youson 1981
Anuran Larvae (tadpoles of most families and genera)	< 1-≈10 cm	Algae, detritus	Wassersug 1975; Seale and Beckvar 1980; Seale 1980 (plus other references cited therein)
Anatidae (Anatine ducks) many species in genera such as: *Anas* (mallard, shovelers), *Stictonetta* (freckled duck), *Malacorhynchus* (pink-eared)	35–80 cm	A variety of phyto- and zooplankton, such as *Daphnia*, calanoid copepods, and other microcrustaceans; seeds of terrestrial and aquatic herbs and grasses. Particles as small as 0.2 mm and as large as 4.4 mm depending on the species.	Douthwaite 1977; Crome 1985; Kooloos et al. 1989 (plus other references cited therein)
Phoenicopteridae (Flamingos)			
Phoenicopterus sp. (greater flamingos)	125–145 cm	Assorted small invertebrates, including gastropods (e.g., *Cerithium*), crustacea, insects (e.g., chironomid larvae), seeds, some algae. Preferred food between 1–10 mm.	Jenkin 1957; Hurlbert et al. 1986
Phoeniconaias minor (lesser flamingo)	80–90 cm	Primarily blue-green algae, diatoms, some small invertebrates. Preferred food between 0.02–0.1 mm.	Jenkin 1957
Phoenicoparrus sp. (Andean flamingos)	≈150 cm	Similar to *Phoeniconaias*	Jenkin 1957

lack gill slits and have lamellae at the margins of their jaws that form the filters. For them, entrapment surfaces are anatomically independent of respiratory surfaces.

All of the continuous suction feeders have a reduced oral gape with sensory structures at the margin to assess the size and texture of particles

entering the mouth. They also all have ways of excluding particles above a certain size. Such adaptations are not necessary for continuous ram feeders because they feed in the open water where there is normally little abiotic material to clog their filters.

Intermittent Suction Feeders. Compared to continuous suction feeders, species in this category generate suction with aperiodic pulses. Teleost fishes are the only vertebrates clearly documented to feed in this manner (table 2.5), although the megamouth shark is thought to use this feeding mode (Compagno 1990). Drenner, O'Brien et al. (1982) referred to intermittent suction feeding in fishes as "pump filter feeding," but this term does not allow a distinction between continuous suction feeding and intermittent suction feeding.

The way water is transported into the mouth by intermittent suction feeders is similar to that used by the myriad of planktivorous fishes that visually locate, attack, and engulf individual prey items using suction (Drenner 1977). However, during suspension feeding, the predator does not usually alter its swimming speed or direction to focus attention on individual plankters (Johnson and Vinyard 1987; Gibson and Ezzi 1985; Drenner, O'Brien et al. 1982; Drenner 1977). In terms of the frequency, duration, and magnitude of mouth opening, intermittent suction feeding is intermediate between continuous ram feeding and suction feeding on individual prey.

Under various circumstances, fishes in this category may use a number of prey-capture techniques in addition to intermittent suction, including attacks on individual plankters and continuous ram feeding (e.g., Hoogenboezem et al. 1992; Batty et al. 1990; Gibson and Ezzi 1990; Ehlinger 1989; Drenner, Vinyard et al. 1982; Holanov and Tash 1978; Janssen 1976, 1978). The size of the predator, the size and density of the prey, and the ambient light level determine feeding behavior in such species (Crowder 1985). A predator with a gape that is large enough to engulf more than one prey at a time may use intermittent suction feeding when the prey are not dense enough or are too large to elicit continuous ram feeding (Gibson and Ezzi 1985; Janssen 1976). Janssen (1976) described three distinct feeding behaviors in the alewife that are dependent on the size of the fish. Small specimens are "particulate" feeders in that they visually select and engulf individual zooplankton, large fish are continuous ram feeders, and medium-sized fish use an intermittent suction-feeding technique that Janssen termed "gulping."

Morphological Patterns

Continuous Ram Feeders. ***Head Size and Shape.*** In continuous ram feeders, the head tends to be a very large portion of the body. Cranial dimen-

TABLE 2.5 Intermittent suction feeders

Family, species	Body length[1]	Prey[2]	Reference
Atherinidae			
Menidia audens[3] (Mississippi silverside)	5.6 cm SL	Z	Drenner and McComas 1980
Catostomidae			
Ictiobus cyprinellus (bigmouth buffalo)	24–83 cm TL	Z	Starostka and Applegate 1970
Cichlidae[4]			
Enterochromis nigripinnis	6.2–8.0 cm TL	P	Moriarty et al. 1973; Moriarty and Moriarty 1973
Oreochromis aureus[3] (blue tilapia)	7–25 cm SL (> 7 μm)	Z, P, D, B, S	Spataru and Zorn 1978; Drenner, Taylor et al. 1984; McDonald 1987; Vinyard et al. 1988
Oreochromis esculentus (tilapia)		P	Denny et al. 1978
Sarotherodon galilaeus[3] (Galilee Saint Peter's fish)	2.0–12.7 cm SL	Z, P (> 6–10 μm)	Drenner, Vinyard et al. 1982; Drenner, Hambright et al. 1987; Vinyard et al. 1988
Oreochromis mossambicus (tilapia)	16–36 cm TL	Z, P, D, B, S	Bowen 1982; Maitipe and De Silva 1985
Oreochromis niloticus[3] (tilapia)	15.7–22.1 cm TL	P, suspended bacteria	Moriarty et al. 1973; Moriarty and Moriarty 1973; Beveridge et al. 1989; Northcott et al. 1991
Clupeidae			
Alosa pseudoharengus[3] (alewife)	12–16 cm	Z	Janssen 1976, 1978
Clupea harengus[3] (herring)	15–16 cm TL	Z	Gibson and Ezzi 1985
Dorosoma cepedianum[3] (gizzard shad)	> 2.4 cm TL	Z, P, D, B (≥ 10 μm)	Bodola 1966; Cramer and Marzolf 1970; Drenner 1977; Drenner, Mummert et al. 1984; Drenner, O'Brien et al. 1982; Kutkuhn 1958; Pierce et al. 1981
Dorosoma petenense[3] (threadfin shad)	4–14 cm TL	Z, P, B	Holanov and Tash 1978; Miller 1967
Cyprinidae			
Abramis brama[3] (bream)	9.5–35.5 cm FL	Z	Lammens 1985
Carassius auratus (goldfish)	1.3–4.3 cm TL	P (≥ 10 μm)	Iwata 1976
Cyprinus carpio[3] (carp)	8–38 cm SL	Z, P, D, B, S, suspended bacteria (> 250 μm)	Sibbing 1988; Beveridge et al. 1991
Hypophthalmichthys molitrix (silver carp)	6 gm–adult	Z, P, D, suspended bacteria (8–100 μm)	Kuznetsov 1977; Cremer and Smitherman 1980; Burke et al. 1986
Hypophthalmichthys nobilis (bighead carp)	adult	Z, P, D (17–3,000 μm)	Cremer and Smitherman 1980; Jennings 1988
Notemigonus crysoleucas[3] (golden shiner)	5.8–11.0 cm SL	Z (360–1,100 μm)	Ehlinger 1989; Hall and Ehlinger 1989
Orthodon microlepidotus[3] (blackfish)	5.1–30.8 cm SL	Z, P, D, B, S (≥ 20 μm)	Byers and Vinyard 1990; Johnson and Vinyard 1987; Murphy 1950
Megachasmidae			
Megachasma pelagios (megamouth shark)	4.5 m	Z	Taylor et al. 1983; Compagno 1990
Mochokidae			
Brachysynodontis batensoda (scaleless catfish)	12.0–13.0 cm SL	Z, D (≥ 80 μm)	Gras et al. 1981
Mugilidae			
Mugil cephalus[3] (striped mullet)	> 3 cm SL	P, D, B, S	Odum 1970
Osteoglossidae			
Heterotis niloticus (abuli)	40–60 cm SL	P	d'Aubenton 1955
Rhiniodontidae			
Rhiniodon typus[3] (whale shark)	14 m	small fishes	Gudger 1941b
Salmonidae			
Coregonus artedii[3] (cisco)	13–26 cm TL	Z	Engel 1976; Janssen 1978
Coregonus hoyi[3] (bloater)	9–26 cm TL	Z	Janssen 1978

[1]TL = total length from tip of snout to end of caudal fin rays; SL = standard length from tip of snout to start of caudal fin rays; FL = fork length from tip of snout to start of fork in caudal fin rays.

[2]Z = zooplankton; P = phytoplankton; D = detritus; B = benthic organisms; S = sediment.

[3]Direct observations of feeding made in field or laboratory. Species not observed feeding are thought to be intermittent suction feeders, rather than continuous ram feeders, on the basis of morphological features.

[4]Additional cichlid species reviewed in Reinthal 1990a, b; and Bowen 1982.

sions in these fishes and whales clearly relate to buccal volume (and opercular volume, in the case of the fishes) and to area of the filtering structures. In the basking shark and whale shark, the head length from the snout tip to the fifth gill slit is 25 to 28% of the total body length (Uchida 1983; Matthews and Parker 1950). The cranial cavities of these sharks are generally much larger than their brains (Matthews and Parker 1950; Denison 1937), and the increased skull size is used to support massive filtering structures. Head lengths of the mackerels *Scomber* and *Rastrelliger,* measured from the snout to the posterior margin of the opercle, are 20 to 26.5% of the standard length (Matsui 1967; Kishinouye 1923). In these teleosts, however, the large head size is due to the large opercular bones rather than the neurocranium (Allis 1903).

In balaenid whales, the head can be up to a third the total length of the animal (Matthews 1978). Such a large cranium results principally from rostral expansion, with specialized processes of the maxillae extending caudally to brace the palate to the braincase. The elongated rostrum supports the baleen plates. This cranial morphology is part of the telescoping of the cetacean skull discussed in detail in Miller (1923), Kellogg (1928), and Howell (1930). However, the rostrum of the paddlefish is an elongated protrusion that does not support the filtering apparatus (Gregory 1933; Imms 1904). In the whale shark, the width of the neurocranium greatly exceeds the length, and the rostrum is extremely reduced (fig. 2.4a).

The basking shark and mysticete whales in general have smaller brains than their non–suspension-feeding relatives (Denison 1937; Krushinskaya 1986; Worthy and Hickie 1986). The orbits and eyes are also reduced, and the eyes are directed laterally, as they are in most suspension-feeding vertebrates. In these species, vision is not an important factor in prey selection and capture. However, the anchovy *Engraulis* (fig. 2.4b) and the mackerels have large orbits, occupying as much as one half the length of the skull in the Atlantic mackerel. Anchovies and mackerels are rapid swimmers that are reported to switch from ram feeding to feeding on individual prey particles, depending on prey size, density, and location (Runge et al. 1987; O'Connell and Zweifel 1972; Loukashkin 1970; Hatanaka et al. 1957; Rao and Rao 1957).

Chapman (1944a) reported that the bones of the palatine and hyoid arches in the anchovy *Anchoa compressa* tend to be large and heavily ossified. He suggested that this strengthening was related to the feeding behavior of anchovies, in which the gill covers and associated structures flare at an angle of 30 to 45° from the vertical. The opercular bones themselves are thin and without strengthening ridges (Chapman 1944a). From their experiments on sunfish, Lauder and Lanyon (1980) determined that opercular bone strain results from the rapid reduction of pressure in the opercular cavity occurring during suction feeding. Two prominent orthogonal

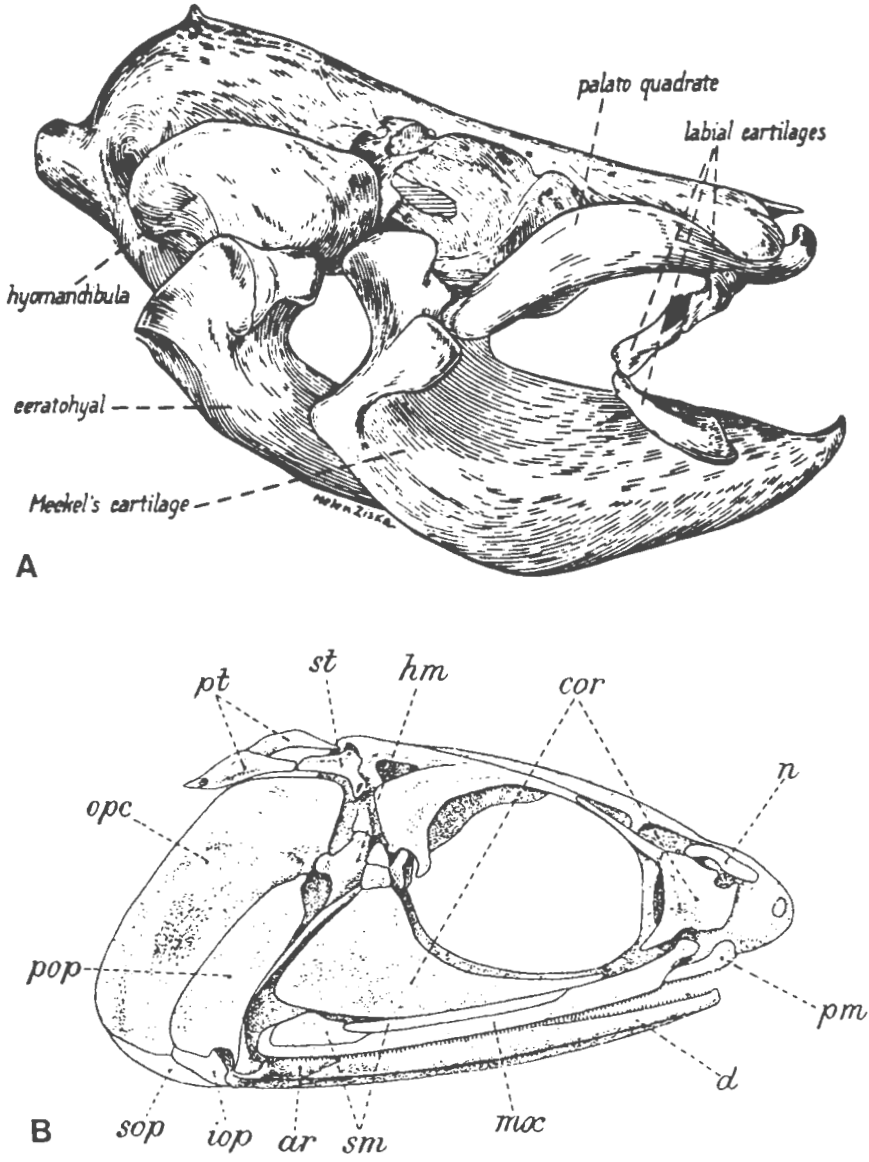

Fig. 2.4. A. Lateral view of skull in the whale shark, *Rhiniodon typus,* a continuous ram feeder and intermittent suction feeder. (From Denison 1937). B. Lateral view of skull in the anchovy, *Engraulis,* a continuous ram feeder. Abbreviations: ar, articular; cor, circumorbital bones; d, dentary; hm, hyomandibular, iop, interopercular; mx, maxilla; n, nasal; opc, opercular; pm, premaxilla; pop, preopercular, pt, post-temporal; sm, surmaxilla; sop, subopercular; st, supratemporal. (From Ridewood 1904)

bony struts on the medial opercular surface appear to resist the medial deformation caused by the generation of negative pressure. Lauder and Lanyon (1980) suggested that this thickening of the operculum is a functional correlate of an inertial suction strategy of prey capture. Consistent with this hypothesis, the anchovy feeds on plankton primarily by utilizing forward body velocity and has not evolved bony reinforcements on the operculum.

All mysticete whales have a large, anteriorly sloping occipital shield compared to odontocetes, although this feature is not as extreme in balaenids as it is in balaenopterids (Miller 1923; Howell 1930). The occipital expansion increases the area for the attachment of epaxial muscles, which may help to dorsiflex the head, but more probably contract isometrically to resist the downward torque on the head when the mouth is open. The problem of torque is partially reduced in balaenid whales because of the enormous arching of their skulls, which brings the open mouth in line with the long axis of the vertebral column. Furthermore, the balaenid whales have the shortest cervical region of any mammal (2.4% of body length in *Eubalaena;* Howell 1930). The cervical vertebrae are fused, greatly limiting any movement of the head on the body. Continuous ram-feeding fishes may have similar adaptations to stabilize the head on the body when the mouth is open. In the mackerel *Scomber,* anterior extensions of the epaxial muscles are located in two deep longitudinal grooves that begin near the lateral edge of the skull, posterior to the middle of the orbit, and widen posteriorly to occupy most of the dorsal surface of the skull (Allis 1903).

Oral Size and Shape. In continuous ram feeders, the mouth aperture is in a plane perpendicular to the direction of forward movement (e.g., mackerels, Matsui 1967; clupeids, Harder 1958). The independent evolution of continuous ram feeding in three families of elasmobranchs (Cetorhinidae, Mobulidae, and Rhiniodontidae) has, in each case, shifted the mouth from the ventral position found in other extant sharks back to its presumed ancestral position at the front of the snout (Moss 1981).

The oral orifice of continuous ram feeders tends to have a very large cross-sectional area. For a basking shark with a total length of approximately 7 m, the area of the open mouth was calculated by Matthews and Parker (1950) to be at least 0.5 m^2. At a swimming speed of about 3.7 km/hr while feeding (Matthews and Parker 1950), the volume of water filtered must be at least 1,850 m^3/hr.

In a whale shark 9.6 m long, the width of the slightly opened mouth was 1.1 m (Gudger 1941a). The tremendous transverse enlargement of the mouth in this species results from the laterally directed suspensorium (Denison 1937). The hyomandibula is a massive cartilage that projects almost directly laterad from the cranium. A groove and two flanges on the

hyomandibula articulate with the otic region of the cranium. These flanges restrict antero-posterior movement of the hyomandibula, but dorso-ventral movement is free except for the dorsal limit of the opisthotic process of the cranium. The levator hyomandibuli is a large, powerful muscle (Denison 1937).

Balaenid whales have an anterior gap between their left and right baleen rows, through which water flows into the mouth when the jaws are depressed. Although the jaws do not open very far during ram feeding in the right whale, Nemoto (1970) still estimated a cross-sectional area of 8.9 m^2 for the oral orifice. The oral cavity in balaenids is largely filled with the muscular tongue (see for example figures in True 1904), which can deflect water laterally toward the baleen, but limits buccal volume. Still, because of the high arch of the skull, when the tongue is depressed the buccal volume can be enormous in these whales. Howell (1930) estimated that the buccal volume exceeds the combined volume of the thoracic and abdominal cavities. While this is probably high, there is no question that the buccal volume exceeds the volume of the rib cage.

Upper and Lower Jaws. Continuous ram feeders are characterized by dentition that is either reduced or absent (e.g., Taylor et al. 1983; Moss 1981; Monod 1961; Moona 1959; Chapman 1944b; Gudger 1935; Kishinouye 1923; Radcliffe 1914; Imms 1904; Kellogg 1928). Baleen whales have teeth only as fetuses. While other sharks in the order Lamniformes have fewer than 60 rows of teeth in each jaw, the basking shark has more than 200 rows of small teeth (Taylor et al. 1983). Each jaw of a large whale shark (> 9 m) may have 3,000 to 3,500 backwardly pointed teeth about one eighth of an inch long (Gudger 1941a). Within the teleost group Clupeomorpha, there is a repeated evolutionary trend toward loss of teeth (Nelson 1973).

The bones of the upper and lower jaws may be elongated and broadened (Moss 1981) but usually are not thickened or heavily ossified in continuous ram feeders (Whitehead 1985; Taylor et al. 1983; Moss 1981; Chapman 1944a; Kishinouye 1923). This is consistent with their function as regulators of water flow into the oral cavity rather than as active elements of prey capture.

The maxillae and intermaxillary elements of mysticete whales are relatively narrow. The rostrum of mysticetes is therefore narrow, particularly in the right and bowhead whales. The lower jaws, however, bow outward, allowing them to corral the baleen plates, which hang down from above, when the jaws are closed. In lateral view, the dentary of these balaenid whales is straight, thin, and lacks a coronoid process. There is little room for the attachment of adductor muscles and, as expected, adductor musculature is reduced compared to that of the odontoceti or even the Balaen-

opteridae. Because the rostrum arches upward in balaenid whales but the mandible does not, the sides of the mouth would remain open with baleen plates exposed even when the jaws were closed, except for the presence of a tall (approaching 2 m), tough, and resilient lower lip that rises from the lower jaw to cover the sides of the mouth (Slijper 1979; Matthews 1978).

The palatoquadrate cartilage of the whale shark is slender and atrophied compared to Meckel's cartilage, which is wide but extremely thin (White 1930). In a whale shark 9.6 m long, the palatoquadrate articulated with Meckel's cartilage at two points, at the knob that formed its proximal end and at a concave facet approximately 10 cm antero-mesiad. Although Denison (1937) suggested that this type of double articulation indicates that the mouth is kept open habitually, Moss (1972) reported a similar articulation in carcharhinid sharks that consume a variety of larger prey.

Intermittent Ram Feeders. The rorqual whales that constitute the intermittent ram feeders are characterized by longitudinal grooves in their gular region that can extend back to the umbilicus. The grooves allow the skin to expand when water is taken into the mouth (Tomilin 1967; Brodie 1977). That expansion can be astonishing (fig. 2.3): the lower jaw rotates back some 45° (P. Brodie, personal communication), and possibly as much as 90° (Gaskin 1976). According to one estimate, a blue whale can, in a matter of seconds, increase its volume by more than 600% (Storro-Patterson 1981). A more common and realistic estimate is that a full-grown blue whale engulfs 60 m^3 or 60 metric tons of water, approximately 50% of its body volume (Orton and Brodie 1987; Pivorunas 1979; Sears 1983).

Essential for this process is the large size and high inertia of the swimming whale. Orton and Brodie (1987) modeled the pressure head on a fin whale as it opened its mouth. Using data from their stress/strain analysis of soft tissue in the throat region of fin whales, they concluded that "there is enough force generated by static pressure at a velocity less than 3.0 m/s to completely expand the buccal cavity." Thus, no buccopharyngeal pump is necessary and cranial specializations for intermittent ram feeding are largely of the soft tissue that must expand to contain the water.

The tongue of the adult blue whale has been described as weighing as much as an elephant, i.e., 2.5% of the whale's total weight (Slijper 1962). Whereas this value may have been inflated by the inclusion of sublingual tissue in the estimate (A. Pivorunas, personal communication), there is no question that mysticete tongues in general constitute a much larger proportion of total body mass than the tongues of non–suspension-feeding mammals. The balaenopterid tongue differs from that of balaenid whales in that it is made predominantly of spongy connective tissue, rather than

muscle, and lies as a flaccid, immobile mass on the buccal floor (Lambertsen 1983). The tongue has a midline cleft and, under the impetus of the inflowing water, inverts completely into an intermuscular fascial cleft below it (the *cavum vertrale* of Schulte 1916), partially lining the water-filled buccal pouch (Pivorunas 1979).

A musculoskeletal feature associated with this first stage, the filling stage, of intermittent ram feeding is the large area for attachment of the semispinalis capitis on the occipital shield above the occiput. This muscle can contract in concert with the remainder of the erector spinae musculature, to resist forward pitch when the mouth opens. The horizontal fluke of the whale may be brought into play to further control forward pitch or even to extend the head and back. Side-to-side rolling motions and pitching over onto the back are common body motions observed during feeding in rorqual whales (e.g., Watkins and Schevill 1979; Storro-Patterson 1981; Sears 1983).

The jaws must close quickly around the mouthful of water to prevent prey from swimming out. This is accomplished by specializations of the mandibular joints and adductor musculature. Mysticete mandibles are not fused at the symphysis but form a loose, kinetic joint (Brodie 1977). The jaw symphysis resembles an intervertebral disc with a nucleus pulposus and anulus fibrosus (Lillie 1915). The articular heads of the mandibles are balls that fit into open sockets, rather than hinge joints. Thus the mandibles are free to rotate around their long axes as well as to swing up, down, left, and right. The right whale has a synovial temporomandibular joint, but in some, if not all, rorquals, that joint is replaced partially or fully by a fibrocartilage mass (Perrin 1870; Beauregard 1882; van Beneden 1882). As the jaw opens and the buccal floor stretches, the dorsal edge of each mandible rolls laterally (Lillie 1915; Pivorunas 1977). This has the effect of increasing the space between the rami by as much as three quarters of a meter in a 12 m humpback whale.

Two mechanisms assist in returning the jaw to its normal position. First, the fibrous tissue in the temporomandibular and intermandibular joints stores energy as elastic strain when the jaws are forced open by the oncoming water. Thus, in one sense, the jaws are spring-loaded and designed to snap shut automatically. Second, balaenopterid whales retain a coronoid process and have extensive temporal fossae for the attachment of large external adductor muscles of the mandible. The masseter and temporalis are not balanced by large internal adductors; rather the pterygoidei, and the pterygoid fossae from which they would originate, are greatly reduced (Carte and Macalister 1868; DeLage 1886; Schulte 1916). Therefore, a net torque is applied to the dentary along its long axis when the adductors contract. The result is not only that the jaws close but that the

upper edge of the mandible rolls inward to press against the lateral margins of the baleen plates (Lillie 1915). This helps to buttress the baleen, keeping it from being pushed outward as the water flows out of the buccal cavity.

It is important that the lower jaws encircle the baleen plates as the mouth is closed, so that the baleen remains medial to the jaws despite the outward pressure of water extruded from the mouth. The rolling movements of the jaws just described may assist in this action. The fact that each lower jaw can roll somewhat independently inward and outward between the temporomandibular and the symphysis should help the mandibles clear the baleen during closure. Gross body movements, which alter the pressure of the water against the jaw (Brodie 1977) and swing the jaws from side to side, may also aid in repositioning the mandible.

Continuous Suction Feeders. ***Ammocoetes.*** Ammocoetes feed within burrows and are the most sessile of all vertebrate suspension feeders. Mallatt (1982) viewed them as specialized for pumping water at a slower rate than other suspension feeders but able to handle very concentrated suspensions. Forward-directed oral cirri surround the entrance of the mouth and act as a screen to prevent large particles from entering. In *Petromyzon marinus* the cirri exclude particles larger than 340 μm (Youson 1981).

Ammocoetes propel water into their mouths by rhythmic contractions of the pharyngeal wall and by oscillations of the velum, a pair of muscular flaps that lie between the oral orifice and the pharynx. Contraction of the pharynx is achieved by circular constrictors acting on a cartilaginous lattice, the branchial skeleton (Hardisty 1981). Elastic rebound in the branchial basket reduces intrapharyngeal pressure and draws water into the mouth (fig. 2.5). Mallatt (1981) considered the parabranchial chambers of ammocoetes to be similar to those of Chondrichthyes and felt that the ventilatory mechanism was fundamentally the same between fishes that use a dual ventilatory pump (the "force-suction pump" of Hughes 1960a, b) and ammocoetes. However, when lamprey larvae are undisturbed, the amplitude of pharyngeal contractions approaches zero (Rovainen and Schieber 1975). In that situation, velar movements continue as the sole pumping mechanism.

The velar flap on each side has an internal mucocartilage skeletal bar and protracting/retracting muscles. The medial edges of the velar flaps approximate as they move backward and separate as they move forward; thus they can fulfill both a piston and valvular function (Mallatt 1981). Flaps across the external branchiopores also act as branchial valves, opening and closing with each contraction of the branchial baskets (fig. 2.5). They act passively such that there is some reflux of water into the pharynx through the branchiopores as the pharynx begins to expand.

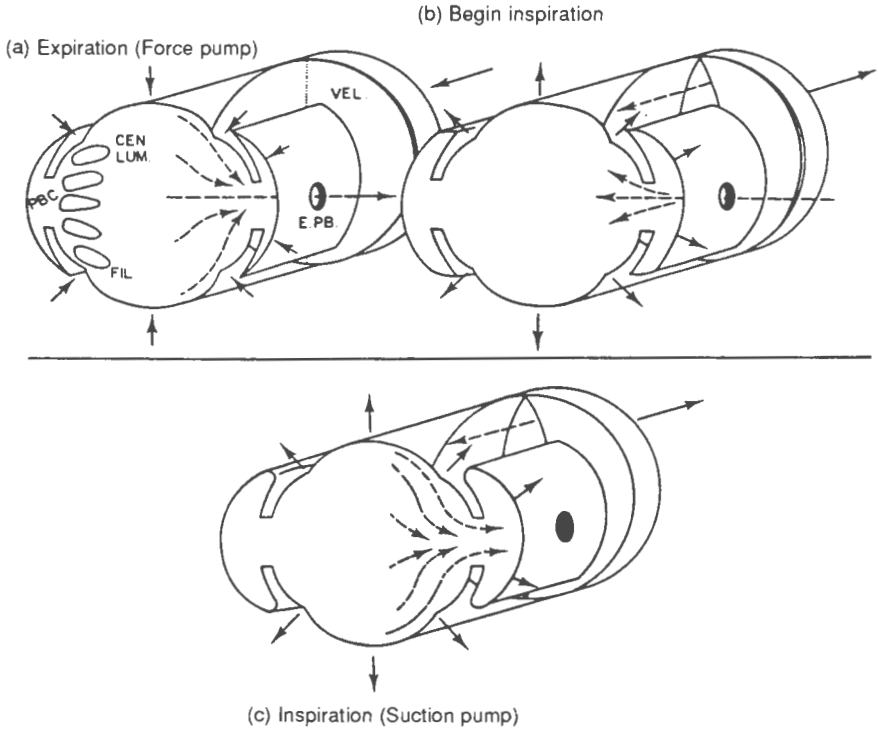

Fig. 2.5. Model of water flow within the ventilating ammocoete pharynx. The pharynx is viewed from behind, anterior is to the right. Only one of seven pharyngeal segments is represented; central lumen and gill pouch are treated as a single unit. Water flow directions are indicated by dashed arrows, while movements of pharyngeal structures are indicated by solid arrows. Positions of the gill filaments are indicated in the left half of the top left diagram. During expiration (top left), the pharynx contracts and the velum moves posteriorly, forcing water over gill filaments and out the external branchiopore. At the onset of inspiration (top right), the velum moves forward and the pharynx begins to expand. Enlargement of the central lumen and parabranchial chambers draws some water in through the branchiopore under the still-closing branchial valve (black), and flow over the gills is medial. Later in inspiration (bottom center), the gill pores are entirely shut, and the expanding parabranchial chambers draw water laterally again across the filaments. Steps (a) and (c) comprise the force and suction pumps respectively of the classic piscine ventilatory mechanism (Hughes 1960a, b). Occasionally during ventilation, no pharyngeal movements occur. When that is the case, flow patterns of steps (a) and (b) do not differ from the above, but in step (c) no lateral flow across the gill occurs. CEN. LUM. = central lumen of pharynx, E.PB. = external branchiopore, FIL. = gill filament, PB.C. = parabranchial chamber, VEL. = velum. (From Mallatt 1981, courtesy of the Zoological Society of London)

Tadpoles. Tadpoles feed from a stationary position either midwater (e.g., most pipids and microhylids) or along the substrate (most other tadpoles). Facultative suspension-feeding tadpoles (Seale 1982) are benthic grazers that have external keratinized beaks and denticles, which they use to reduce detritus, macrophytes, and periphytic films to a size small enough to be brought into the mouth in suspension (Duellman and Trueb 1985; Altig and Johnston 1986). Obligate suspension feeders that live in midwater lack keratinized mouthparts. In both cases, the water transport system and particle entrapment mechanisms used are essentially the same (Seale and Wassersug 1979; Wassersug 1980).

The buccal pumping mechanism of anuran larvae has been investigated by a number of workers in recent decades. The most comprehensive studies are those of DeJongh (1968), Kenny (1969a), and Gradwell (1968, 1971, 1972a, b, 1975); older studies are cited therein. The essential feature of the pump is a medially expanded ceratohyal plate on each side that articulates laterally with the palatoquadrate. The ceratohyal plates serve as the piston for the buccal pump (fig. 2.6). Muscles that run from the lateral arm of the ceratohyal to the muscular process of the palatoquadrate, primarily the orbitohyoideus (Satel and Wassersug 1981; Wassersug and Pyburn 1987), cause the central portion of the ceratohyal to drop when they contract. A transverse sling of muscle below the ceratohyal that also attaches to the lateral arms of the ceratohyals, the interhyoideus, elevates the buccal floor when it contracts. Gradwell (1972b) has pointed out that the musculature of the ceratobranchials behind the ceratohyals may constrict and elevate the branchial baskets, thus acting as a secondary pump. It is not known, however, whether the slight movements of the branchial baskets observed when the tadpole buccal floor oscillates during normal feeding and breathing are passive or active.

Severtzov (1969) contrasted the horizontal expansion and ventral/dorsal movement of the tadpole ceratohyal with the fore-aft movement of the urodele larva's gill arches. An important aspect of the plane of movement of the tadpole buccal pump is the extreme elongation and horizontal orientation of the palatoquadrates, with which the ceratohyals articulate (Wassersug and Hoff 1982). This orientation of the jaw suspension distinguishes tadpoles from all other vertebrates, including adult frogs. In suspension-feeding tadpoles, this unusual design for the jaw suspension is associated with short Meckel's cartilages and a small oral orifice. At metamorphosis, the tadpole branchial skeleton completely rebuilds: the palatoquadrate shortens and takes up a more vertical orientation, Meckel's cartilage elongates, and the tadpole buccal pump disappears. With that, the anuran goes from being a small-mouthed microphagous tadpole to a big-mouthed macrophagous frog.

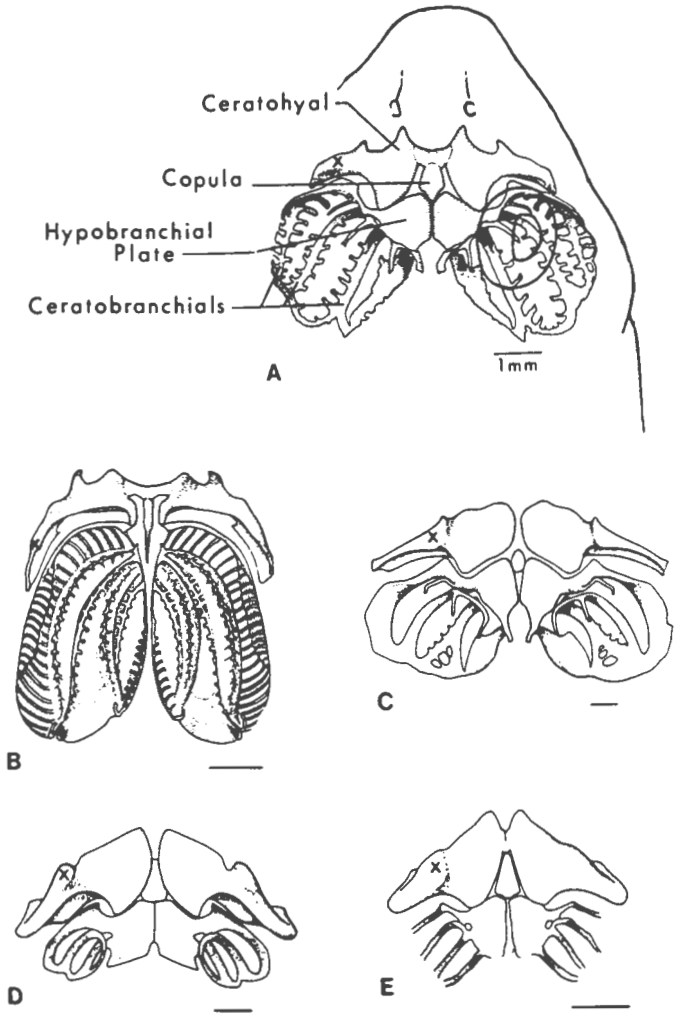

Fig. 2.6. Branchial skeletons in dorsal view for tadpoles from five species, selected to illustrate basic structures and diversity. Anterior is toward the top of the page. The "x" on each drawing indicates the point of articulation of the ceratohyal with the palatoquadrate bar on one side (not shown). The ceratobranchials form the branchial baskets and the gill filters arise from the ceratobranchials. All elements are cartilage. A. *Rana pipiens,* with major structures labeled. This larva is a dietary generalist, feeding on a coarse suspension of particles generated through the action of its keratinized beaks and denticles. B. *Gastrophryne carolinensis,* an obligate suspension feeder. C. *Heleophryne natalensis,* a benthic tadpole adapted to fast flowing water. This larva has a large suctorial mouth and grazes on periphyton. D. *Anotheca spinosa,* an arboreal, macrophagous, carnivorous larva. E. *Hyla microcephala,* a pond tadpole that ingests large filamentous plant fragments and zooplankton. (From Wassersug and Hoff 1979)

There is a spectrum of particle sizes on which tadpoles of different species preferentially feed, and these preferences can be correlated with differences in the buccal pump design among tadpoles (Wassersug and Hoff 1979). At one extreme, there are midwater, obligatorily microphagous larvae (fig. 2.6a, b). They tend to have a ceratohyal with a small medial surface area and short lateral lever arm (poor mechanical advantage). Wassersug and Hoff demonstrated that this was a design that achieved a large buccal volume by depressing a small buccal floor area a relatively long distance, i.e., "a small bore, long stroke" design. This design does not favor sucking in resistant prey, but by having a small buccal floor area these tadpoles have more cranial space left for gill filters. They have, indeed, the most extensive gill filters of any tadpoles. At the other extreme are the larvae of a few species that have evolved into obligatorily macrophagous forms (fig. 2.6c, d, e). These tadpoles have a longer lateral lever arm on their ceratohyal (high mechanical advantage) and a larger buccal floor area. They have a powerful buccal pump (associated with disproportionately large buccal floor depressor musculature; Satel and Wassersug 1981), but one that is not depressed very far, i.e., "a large bore, short stroke" design. They can pull into their mouths large and resistant prey, but space for their large buccal pump is at the expense of their gill filters. These tadpoles have little (e.g., *Anotheca,* Hylidae) or no (e.g., *Hymenochirus,* Pipidae) gill filters and the ceratobranchials—the skeletal elements that support the gill filters—are reduced in length and occasionally even in number (Wassersug et al. 1981).

There are several valves in tadpoles that control one-way flow. The mouth opens as the buccal floor is depressed and closes just before the buccal floor is elevated (e.g., DeJongh 1968; Kenny 1969a). The internal nares have simple, passive, valvular flaps that close as buccal pressure rises (Wassersug 1980; Wassersug and Heyer 1988). There is an elegant, internal valve mechanism built around a nonmuscular flap of tissue, called the ventral velum (not homologous with the velum in ammocoetes). The ventral velum of tadpoles extends caudally from the ceratohyal over the branchial baskets in most tadpoles (fig. 2.7). It has a cartilaginous skeleton made of spicules projecting rearward from the hypobranchial plate. Because the hypobranchial plate is overlapped rostrally by the ceratohyal, when the ceratohyal is depressed, the front of the hypobranchial plate is depressed also. The caudal part of the hypobranchial plate, however, moves upward because the plate rotates around a transverse axis (DeJongh 1968). This pushes the posterior free edge of the ventral velum against the buccal roof and seals the buccal cavity to the front from the pharyngeal cavity behind. As the buccal floor is elevated and buccal pressure rises, the ventral velum comes down and water is injected into the branchial baskets

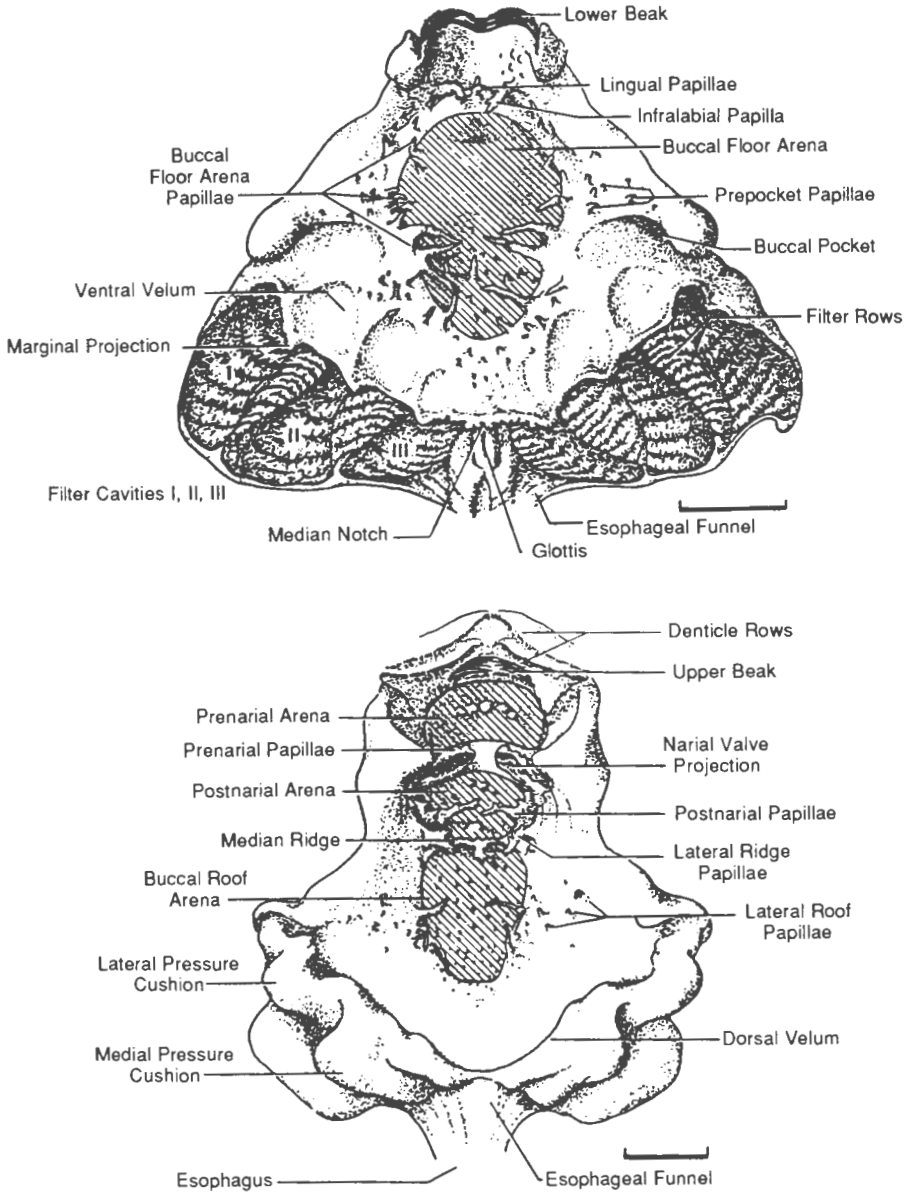

Fig. 2.7. The floor (above) and the roof (below) of a *Hyla femoralis* larva with major morphological features labeled. The complex surface features sense, sort, and direct particulate matter carried into the mouth of the tadpole in water currents. The scale line equals 1 mm. (From Wassersug 1980)

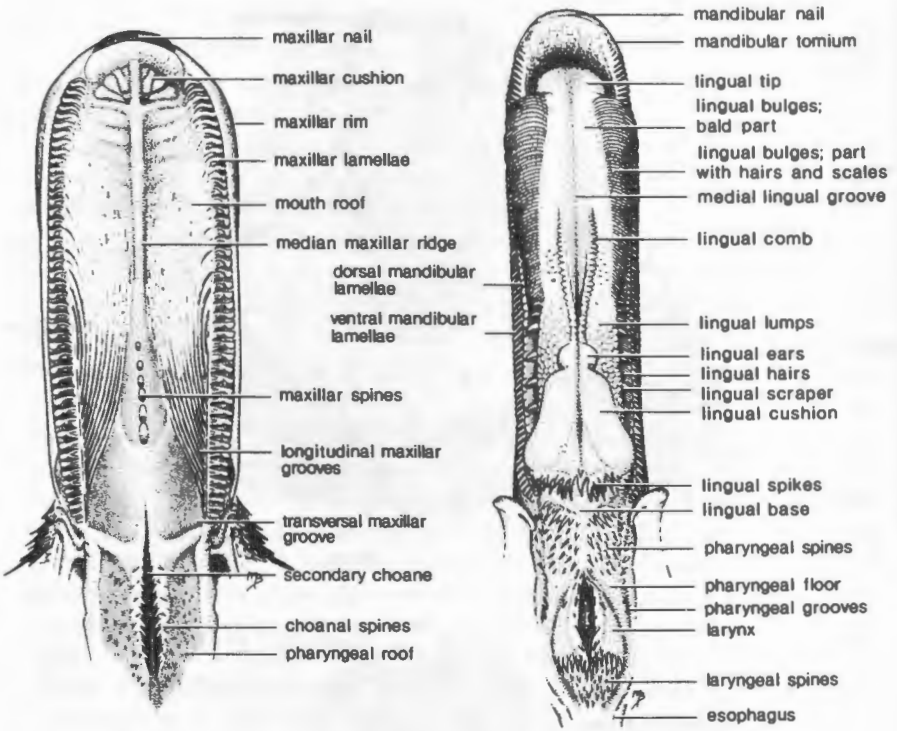

Fig. 2.8. Epidermal structures of the maxilla and pharynx of the mallard, *Anas platyrhynchos*, in a ventral view (left) and of the mandibula, tongue, and pharynx in a dorsal view (right). (Adapted by G. A. Zweers from Kooloos 1986 and Kooloos et al. 1989)

(Gradwell and Pasztor 1968). Another transverse flap, called the dorsal velum, descends from the buccal roof behind the ventral velum and helps to direct the jet of water down toward the gill filters and the mucus entrapment surfaces.

Tadpoles in the genus *Xenopus* (Pipidae) lack a valvular ventral velum. In those species, flaps on the body wall cover the opercular chamber and open and close with each stroke of the buccal pump; they serve as passive valves like the flaps over the branchiopores in ammocoetes.

Ducks and Flamingos. Suspension-feeding ducks (table 2.4) have relatively long and broad bills (Avilova 1978). The larger, upper bill in these birds bows upward in cross section to canopy completely the lower bill and the tongue when the mouth is closed. A row of keratinized lamellae lines the lateral margins of both beaks (fig. 2.8). When the mouth is slightly ajar,

the lamellae on the upper jaw oppose the lamellae on the lower jaw and may act as sieves for straining particles from the water.

Unlike the comparatively amorphous tongue of suspension-feeding mammals, tongues of suspension-feeding birds are morphologically complex (see fig. 2.8 and figures in Crome 1985; Kooloos 1986; Kooloos et al. 1989). In anatines the tongue is broad, with two large, swollen areas that act as pistons to draw water into the mouth (Zweers et al. 1977; Kooloos and Zweers 1991). The more anterior area, the region of the lingual bulges, is pressed against the roof of the mouth as the tongue is drawn backward, but moves away from the roof when that portion of the tongue advances. Thus the bulges act as both a piston and a valve. The more posterior swelling, the lingual cushion, is bounded laterally by projections called lingual scrapers that ride past the lamellae. The cushion terminates posteriorly in a field of spikes. As the cushion oscillates back and forth, the scrapers remove food particles from the lamellae and draw ingested material posteriorly toward the esophagus. The spikes ultimately help to drive particles into the esophagus.

The tongue moves rapidly; in *Anas platyrhynchos* the tongue tip travels back and forth 11 mm in cycles that last 60–70 msec (Zweers et al. 1977). Cycle frequencies are only slightly lower in other species (Kooloos et al. 1989). The underlying musculoskeletal system that allows these complex lingual movements to take place so rapidly is described in detail in Zweers (1974).

With each cycle, the jaws open and close slightly (maximum and minimum gape during feeding in *A. platyrhynchos* equal 14 mm and 3 mm, respectively; Zweers et al. 1977). This is accomplished as much by elevation of the maxillae, which rotate through $\leq 13°$ with each cycle, as by depression of the mandible. The fast oscillations of the jaws help suck water into the mouth and give it momentum. Since these beak movements take place against the resistance of water and often mud, they require some force. Anatine ducks are characterized by a large retroarticular process on the mandible for the insertion of a large depressor muscle complex. The jaw adductors, specifically the vertically oriented pterygoid muscles, are equally large. Heavy jaw protractor muscles arise from a large lateral extension of the lacrymal bone. The lacrymo-mandibular and occipitomandibular ligaments, which help control jaw kinetics, are also very large, as are, of course, the surfaces from which they originate.

The jaw and tongue movements together bring water into the front of the mouth as a thin sheet. Water is then expelled from the mouth along the posterior 70% to 95% of the rim (Kooloos et al. 1989). It takes from 2 to 7 cycles for food particles to travel from outside the mouth, past the lingual bulges, and onto the collecting surfaces. It takes another 3 or 4 cycles for that ingested material to reach the esophagus.

One can contrast some of these features of ducks with those of the ultimate suspension-feeding birds, the flamingos. In flamingos, the tongue is a narrower, more cylindrical structure which lies in a bony trough formed within the deep lower jaws. Depending on the genus, the upper beak has either a deep or shallow median keel that descends toward the tongue and forms a cap over the lingual trough. Multiple rows of fine lamellae cover the interfacing regions of the upper and lower jaws (Jenkin 1957). The shape of the tongue and its tight confinement suggest that it functions as a simple piston, although the details of its movements have not been described. There are spines on the tongue posteriorly that may help to move food particles toward the esophagus, but the contact region for those spines with the lamellar fields on the beaks is far less than in the ducks.

In both flamingos and suspension-feeding ducks, the mouth opens and closes slightly with each tongue cycle. The mesokinetic skull of flamingos allows the upper jaw to be elevated when the lower one is depressed, but there are no quantitative data on how much rotation actually takes place for either jaw during a typical feeding cycle, as there is for ducks (Zweers et al. 1977; Kooloos 1986; Kooloos et al. 1989).

As in ducks, the feeding cycles are rapid; Jenkin (1957) reported four hyoidean/tongue cycles per second for *Phoenicopterus antiquorum,* whereas deJong and Zweers (1981) gave cycle lengths of 60 msec for the closely related *Phoenicopterus ruber.* According to Jenkin, in *Phoenicopterus* water is drawn in along the sides of the beaks and not just at the front. Lateral head movements are a common part of flamingo feeding and are thought to stir up water and bottom material, but may actually be part of the driving force propelling water through the beaks (deJong and Zweers 1981).

The small gape of all suspension-feeding birds helps exclude unwanted material from the mouth. Although it has not been rigorously documented, Jenkin (1957) inferred from the anatomy of the flamingo that the role of valves—crucial for assuring one-way flow—is achieved by the subtle movements of the jaws in relation to each other. By opening and closing the jaws, or possibly by lateral movements of the jaws, the spacing between lamellae can be greatly modified and the resistance to flow altered (Jenkin 1957). The jaw movements that are possible differ between ducks and flamingos. This is testified to by the quadrate-articular joint, which is a flat, open joint in the former and a ball and socket in the latter.

Both anatine and phoenicopterid birds share unusually long retroarticular processes for the attachment of jaw depressors. The beaks are narrower in flamingos than in ducks, so resistance from the surrounding water to jaw depression may be less; however, flamingos face the unique problem

of having to depress their lower jaws against gravity since they feed with their heads upside down.

Similarities between anatine and phoenicopterid feeding structures vary with the species compared. According to Crome (1985), the freckled duck *Stictonetta naevosa* "has bill features more characteristic of flamingos," than other ducks. Based on the features just outlined it is too simplistic to say, as did Olson and Feduccia (1980b, ii), that "the structure of the feeding apparatus of flamingos is . . . entirely different from that of the Anseriformes" (see "Discussion").

Intermittent Suction Feeders. A large number of species in the cichlid genera *Oreochromis* and *Sarotherodon* are planktivorous (Bowen 1982; Philippart and Ruwet 1982). While only a few of these species have been observed to use intermittent suction feeding (Gophen et al. 1983; Drenner, Vinyard et al. 1982), the presence of phytoplankton in the diets of other species indicates that they use a mode of suspension feeding. These species demonstrate remarkable trophic plasticity, feeding opportunistically on phytoplankton, benthic algae, aquatic macrophytes, detritus, zooplankton, and periphyton (Bowen 1982; Philippart and Ruwet 1982). Since the mode of suspension feeding that we refer to as intermittent suction feeding is very similar to suction feeding on individual prey items, it is not surprising that intermittent suction feeders do not appear to possess unique morphological features related to the transport of water into the mouth. Like continuous ram feeders, however, intermittent suction feeders tend to have reduced dentition (e.g., *Coregonus:* Dorofeyeva et al. 1980; Vladykov 1970; Norden 1961; *Dorosoma cepedianum:* Miller 1960) and, in the case of suspension-feeding sharks, reduced heterodonty (Compagno 1990).

Although there have been no observations of feeding in megamouth sharks (*Megachasma pelagios,* Megachasmidae), this species can generate suction to draw water into its mouth during respiration (Lavenberg 1991), and the consensus is that it feeds using suction (Compagno 1990; Lavenberg 1991). Taylor et al. (1983) noted a number of morphological features that distinguish *Megachasma* from the basking and whale sharks. While the basking shark has slightly protrusile jaws, megamouth can protrude its jaws forward to expand the oral orifice well in front of the snout. Taylor et al. (1983) suggested that the hyomandibulae and the jaws move downward, anteriorly, and laterally during protrusion. Megamouth's stout jaws, which are much longer than its cranium, contrast with the slender, weak jaws of continuous ram feeders. The enlarged jaws increase the diameter of the oral orifice, and the thick hyaline cartilage provides support. Relative to these huge jaws, the adductor mandibulae muscles are, as expected of suspension feeders, small and weak (Taylor et al. 1983).

Compagno (1990) also discussed important differences between the morphology of the continuous ram-feeding basking shark and that of megamouth. The basking shark has: (a) a small, flat tongue, (b) gill rakers that do not substantially impede water flow through the gill openings, and (c) enormously enlarged gill openings that extend onto the dorsal and ventral surfaces of the head. Megamouth, in contrast, has: (a) a large, thick, and broad tongue enclosing a greatly enlarged basihyoid cartilage, so that the tongue almost fills the oral cavity when the jaws are closed, (b) papillose gill rakers in dense clusters that screen the internal gill openings, and (c) moderately large gill openings that do not extend onto the dorsal or ventral surfaces of the head. In addition, Compagno (1990) diagrammed how the hyoid of megamouth can reverse direction, to lie with the hyomandibulae and ceratohyals anteroventral to their normal position. This movement of the hyoid would cause the tongue, basihyobranchial skeleton, and pharynx to be depressed ventrally, increasing the volume of water in the mouth. Compagno (1990) also noted a cranial morphological feature of megamouth that allows the upper jaws to tuck in under the cranium. The orbital processes of the palatoquadrates fit into a deep, prominent pit in the basal plate on each side of the ventral surface of the cranium. These characteristics of megamouth, in combination with its weak body musculature and soft fins, indicate that megamouth is an intermittent suction feeder (Compagno 1990).

Iridescent tissue has been reported on the upper jaw and palate of megamouth (Compagno 1990), and Taylor et al. (1983) suggested that the skin of the lower jaw and tongue might be luminescent. Although Diamond (1985) speculated on the possible advantages of luminescent tissue in attracting prey, Lavenberg (1991) stated that there was no evidence of luminescence in a live specimen observed in captivity.

TRANSPORT OF WATER PAST THE FEEDING STRUCTURES AND OUT OF THE MOUTH

Water transported into the mouth must be moved past the feeding structures and must exit the mouth. The forward motion of continuous ram feeders directs water posteriorly through the gape and past the feeding structures. Water exits laterally from the corners of the mouth in continuous ram-feeding whales or from the gill slits in fishes. Contraction of the buccal floor directs water into and through the baleen plates in intermittent ram-feeding whales. All continuous and intermittent suction feeders possess valves to preclude reflux of unprocessed water and use their lingual, pharyngeal, or buccal pumps to force the water through feeding structures.

Continuous Ram Feeders. Swimming fishes in general use the reduced pressure behind the operculum or gill slits, induced by the Bernoulli effect, to draw water out the gill slits (Vogel 1988). Continuous ram-feeding whales possibly make use of this phenomenon also, but this is strictly conjecture since no data are available on water pressures around the heads of freely swimming and feeding whales. The large tongue in balaenid whales directs water toward the baleen fringe. When right and bowhead whales are skimming at the surface, the arch of their rostra means that a pressure head of water can build up within their mouths between the tongue and baleen. Gravity may then help drive water through the baleen plates posteriorly.

Intermittent Ram Feeders. Next to moving their tails up and down, the expelling of water from their mouths by rorqual whales is the most massive, single action taken by any organism that has ever lived. Yet the process is largely unstudied. From the many descriptions of water rushing out of the mouths of these whales as they pitch over and roll on the ocean surface, there is no question that inertial and gravitational forces are of paramount importance. The major question concerning this action is how much of the compression of the buccal cavity is due to passive elastic rebound in the stretched tissues of the buccal floor as opposed to active muscle contraction. On the one hand, the older literature (e.g., Carte and Macalister 1868; Lillie 1915; Howell 1930) credits the musculature below the *cavum ventrale,* principally the mylohyoideus, with compressing the pouch. On the other hand, more recent studies of the histology and mechanical properties of the skin, blubber, and muscles all indicate that elastic recoil plays a major role in the return of the buccal floor to its resting position (Slijper 1962; Orton and Brodie 1987). Clearly both play a part (Lambertsen 1983).

Pivorunas (1977) demonstrated that the anterior portion of the pouch has a fibrocartilage skeleton formed as a bifid caudal extension of the mandibular symphysis. This structure gives some rigidity to the buccal floor and should help to elevate the floor, if it is strained during buccal expansion. Lambertsen (1983) suggested that the genioglossus pulls the tongue forward and upward near the end of expulsion. As the tongue comes up, its left and right lobes may be separately wedged between the baleen plates and the central keel of the rostrum. This would force the last remaining water out of the mouth.

Continuous Suction Feeders. For continuous suction-feeding forms with gill slits, the expulsion of water through the gill slits is the compressive half of the oscillating pump cycle (see above). This has been covered above in the section "Transport of Water into the Mouth." The role of the tongue

in driving water through the lamellae in ducks and flamingos also has been discussed. In ducks, the topography of the buccal roof and the dorsum of the tongue necessarily directs feeding currents laterally to the marginal lamellae as the tongue is retracted and the upper beak depressed during each feeding cycle. Ciné x-ray analyses have confirmed the exact relationship between tongue movements and the extrusion of water in *Anas platyrhynchos* (Zweers et al. 1977; Kooloos et al. 1989). In flamingos, the tongue and jaw movements are also presumed to control the outflow of water (cf. Jenkin 1957); however, there has been no functional morphological analysis comparable to the work on ducks to test Jenkin's conjectures on this topic.

Intermittent Suction Feeders. The alewife and two *Coregonus* species have been reported to open and close the mouth several times at a rate of approximately two to three times per second, then pause for about 0.5 sec with the mouth closed before resuming feeding (Janssen 1976, 1978). Drenner, O'Brien et al. (1982) described "swallowing" movements that interrupt the feeding of gizzard shad.

These fishes can simply use the upper and lower jaws as a valve to prevent water from exiting anteriorly, or may close a pair of membranous valves (oral valves) that are located in the anterior region of the buccal cavity. With the mouth or oral valves closed, water is drawn through the branchial apparatus to retain food particles. The functional morphology and hydrodynamics of this process during suspension feeding in intermittent suction feeders have not been investigated, but there is no reason to suspect that they differ from those of other suction-feeding fishes. To return the mouth cavity to its resting volume, other suction-feeding species contract the adductor musculature of the jaws and the suspensory apparatus (Liem 1980). Negative pressure is generated in the opercular cavity as the opercular apparatus is abducted, contributing to the posterior flow of water (Lauder 1983).

SEPARATION OF PARTICLES FROM THE WATER

The dimensions of the entrapping structures, and the density and velocity of the food particles, affect entrapment processes for suspension feeders. Retention of particles on filters with a pore size smaller than the particles themselves ("straining" or "sieving") is only one of several possible entrapment mechanisms. Other mechanisms that may operate separately or simultaneously with sieving in vertebrates include direct interception, inertial impaction, and electrostatic entrapment (Rubenstein and Koehl 1977).

LaBarbera (1984) suggested that, based on morphology, sieving is likely to be the major particle-capture mechanism in suspension-feeding fishes and baleen whales. Most suspension feeders capture particles with an efficiency dependent on the size and shape of the particles (Jørgensen 1966). That is consistent with, but does not confirm, sieving as an entrapment mechanism. A sieve with a uniform mesh size should theoretically retain 100% of the particles above a certain size threshold and 0% below that threshold (Rubenstein and Koehl 1977). Few data are available that test this prediction for the gill arch structures of continuous ram-feeding and intermittent suction-feeding fishes.

In teleost suspension feeders and in the paddlefish, each of the anterior four gill arches possesses one or two rows of gill rakers. Where two rows are present, the rakers of one row are directed anterolaterally and those of the other are directed medially or posteromedially. The fifth gill arch usually possesses one row of gill rakers directed anterolaterally. The rakers generally consist of a bony or cartilaginous core covered by epithelium that may contain cuticle-secreting cells, mucus cells, and taste buds (Friedland 1985; Sibbing and Uribe 1985). The number of gill rakers, their length, and the size of the spaces between them may increase with the age and length of the fish (e.g., MacNeill and Brandt 1990; Gibson 1988; Ciechomski 1967; Krefft 1958).

Mummert and Drenner (1986) developed a mechanical-sieve model of filtering efficiency for gizzard shad (an intermittent suction-feeding fish), based on the cumulative frequency distribution of the distances measured between gill rakers. The ingestion rates for different particle sizes, as determined in laboratory feeding experiments, were consistent with the predictions of the model (Mummert and Drenner 1986). Durbin and Durbin (1975) and Friedland et al. (1984) reported that the retention efficiency of menhaden (a continuous ram-feeding fish) increased in a continuous rather than step fashion with the size of the food particles, a result that is not consistent with a sieving mechanism involving a mesh with pores of a single size. They pointed out, however, that detritus and the flocculation of phytoplankton could lead to the retention of some particles smaller than the pore size of the sieve.

From x-ray films of bream (an intermittent suction-feeding fish) with platinum markers implanted in the gill arches, Hoogenboezem et al. (1990) concluded that the distance between adjacent arches was too wide and variable for zooplankters to be sieved by the passive interdigitation of gill rakers on adjacent arches. Additional x-ray films by Hoogenboezem et al. (1991) indicated that 25% of individual *Daphnia* with a 1-mm-diameter iron sphere glued to their carapaces were retained in the channels between adjacent gill rakers on each arch. They proposed a model in which lateral rakers of bream move actively into the channel between me-

dial rakers on the adjacent arch, forming a sieve with an adjustable mesh.

Particles that are small enough to pass between the elements of the filtering array are commonly retained by both invertebrate (Jørgensen 1966) and vertebrate suspension feeders, indicating that entrapment mechanisms other than sieving, such as direct interception and inertial impaction, are operative (Rubenstein and Koehl 1977). Inertial impaction as a particle encounter mechanism may come into play in animals that feed on relatively large, dense particles in high flow velocities (Rubenstein and Koehl 1977), including large fishes that are continuous ram feeders and whales in particular.

The mucus-secreting cells and the copious amounts of mucus found on the branchial elements of lamprey larvae, tadpoles, and some fish species (see, e.g., Hampl et al. 1983; White and Bruton 1983; Weisel 1973; Greenwood 1953) also point to capture mechanisms other than sieving. Food particles observed by Wassersug (1972) in mucus on the branchial food traps of tadpoles certainly could not have been collected by sieving, for those organs are not porous. The small size of tadpoles and ammocoetes means that they perform in a Reynolds number range where viscous forces are relatively significant and prohibit simple sieving (Wassersug 1989). Not surprisingly, none ram feed.

However, the presence of mucus on gill arches does not, of itself, preclude sieving as an entrapment mechanism. Whereas Friedland (1985) found mucus cells in the epithelium of the gill rakers and gill arches of menhaden, they were not present on the smallest units of the branchial apparatus, the branchiospinules on the rakers, which he considered the principal site of prey retention. Consequently, he concluded that sieving and not some form of mucus entrapment was the primary mechanism used in particle capture by the menhaden. Although mucus cells have been noted on the branchial apparatus of paddlefish (Weisel 1973), plankton smaller than the mean space measured between the gill rakers are ingested in a low proportion compared to their concentration in the environment (Rosen and Hales 1981). This led Rosen and Hales to suggest that mucus does not play an important role in paddlefish feeding.

Although gill arch structures have been assumed to be the site of particle retention in suspension-feeding fishes (e.g., Lammens 1985; Mummert and Drenner 1986; MacNeill and Brandt 1990; but see Harrison and Howes 1991), Sanderson et al. (1991) showed that water does not pass between the gill rakers of intermittent suction-feeding blackfish, and that the rakers do not serve as filters. Measurements of flow patterns and water velocities inside the oral cavity of blackfish, made with a fiberoptic endoscope and thermistor flow probe, found that the rakers act as barriers that direct particle-laden water to the mucus-covered roof of the oral cavity,

where particles are retained. This filtration mechanism cannot operate in clupeids and engraulids that lack an expansive, mucus-covered oral roof. Further study will determine whether particles are retained on the gill rakers in such species, and whether transport of particles toward the esophagus is mediated by water currents directed passively by the morphology of the branchial apparatus itself during continuous ram feeding.

The problem of determining the filtration mechanism(s) operating at any instant is particularly difficult in intermittent ram feeders and both types of suction feeders because of unsteady flow. These organisms create a current which accelerates from zero or near zero and then decelerates back to that starting point. As the velocity increases, inertial impaction of particles should increase (Rubenstein and Koehl 1977). But as an additional complexity, the filters are flexible in most vertebrate suspension feeders and their pore size is not fixed. Even in those filters that are relatively rigid, such as the gill rakers of fishes and the lamellae of birds, the porosity varies as the gill arches abduct and adduct (Lauder 1986) or the jaws open and close (Kooloos et al. 1989), respectively. Filters in forms such as tadpoles and whales are arranged in such a way that they are compressed by the pressure of the water passing through them, so that their porosity varies with pressure. The pressure, in turn, changes in response to the density of prey and other material on the filters. All of these dynamic factors change the flow at the microscopic level and make it difficult to establish what entrapment mechanism(s) is (are) effective at any instant during vertebrate suspension feeding.

Jørgensen (1983), who was primarily concerned with invertebrates, stated that the Reynolds numbers that apply to the feeding structures of suspension feeders are very low, $<< 1$. Shimeta and Jumars (1991) presented data indicating that the filter elements of some benthic invertebrate suspension feeders may operate at Reynolds numbers from 10 to 40. Compared to invertebrates, vertebrate suspension feeders typically encounter higher flow velocities and possess larger feeding structures ("more porous filters," Jørgensen 1970), and thus may operate at somewhat higher Reynolds numbers. One of the few attempts to calculate a Reynolds number at entrapment surfaces for a vertebrate suspension feeder is that of Friedland (1985) for menhaden. He reported a conservative figure of 2 to 3, using the smallest unit in the feeding apparatus (the branchiospinule) as the relevant length dimension. Vogel (1981) suggested that the baleen whales may be the only suspension feeders operating at a high Reynolds number.

The flow regime around entrapment surfaces for virtually all vertebrate suspension feeders is too poorly known to estimate Reynolds numbers realistically, let alone characterize the specific physical mechanisms involved in particle encounter. Quantitative laboratory investigations of

particle encounter and retention, combined with detailed histological, morphological, and fluid dynamic studies, will be needed to solve the problem.

Continuous Ram Feeders. The bones comprising the gill arches of continuous ram feeders may be laterally compressed (Kishinouye 1923); this is carried to an extreme in the paddlefish, which has ceratobranchial and epibranchial elements that are 15–20 mm wide in large specimens but only 1–2 mm thick in cross section (Grande and Bemis 1991). Water must pass between the rakers and the gill arches to reach the gill filaments and to enter the opercular cavity. The tips of the lateral rakers on the first arch abut the side of the oral cavity, and the lateral rakers of each successive arch extend anteriorly to the preceding arch. Continuous ram feeding fishes are characterized by extensive elaboration of the branchial apparatus, including spectacular increases in the length, number, and structural complexity of branchial elements. For example, the rakers of adult mackerel (*Rastrelliger*) are longer than the gill filaments and protrude forward past the corners of the gape when the mouth is open (Collette and Nauen 1983). In addition, denticles or branchiospinules are found on the surfaces of the rakers in many species (Bornbusch 1988; Gibson 1988; Friedland 1985; Collette and Nauen 1983).

There is little information on the extent to which the gill rakers are movable. In the paddlefish, Imms (1904) described muscle fibers on the outside of each raker that attach to the cartilage of the gill arch. He suggested that contraction of these muscle fibers would cause the rakers to be pulled outward at an angle of approximately 60° to the arch. Elastic fibers also attach the basal part of each raker to the arch. Imms (1904) hypothesized that these elastic fibers cause the rakers to lie against the arch when not in use. Matthews and Parker (1950) observed a similar system of muscle fibers and elastic fibers in the basking shark. In a model proposed by Kirchhoff (1958), the rakers of the herring spread and rotate as an elastic membrane at their bases is stretched during mouth opening. This appears to be the only report on the action of such an elastic membrane in teleosts.

In most clupeid and engraulid fishes, a number of gill arches meet in the dorsal midline, allowing the gill slits and rakers to extend further medially than usual. Rows of rakers replace the teeth that are typical in this location (Nelson 1967b). The mediopharyngobranchial is a cartilaginous element present in some of the clupeid fishes that have gill arches meeting in the dorsal midline. According to Nelson (1967b), this element bears rakers and has no apparent homologue in the gill arches of other vertebrates. He also noted that the dorsal attachment of gill arch elements pre-

vents expansion of the pharynx in that area, and tends to be absent in "predaceous" fishes.

In the anchovy *Anchoa,* the gill arches extend far anteroventrally (Chapman 1944a). The hypohyals articulate with the anterior end of the first basibranchial directly behind the symphysis of the lower jaw. There is no glossohyal and, in fact, there is not sufficient space for a tongue. The basibranchials of mackerels, which are very narrow and laterally compressed (Kishinouye 1923), also extend far anteriorly (Matsui 1967). Consequently, the glossohyal is very small, as is the smooth tongue (Kishinouye 1923).

Proliferation of gill rakers, loss of teeth, and development of accessory organs known as epibranchial organs has been a dominant evolutionary theme in clupeid fishes (Nelson 1967a). Epibranchial organs are a pair of diverticula arising from the posterior roof of the pharynx above the esophagus. Small food particles appear to be channeled by gill rakers into the epibranchial organs, where the food is thought to be coalesced into a bolus that is then swallowed. Epibranchial organs are associated with microphagy and have been identified in five of the teleost families listed in tables 2.2 and 2.5. They occur in five groups of "lower" teleosts: the Cypriniformes, Salmoniformes, Gonorynchiformes, Osteoglossiformes, and Clupeiformes (Bertmar et al. 1969). The similarities in the structure and development of the epibranchial organs in these groups led Bertmar et al. (1969) to conclude that these fishes probably derive from a common ancestral group such as pholidophorids. Nelson (1967a), however, attributed the similarities to convergence. Since the functional morphology of these organs relates to the transport of food to the esophagus and involves primarily soft tissue, their structure will not be discussed further.

As in the teleosts, the evolution of continuous ram feeding in elasmobranchs has involved tremendous increases in the length and number of gill rakers (Moss 1981). The comblike gill rakers of the basking shark are arranged in a single series on the edge of each arch, directed anteriorly, as is a strip of hooked denticles (Matthews and Parker 1950, Schnakenbeck 1955). A thick epithelial layer at the bases of the rakers was thought to be the source of much of the abundant mucus found in the stomach (Matthews and Parker 1950).

The whale shark differs from the other two suspension-feeding shark species in that the elements of the feeding apparatus are not restricted to the margins of the internal gill openings (Taylor et al. 1983). Lateral to the five gill arches is a series of parallel compressed plates that connect adjacent arches (Gudger 1941a). These plates have a cartilage core and support a medial spongy tissue grid that is covered with denticles. The mesh of this grid is too fine to permit rapid processing of large volumes of water. Taylor

et al. (1983) suggested that this dense screen, combined with a very long, broad, low pharynx and relatively small gill openings, allows the whale shark to generate suction as well as to suspension feed. Small food particles are collected on the feeding apparatus during continuous ram feeding, but intermittent suction feeding is reportedly used to capture fishes while the whale shark remains relatively stationary in a school of feeding fishes (Gudger 1941b). The basking shark does not appear to be capable of suction feeding (Taylor et al. 1983).

Rays in the family Mobulidae possess a series of gill rakers on anterior and posterior surfaces of each of the first four gill arches, and a series on the anterior face of the fifth arch (Bigelow and Schroeder 1953). Each raker is feathered with pinnately arranged protuberances (*Mobula;* MacGinitie 1947), or is composed of overlapping serrated lobes (*Manta;* Bigelow and Schroeder 1953).

The baleen of continuous ram-feeding whales is similar to that of intermittent ram-feeding whales (see below).

Intermittent Ram Feeders. Probably the best-known single feature of any vertebrate suspension feeder is whalebone. Because baleen is keratin of epidermal origin and not strictly part of the skull or skeleton of whales, it will not be discussed here in detail. There are a few general points though that pertain to the relative feeding capabilities and cranial designs of the different species.

The basic morphology of baleen plates, which across species number from 100 to 400 per side (Tomilin 1967; Pivorunas 1979), is summarized in Matthews (1978) and Slijper (1979). Efforts to quantify baleen morphology so that interspecific variation can be correlated with feeding ecology and diet were begun by Nemoto (1959), and extended by Williamson (1973), Pivorunas (1976), and Kawamura (1974, 1978, and other papers cited therein). A good review on this topic remains Nemoto (1970), who offered this concise distinction: "The shape of plates in right, Greenland and pygmy right whales is slender and elastic, and the fringes along the inner margin of the plates are very fine and numerous. The plates of Balaenopteridae whales (blue, fin, humpback, etc.) are short and tough, and have rather rough baleen fringes." The plates in the Greenland right whale (bowhead) may exceed 3 m in length, which is three times the length of the plates in any rorqual. The plates in the latter, however, may be twice as wide as those of the former. Nemoto (1970) estimated that the gross filter area of a 17 m right whale was 13.5 m^2 compared to only 4.6 m^2 for a 27 m blue whale.

Matthews (1978) cautioned that there is not a simple correlation between the texture of the baleen fringe and the diets of whales. This is because the fringe is flexible and its characteristics vary in life depending on

hydrodynamic factors such as flow direction and water pressure (Pivorunas 1976). Fringe morphology also varies along the length of the baleen plates and from one plate to another along the rostrum. Nevertheless, in light of what is currently known about the diets of whales (e.g., Nerini 1984; Würsig et al. 1985; Ridgway and Harrison 1985; Nelson and Johnson 1987) certain relationships stand out. First, continuous ram-feeding whales have relatively greater filter surface area overall (Kawamura 1974). Secondly, there is a gross relationship between the morphology of the baleen plates, their fringes, and the diets of whales. Those species least likely to take microplankton have stiffer baleen fringes. For example, gray whales, which feed on coarse, abrasive material ram-fed or sucked off the bottom (Ray and Schevill 1974; Nerini 1984; Nelson and Johnson 1987), have stiff, thick, short plates with a coarse, short fringe. At the other extreme, the sei whale, which is the rorqual that has been consistently reported to prefer copepods to larger prey (Kawamura 1974; Watkins and Schevill 1979; Gambell 1985), and even to hunt in a continuous ram-feeding fashion (Nemoto 1970; Mitchell 1974; Gaskin 1976; Krushinskaya 1986), has a finer fringe with both a mean diameter and density per cm of plate more similar to that of balaenid whales than other rorquals.

Continuous Suction Feeders. ***Ammocoetes and Tadpoles.*** The particle entrapment surfaces of tadpoles and ammocoetes are soft tissue and not part of the skull. Thus, we will not discuss them in detail here other than to emphasize the few features that they have in common.

In both forms the smallest particles are trapped directly in mucus generated by special secretory tissue (for ammocoetes see Mallatt 1979, 1981; for tadpoles, Savage 1952; Kenny 1969b; Wassersug 1972; Wassersug and Rosenberg 1979). In the ammocoete these are the goblet cell fields of the parabranchial chambers located laterally and not, according to Mallatt (1981), the medial endostyle as has been erroneously assumed in much of the older literature. Particles can be trapped anywhere along the mucus cords, but larger particles are more likely to be trapped medially (figs. 2.9, 2.10).

In most tadpoles, the mucus entrapping surfaces are concentrated on the ventral surface of the ventral velum and have been called the branchial food traps by most recent authors (fig. 2.7). In the case of pipids, which lack a ventral velum, the branchial food traps are dorsally facing on the pharyngeal floor above the gill filters (Gradwell 1975; Viertel 1987). In macrophagous forms, the branchial food traps are reduced in size or absent (Wassersug et al. 1981; Lannoo et al. 1987).

In tadpoles, there are papillary fields on the buccal floor and roof that can act as both sieves and funnels (Wassersug 1980; Viertel 1982, 1985; Sokol 1981); they can direct large particles toward the esophagus directly

and smaller particles into the pharynx. Particles aggregated in mucus can be caught on the gill filters proper, which extend upward from the gill bars. The mucus, however, comes from the branchial food traps or elsewhere in the mouth since there is little secretory tissue associated with the filters (Kenny 1969a, b). The size and porosity of the gill filters correlate roughly with the size of particles that tadpoles of different species ingest (Wassersug 1980; Wassersug and Heyer 1988) but, as noted above, particles much smaller than the pore size of the filters are commonly ingested. The pore size itself is clearly not static and direct interception seems more important than sieving.

Food and mucus are transported by cilia to the esophagus, but water movements play a motive role as well. The evidence for this is that the

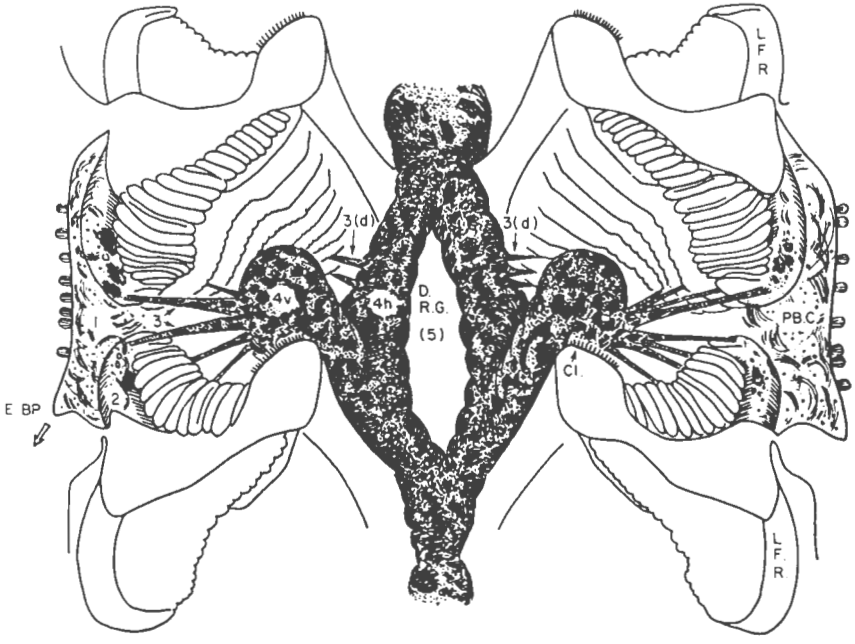

Fig. 2.9. Diagram of the feeding configuration for a lamprey larva, including portions of the mucus complex not visible in Fig. 2.5. The pharynx is shown in frontal hemisection, dorsal half, single gill pouch. Anterior is above. Note the outline of the dorsal ridge under the mucus in the center. Segments of the mucus complex (1–5) are depicted, as is the relative degree of particle aggregation within each. Note how the extreme dorsal gill pouch strands, 3(d), are attached medially to the horizontal band (4h) on the dorsal ridge. L.F.R. = lateral region of gill filament, E.BP. = external branchiopore, D.R.G. = dorsal ridge, CI. = ciliary tract, PB.C. = parabranchial chamber. (From Mallatt 1981, courtesy of the Zoological Society of London)

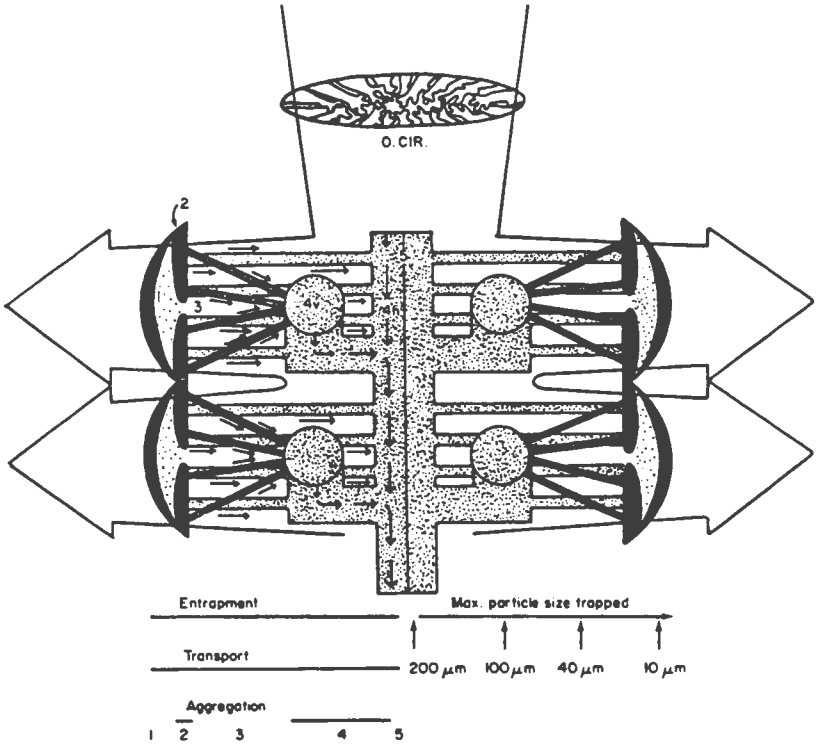

Fig. 2.10. Summary of the ammocoete feeding mechanism. Only the mucus complex (stippled) is shown; its segments are labeled as in fig. 2.9. The very large, unshaded arrows indicate the average path of water flow. For simplicity, only two of the seven gill pouches are shown. Mucus is continually manufactured laterally by the epithelium of the lateral regions of the filaments and the parabranchial chambers (black), then moved medially, then posteriorly, as indicated by small arrows. The three lines at bottom left indicate that while entrapment and transport of particles occur throughout the complex, aggregation occurs only at the lateral regions of the filaments (2) and on the ciliary tracts (4v, h). The line at bottom right indicates that the maximum size of particles trapped decreases from the medial to the lateral parts of the mucus complex. The oral cirri prefilter water entering the pharynx. O.CIR. = oral cirri. (From Mallatt 1981, courtesy of the Zoological Society of London)

ciliary tracts that move the mucus and the goblet cells where the mucus is generated are topographically separated.

Ducks and Flamingos. Until recently the particle capture mechanism for all suspension-feeding birds was presumed to be strictly sieving on lamellae. The fine structure and morphometry of the lamellae in both ducks and flamingos have been studied in great detail (see Crome 1985; Kooloos

et al. 1989; Jenkin 1957, and references therein). As with the filters of other suspension-feeding vertebrates, from tadpoles to whales, there is a general relationship between how fine, dense, and numerous the filters of suspension-feeding birds are and the modal size of particles either found in their guts or handled most efficiently by them in the laboratory (Avilova 1978). Unfortunately the pattern is not absolute; the diet of some ducks, but not all, can be predicted from the morphology of their lamellae (Crome 1985; Kooloos et al. 1989). There are two reasons for this imprecision. First, as shown experimentally by Kooloos et al. for ducks and inferred by Jenkin for flamingos, these birds adjust the porosity of their filtering mechanism to the particle size they are feeding on by continuous fine alterations of gape and maxillary elevation. Secondly, some ducks, such as mallards and the tufted duck (*Aythya fuligula*), can maintain feeding efficiency even after fairly extensive ablation of their sieving lamellae (Kooloos et al. 1989), so mechanisms of filtration other than simple sieving must be operating.

Kooloos et al. (1989) suggested that, in addition to sieving, ducks capture particles by inertial impaction secondary to the induction of vortices in their feeding currents. This suggestion is based on a high, but rough, estimate of a Reynolds number of < 2000 at the surfaces where entrapment takes place. Separation of particles by this mechanism, which is a form of centrifugation, requires that the density of the particles be great relative to the water, and particle density was not incorporated in their analysis. Kenny (1969a) criticized vortex separation when it was previously hypothesized by Savage (1952) as a suspension-feeding mechanism for tadpoles. Despite these problems, for the moment there is no better proposal or more sophisticated analysis on how ducks capture particles after lamellar ablation.

The position and orientation of the lamellae on the beaks of both flamingos and ducks, and the fact that they use fine changes in gape to regulate the mesh size of their filters, help explain some of the strange curvatures in the beaks of these birds. The famous, nearly right-angle bend of the beaks in flamingos and the very tight conformity of their jaws mean that a uniform distance across from one jaw to the other can be maintained distal to the bend at any angle of jaw opening (see Jenkin 1957, 466, 489). The bend thus helps maintain uniform spacing of opposing lamellae from the tip of the beaks back to the bend regardless of the gape. Because of the transverse arching of the beaks in ducks the same principle applies, but in a different plane. The facing lamellar surfaces of the upper and lower beaks in ducks are not in the horizontal plane, but are turned slightly vertical. This reorientation helps to maintain a more uniform spacing, as the jaws open, between the lamellae on one surface and those on the other along the length of the facing surfaces (Sanderson and Wassersug 1990).

Intermittent Suction Feeders. In the fishes that are both intermittent suction feeders and continuous ram feeders, the separation of particles from the water is likely to be achieved by the same mechanisms during both suspension-feeding modes. These mechanisms have been described above.

Species in the family Cichlidae have been reported to suspension feed using only intermittent suction. Greenwood (1953) suggested that the gill rakers on the arches of *Oreochromis esculentus* can sieve coarse particles, such as copepods, but are unable to retain phytoplankton. However, phytoplankton may adhere to mucus secreted by abundant mucus cells on the posterior mid-dorsal surface of the oral cavity, the gill arches, and the upper and lower pharyngeal jaws (Greenwood 1953; Northcott and Beveridge 1988). Greenwood (1953) envisioned aggregates of particle-laden mucus becoming entangled in the anterior teeth of the lower pharyngeal jaw, and being raked into the esophagus by subsequent movements of the upper and lower pharyngeal jaws.

Microbranchiospines ("micro-gillrakers") are minute structures in a row posterior to the gill rakers on the lateral faces of the second, third, and fourth gill arches of *Sarotherodon, Tilapia,* and *Oreochromis* species. Each microbranchiospine is approximately 250 μm long and 100 μm wide, with two rows of 8 to 16 teeth (Whitehead 1959). The teeth are approximately 35 μm in length and are spaced at 10μm intervals (Gosse 1955). The points of teeth are curved anteriorly, and they generally meet or overlap the teeth on the adjacent microbranchiospines. Whitehead (1959) hypothesized that microbranchiospines may comb the medial face of the gill filaments on the preceding gill arch, concentrating mucus and preventing the mucus from exiting with the water. Gosse (1955) proposed that the microbranchiospines may function as sieves or may retain particle-laden mucus. However, Beveridge et al. (1988) described well-developed microbranchiospines in a *Tilapia* species that consumes primarily macrophytes and benthic invertebrates rather than suspended particles.

Drenner, Taylor et al. (1984) reported that *Oreochromis aureus* captured particles as small as 7 μm and selectively consumed particles larger than 25 μm while intermittent suction feeding. They suggested that planktivorous cichlids strain particles with gill rakers and may also collect smaller particles on microbranchiospines. To test this hypothesis, Drenner, Vinyard et al. (1987) removed the gill rakers and microbranchiospines of *Sarotherodon galilaeus*. They noted no changes in particle ingestion rates or selectivity resulting from the surgical manipulation. Consequently, the mechanism of particle entrapment and the functions of gill rakers and microbranchiospines have not been established.

Jirasek et al. (1981) and Pichler-Semmelrock (1988) described narrow and dense lamellae, approximately 37 μm wide and 49 μm high, attached perpendicularly to the medial face of each raker in the silver carp. The

distance between lamellae ranged from 12 to 26 μm. The lamellae are formed from thin plates of collagenous connective tissue (Hampl et al. 1983). Murphy (1950) described the unusual tufted appearance of the rakers in adult blackfish.

ADDITIONAL EXTANT SUSPENSION FEEDERS

Tables 2.2 through 2.5 give a partial list of the heterogeneous array of vertebrates that can suspension feed. Not included are a few species that are unquestionably suspension feeders, but which do not readily fit our simple four-way classification for suspension-feeding types.

First and foremost is the gray whale, *Eschrichtius robustus* (family Eschrichtiidae). This baleen whale shows a tremendous versatility in feeding, with reports encompassing continuous and intermittent ram feeding, intermittent suction feeding, and suction or ram feeding on benthic prey (Nelson and Johnson 1987; Taylor 1987; Nerini 1984; Ray and Schevill 1974). The gray whale has a small gap separating the baleen plates at the front of the mouth, a feature shared with continuous ram feeders. At the same time it has for its size a large hyoid and a large, muscular tongue, which suggest that it actively pumps water into its mouth. The most common feeding behavior for gray whales is scooping up benthic prey from the ocean floor, leaving trails as they gouge the mud substrate (Nelson and Johnson 1987). What is not clear is whether this action is achieved by ram feeding, suction feeding, or both. Most authors assume that gray whales suck prey off the bottom because the only *E. robustus* specimen observed in captivity (Ray and Schevill 1974) sucked prey off the bottom of its tank. The problem is that that individual was a juvenile and powerful oral suction occurs in all juvenile mammals. Whereas suction feeding is definitional to mammals before weaning, it is not commonly retained after weaning. The gray whale is large enough and swims at a high enough velocity that it is not impossible that it rams through bottom sediments.

Next are the prions. Prions are petrels of the genus *Pachyptila* (family Procellariidae; Warham 1990), which have also been called whale-birds because of the morphological features that they share with right whales (Murphy 1936). There is no question that the three largest species with the broadest bills (*P. desolata, P. vittata,* and *P. salvina*) can subsist on small zooplankton captured without being detected individually (Imber 1981; Prince and Morgan 1987); for example, one 16.0 g gut sample from a Dove prion, *P. desolata,* contained 41,000 copepods (Prince 1980). These species, however, are treated here separately from other suspension-feeding birds because so little is known about their morphology and feeding behavior.

The most conspicuous cranial features of the suspension-feeding *Pachyptila,* in contrast to their non–suspension-feeding congeners, are: a broad bill (extremely so in the aptly named broad-billed prion, *P. vittata*); a wide, muscular tongue; keratinized lamellae descending from the posterior lateral margins of the upper beak; and redundant folds of skin between the lower jaws that allow the buccal floor to expand in a pelicanlike fashion. The lamellae are similar to baleen in that they are closely packed plates, approximately 40 per cm of jaw margin in *P. desolata* (pl. 1c in Prince 1980), and are oriented perpendicular to the margin of the beaks. In *P. vittata* the lamellae number 150 or more per side (Murphy 1936) and reach a maximum length of 3.5 mm.

In lateral view the front half of the beak bows upward whereas the back half bows downward (illustrated in Murphy 1936; Fleming 1941; Prince 1980). As a result, the lamellar fringe at the back of the upper beak descends below the plane of the oral orifice when the mouth is partially open. Theoretically, then, water and food can enter the front of the mouth and be simultaneously strained out the back as the animal swims forward, in continuous ram-feeding fashion. One account of the feeding posture in these prions hints that they may, in fact, continuously ram feed. Ashmole (1971), following Murphy (1936), described these birds as resting on the surface with wings outstretched, bill underwater and propelling themselves forward with their feet. According to Ashmole, since "the power for filtering is provided by motion through the water . . . [this] is a fair analogue to a towed plankton net." On the other hand, they may more commonly feed in intermittent ram or pulse fashion. Murphy (1936) reported that *P. desolata* thrust their heads under water and "scoop for food." We are ignorant of whether the buccal cavity fills passively or actively during this scooping. There are no morphological studies that might give clues to tongue and cranial movements during suspension feeding in *Pachyptila.*

Arguably the most bizarre tadpole in the world is that of the microhylid frog *Otophryne robusta.* It is our final example of a vertebrate that clearly suspension feeds, but does not comfortably fit with either ram or suction feeders. This tadpole has been found shallowly buried in sand only at the bottom of streams in northern South America. It has a spiracular tube that is so long that it can extend above the sand even when the remainder of the larva is concealed. Wassersug and Pyburn (1987) suggested that the *Otophryne* tadpole filter feeds while buried. In a flowing stream the water pressure would necessarily be lower at the exposed tip of the spiracle than at the mouth and, in theory, a current could be drawn through the oral cavity by the Bernoulli effect (cf. Vogel 1988). If this speculation is correct, then the *Otophryne* tadpole would be the first vertebrate capable of filter feeding passively, without either ram feeding or suction feeding. The chondrocranium of *Otophryne* has a plethora of odd

features, directly related to its combined fossorial/filter-feeding way of life (see table 1 in Wassersug and Pyburn 1987). These include: laterally expanded and thickened trabecular horns and suprarostral cartilages, to stiffen and brace the front of the snout; expansion and inversion of the muscular process of the palatoquadrate, to form a protective cap of cartilage over the more superficial hyoidean depressor muscles; and expansion of a cartilage lattice lateral to the otic capsule, as a protective cap over the branchial baskets. In general, there is hypertrophy of cranial cartilage which increases cranial density and helps the skull resist deformation during burrowing. The structures involved directly in particle capture (e.g., the filter plates in the branchial baskets and the mucus-secreting branchial food traps), however, differ little from those of *Otophryne*'s microhylid relatives that are obligate midwater suspension feeders.

FOSSIL SUSPENSION FEEDERS

No fossil forms are listed in tables 2.2 through 2.5, but a variety of extinct fish taxa could be added, such as the early teleost family Leptolepidae (Cavender 1970). Mallatt (1984a, b, 1985) argued forcefully that the earliest vertebrates, agnathan forms such as *Astraspis* (Darby 1982), were relatively sessile, benthic suspension feeders. If so, they must have been continuous suction feeders, like ammocoete larvae today. Close fossil relatives of extant forms known to suspension feed also are likely to have been suspension feeders, particularly if they are morphologically similar. Thus, for example, fossil anuran larvae of the extinct family Paleobatrachidae (Spinar 1972), which look very much like midwater, obligate, suspension-feeding pipid tadpoles, such as *Xenopus,* may safely be considered suspension feeders. *Presbyornis,* a charadriiform bird close to the ancestry of ducks, also has been considered a suspension feeder (Olson and Feduccia 1980a).

Several extinct plesiosaurs and pterosaurs have been deemed suspension feeders ostensibly because they had long thin teeth that paleontologists thought must have functioned better as sieves than as piercing/grasping structures. Of these, the pterosaur *Pterodaustro* (Pterodaustriidae) best fits our idea of a suspension-feeding vertebrate. The teeth on the lower jaw of *Pterodaustro* are extremely long, numerous, and closely packed (Bonaparte 1971; Sanchez 1973). They are so thin that to function in piercing prey seems out of the question (fig. 2.11). The teeth are, in fact, so thin that they appear to have been flexible (which is consistent with the observation that the porosity of biological sieves is not immutable in extant suspension feeders). Other putative suspension-feeding fossil reptiles, for example the

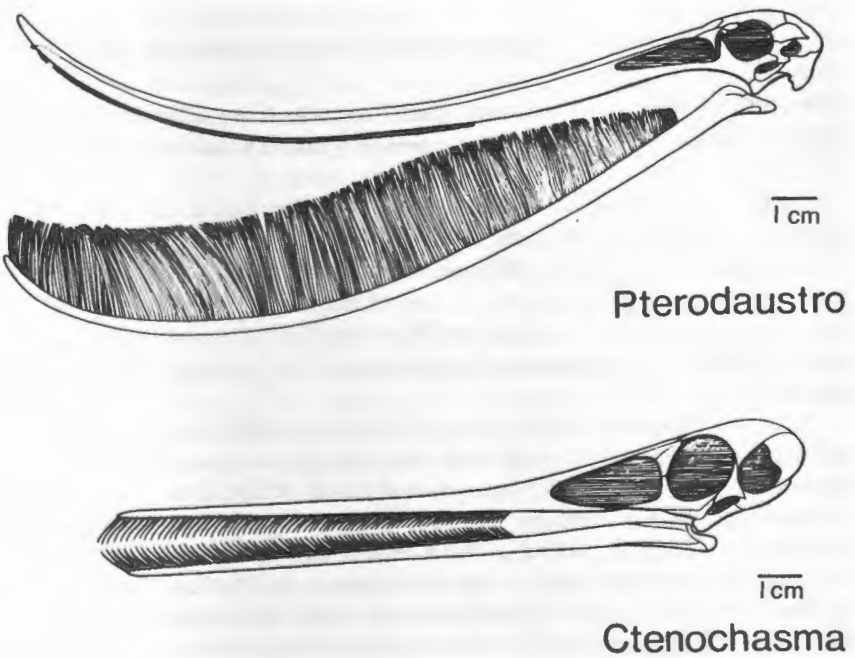

Fig. 2.11. Skulls from two fossil pterosaurs that have been considered suspension feeders. The case for *Ctenochasma* being a suspension feeder is more equivocal than for *Pterodaustro*, whose long, flexible mandibular teeth would seem to preclude grasping individual prey. *Pterodaustro* has been likened to flamingos (Bakker 1986). The teeth would have served as a filter. (From Wellnhofer 1981)

pterosaurs *Ctenochasma* and *Gnathosaurus* (Broili 1924; Sanchez 1973; Wellnhofer 1981) and the plesiosaur *Kimmerosaurus* (Brown 1981), have in comparison much shorter, stouter, more widely spaced teeth. They may have been piscivorous or eaten soft-bodied invertebrates, but we are skeptical that they were obligate suspension feeders.

Pterodaustro was approximately the size of the greater flamingo and shares with it a curved rostrum, although one that curves upward rather than downward (fig. 2.11). Bakker (1986) reconstructed *Pterodaustro* as a flamingo, feeding while standing in shallow water. This posture precludes ram feeding. We do not know whether the hyoid and tongue served as a pump for suction feeding. Since the filter structures (i.e., the teeth) project up from the mandible rather than descend from the skull, the vestibule between them might have been filled by a dipping motion of the lower jaw using either jaw adductors, neck extensors, or both.

PUTATIVE BUT PROBLEMATIC SUSPENSION FEEDERS

The case for many other living and fossil vertebrates being suspension feeders is dubious. Some of the problematic forms include turtles, salamander larvae, avocets, phalaropes, and seals.

Smith (1961) proposed that fleshy papillae called choanal rakers, which extend across the internal nares in the green sea turtle *Chelonia,* could function as strainers. Such structures may serve to protect the internal nares from obstruction, but in and of themselves they do not establish that sea turtles suspension feed and there has been no subsequent study of either the diet or functional morphology in *Chelonia* supporting Smith's hypothesis.

Certain freshwater turtles (e.g., *Podocnemis unifilis, Chrysemys picta, Kinosternon flavescens*) have been observed skimming small particles off the surface of the water (Mahmoud and Klicka 1979). During this behavior, termed neustophagia by Belkin and Gans (1968), the turtle holds its head with the mouth open and the margin of the lower jaw just below the water's surface. This causes a thin film of water to flow into the mouth by gravity. Ciné film analyses indicated a fourfold expansion of pharyngeal volume in *Podocnemis unifilis* when its hyoid was protracted during neustophagia (Belkin and Gans 1968). These turtles, however, do not have any specialized sieving structures at the margins of their mouths or elsewhere in the oropharyngeal cavity. Small particles are entrapped between nearly closed jaws as water is slowly expelled, just as water is expelled when larger prey are caught in the mouth. Given the absence of any true filters, it is not surprising that neustophagia appears to be neither common nor preferred by the few turtles in which it has been observed.

Tilley (1964) speculated that larval tiger salamanders (*Ambystoma tigrinum,* Ambystomatidae) may filter feed. There is no question that they regularly ingest small zooplankton. But despite much recent study of their feeding behavior (e.g., Leff and Bachmann 1986, 1988), no subsequent evidence has come forth indicating that they feed other than by attacking individual prey.

A few extant charadriiform birds with attenuate beaks, such as the American avocet (*Recurvirostra americana,* Recurvirostridae) and phalaropes (Phalaropodidae) take prey individually (Dodson and Egger 1980; Crome 1985) but have morphological features associated with suspension feeding, including papillae on the beak margins or the palate (Olson and Feduccia 1980b; Mahoney and Jehl 1985a). Phalaropes use water's adhesive and cohesive properties to transport a small amount of water containing the prey from the beak tip to the buccal cavity (Rubega 1990). The prey is then apparently held between lingual lumps and posteriorly facing

palatal papillae as the remaining water is squeezed out of the mouth (Rubega, in preparation). Based on physiological studies of salt-loading in eared grebes (*Podiceps nigricollis*, Podicipedidae, Podicipediformes) feeding in a hypersaline and alkaline lake, Mahoney and Jehl (1985b) suggested that they also act like suspension feeders by pressing their large, fleshy tongues against the palate to separate prey (brine shrimp and brine flies) from water. The extrusion of water from the mouth is, of course, a component of suspension feeding. However, the issue of whether prey are selected individually, a criterion for suspension feeding, is not addressed by Mahoney and Jehl (1985b).

The crabeater seal, *Lobodon carcinophagus* (Phocidae), which has a diet consisting largely of euphausiacean krill, is often presumed to suspension feed (e.g., King 1972; Taylor 1987; Riedman 1990). This presumption goes back at least to Racovitza's (1900) passing comment that *Lobodon* swims with its mouth open, feeding in a manner similar to baleen whales. The crabeater, however, is a crepuscular forager (King 1983), which makes its feeding activity difficult to observe, and morphological evidence for suspension feeding in the animal is, at best, mixed. *Lobodon* has a proportionally longer, narrower snout and smaller orbits than other phocid seals (King 1972), and a scooplike lower jaw (King 1961). Both upper and lower postcanine teeth are triangular, subequal in size, and adorned with elongate, fingerlike cusps (see fig. 4 in Kooyman 1981). When the jaws are closed, upper and lower teeth occlude in an offset fashion such that a sieve is necessarily formed by the spaces between the cusps. Between the last molar and the coronoid process of the dentary is a bony protuberance which has been interpreted as a guard against prey escaping from the oral cavity posterior to the cheek teeth (King 1961).

It is easy to imagine how water captured with krill could be extruded from the mouth through the spaces between the cusps on *Lobodon*'s teeth. Juvenile crabeater seals feeding on fish in captivity sucked them in individually and ejected excess water from the sides of their mouths (Ross et al. 1976). A similar straining role has been proposed for the far less elaborate cusps on the cheek teeth in the ringed seal, *Phoca hispida* (Frost and Lowry 1981). However, these spaces alone do not establish suspension feeding any more than gill slits do in fishes. In contrast to the filters of virtually all confirmed vertebrate suspension feeders, which are made of soft flexible tissue, the teeth of these seals lack the finely adjustable porosity achieved by typical filters. Although the skulls of mysticete whales are more kinetic than those of odontocete whales (Brodie 1977; Pivorunas 1977), the skull and jaws of *Lobodon* do not appear any more kinetic than in other seals. No specialization of the hyoid, tongue, or other soft tissue of the buccal floor for suspension feeding has been reported so far in this genus. The most extensive observations available to date on *Lobodon*

feeding in the wild—merely three sentences reported in Kooyman (1981)—suggest that invertebrate prey are captured one by one. Bonner (1990), however, came to the same conclusion based on an independent interpretation of crabeater seal morphology.

DISCUSSION

Ecomorphological Patterns

Our primary distinction between ram feeding and suction feeding splits the teleost fishes and elasmobranchs into two groups, one of which is placed with whales. Our secondary distinction, between continuous and intermittent feeding, produces some unlikely taxonomic assortments by further dividing the whales (balaenids vs. balaenopterids), and grouping tadpoles with ducks and flamingos. Although this scheme cuts across taxonomic lines, it focuses on biomechanical differences in how water is transported to the entrapping surfaces of suspension feeders. These distinctions have not been emphasized before in literature on suspension-feeding adaptations of vertebrates (see for example fig. 2.12; also Owen 1980; Morton 1967; Taylor 1987), but are important for understanding convergent and nonconvergent cranial designs in these organisms. The distinctions recognize that suspension feeding relates as much to locomotor specializations as to cranial features (see Webb and Buffrénil 1990; Webb 1984, 1988, for a general discussion of the relationship of locomotion to feeding in aquatic vertebrates).

Where locomotion provides the flow to feeding structures (i.e., ram feeding), no cephalic pump is necessary and cranial specializations for suspension feeding—other than the proliferation of filters proper—may be relatively slight. If there is less forward body motion, some cranial adaptations for pumping may be in order (i.e., intermittent suction feeding). Where there is little or no body movement, cranial specializations to ensure adequate flow become essential (i.e., continuous suction feeding). Those latter specializations include not only a lingual or pharyngeal pumping mechanism, but valves to ensure one-way flow. Not surprisingly, those vertebrates that use locomotion totally or partially to deliver water to their feeding structures are best designed for sustained locomotion in the aquatic environment (fishes, whales). Those that feed from a relatively stationary posture and use continuous suction feeding are least designed for sustained aquatic locomotion (birds, lamprey larvae, tadpoles; see Wassersug 1989).

There is some exclusion between cranial designs for continuous ram feeding and those for continuous suction feeding due simply to packing constraints in the vertebrate head. For the ram feeders, maximizing surface

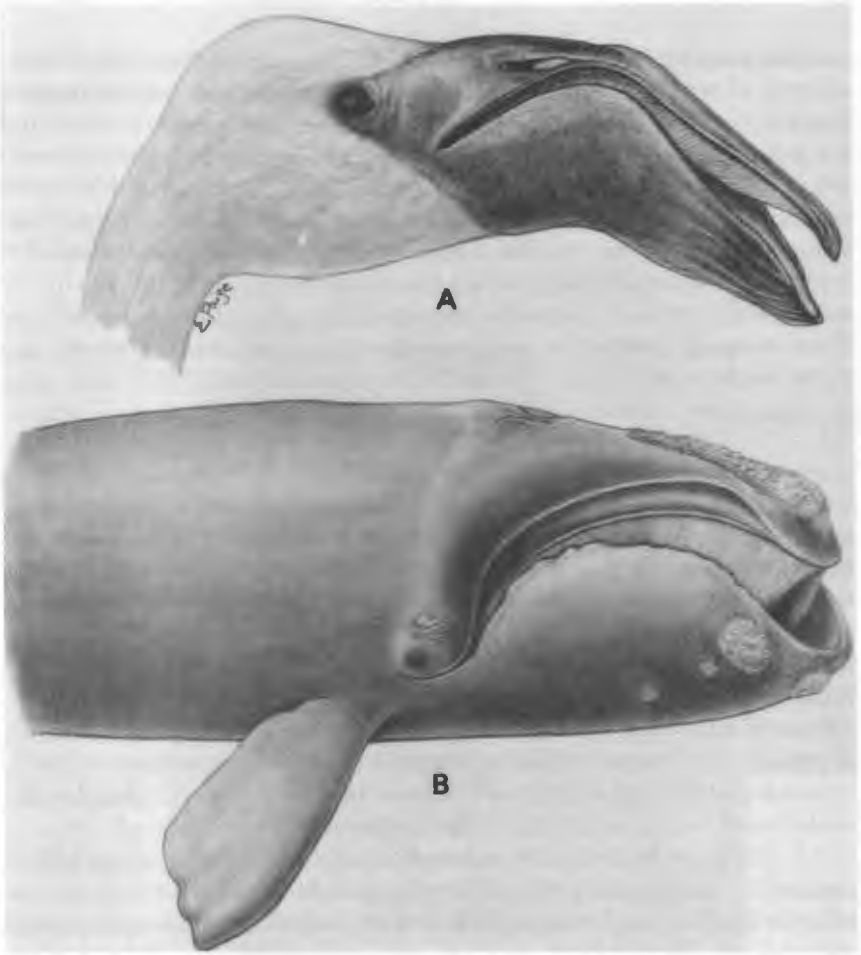

Fig. 2.12. Presumed convergence in the suspension-feeding apparatus of the lesser flamingo, *Phoeniconaias minor,* and the black right whale, *Eubalaena glacialis.* The analogy, however, is superficial. The whale uses continuous ram feeding, whereas the flamingo depends on an oscillating hyoidean suction pump to deliver water to its particle-entrapping surfaces. The whale swims forward as it feeds, whereas the flamingo waves its head from side to side. Water comes in through the front of the mouth in ram-feeding whales through a large gape, whereas it comes in through the side of the mouth in flamingos, through a narrow slit. The flow regimes are not comparable around the filter apparatus of the two animals and it is unlikely that the physical processes used in particle capture are, in fact, the same (see text).

In the right whales only the upper jaw is bowed; the lower jaw is straight in lateral view. This means that at their midpoint the upper and lower jaws are always widely separated, with long baleen plates filling the intervening space. In flamingos the upper and lower jaws have the same arch and are never separated by much distance. The implication of the arch in whales, and the fact that the two jaws do not conform, means extra space for baleen. The implication of the arch for the flamingo is more uniform spacing along the jaws rostral to the bend when the jaws are open. (From Olson and Feduccia 1980b, reprinted by permission of the Smithsonian Institution Press)

area for entrapment becomes essential if they are going to process large volumes of water at reasonably low (viz., energy efficient) body velocities. Large buccal volumes and expansive collecting surfaces are in order, and the cross-sectional area of the mouth in these organisms is typically enormous. This large area is achieved, in part, by reducing or never developing the musculoskeletal components that make up the pump in continuous suction-feeding forms. Besides, a buccal pump would be superfluous since feeding usually takes place when the oropharyngeal volume is already maximal. In contrast, in continuous suction feeders, the room available for entrapping surfaces is comparatively reduced to make space for the pump mechanism.

Summary of Morphological and Ecological Features Shared by Vertebrate Suspension Feeders

1. Teeth are reduced or absent (*Pterodaustro* is a specialized exception) and adductor musculature is concomitantly reduced, compared to macrophagous relatives.

2. Forms that lack gill slits—be they bird or mammal—all have their entrapping surfaces on the jaw margins. Deeper placement of entrapping structures within the mouth would require further transport of water and increase the energetic cost of feeding. None rely on mucus entrapment to capture food. Perhaps, with their entrapment surfaces superficial, the loss of mucus to the water would be too great to make that mechanism profitable. Alternatively, this decreased reliance on mucus may be related to the evolution of birds and mammals in a terrestrial environment.

3. Elasmobranchs and cetaceans that suspension feed are large and all ram feed, with the exception of the megamouth shark. Ram feeding is an effective mechanism for suspension feeding only for organisms that swim at high Reynolds numbers.

4. Below a certain minimum body length (approximately 2–5 cm), teleosts do not suspension feed (Sanderson and Cech 1992; but see van der Meeren 1991). Adult suspension-feeding teleosts, and the paddlefish, begin life as juveniles that use suction to capture individual zooplankton (e.g., Michaletz et al. 1982; Durbin 1979). After the transition, these fish may suspension feed on the same type of zooplankton prey that is consumed by juveniles, or they may switch to phytoplankton (Johnson and Vinyard 1987; Moriarty et al. 1973; Cramer and Marzolf 1970; Ciechomski 1967; Bensam 1964). Whereas fishes can discern increasingly smaller prey as they themselves grow larger (Hairston et al. 1982), the ontogenetic shift to suspension feeding cannot be explained by that fact since, by definition, individual prey items are not sensed and attacked during suspension feeding. The ontogenetic shift in feeding habits suggests that the entrapment mechanisms used by larger fishes may not work with the same

efficiency in the low Reynolds number range in which the juvenile fishes necessarily operate.

5. Most suspension-feeding teleost species swim in schools. This is true of the clupeids and engraulids (Blaxter and Hunter 1982), the cyprinid *Orthodon* (Murphy 1950), some species of *Coregonus* (Koelz 1927), and the mackerels (Collette and Nauen 1983). These schools tend to utilize patchy food resources in pelagic habitats.

6. All of the continuous suction feeders that are capable of generating their own suspensions from the bottom material share not so much a common cranial design, as a capability for moving from patch to patch using seasonally available resources. None are permanent residents in the aquatic habitats where they feed; eventually they either metamorphose (tadpoles), emigrate (avians), or do both (lamprey larvae).

7. A common feature of suspension-feeding vertebrates is greater cranial kinesis than in close, macrophagous relatives. This is true whether one compares baleen and toothed whales or tadpoles and frogs. The kinesis appears to be used for fine regulation of suspension-feeding flow rates.

8. Suspension-feeding vertebrates that lack gill slits generate a bidirectional flow; water must both enter and exit through the mouth. After the water surrounding the prey has been accelerated into the oral cavity, it must decelerate in order for the direction of flow to be altered by as much as 180°. Mobile prey may have the opportunity to escape as the flow decelerates. Lauder and Shaffer (1986) presented data on ambystomatid salamanders indicating that bidirectional flow systems are not as successful at capturing elusive prey as are unidirectional flow systems. The tremendously expandable oral cavity of intermittent ram-feeding whales, however, may allow their morphologically bidirectional flow system to become functionally unidirectional, as proposed by Lauder and Shaffer (1986) for the expandable esophagus in turtles. In these cases, the time at which the flow decelerates and reverses can be delayed until the jaws have closed to a gape too small for the escape of prey.

Unsolved Problems

The transport of food captured on oropharyngeal surfaces to the esophagus and the initiation of swallowing are the two least understood steps in suspension feeding by vertebrates. A description of these processes will require a combination of techniques from the disciplines of functional morphology and biomechanics. But even the basic myology of the lingual and pharyngeal regions for most species has not been examined. This problem is glaring for whales, where stomach contents have been repetitively examined, yet the cranial muscles which let those organisms fill their stomachs remain uninvestigated. The two most comprehensive studies of mysticete cranial myology are still Carte and Macalister (1868) and

Schulte (1916), both on *Balaenoptera*. The first is on a small, decomposing specimen and the second on a fetus. That there are errors of omission and interpretation in both of these works has been known for over half a century (Howell 1930). The lingual movements (if it *is* lingual movements) that transport captured food from the baleen to the esophagus are simply not known. The hyoids of baleen whales in general are not large given the size of the heads in these animals. However, those genera known to have either massive tongues (*Eubalaena*) or powerful tongue movements (*Eschrichtius*) do have much larger hyoids (Omura 1964). This suggests that there must be substantive differences among species in the muscles that insert on the hyoid and indirectly work the tongue.

At the other end of the size spectrum, it has been established for some time (Dodd 1950) that cilia carry food from the pharynx down the esophagus in tadpoles. However, what has not been established is how particulate matter gets from a tadpole's gill filters, which lie at the bottom of its pharynx, to the ciliary groove in the lateral pharyngeal wall. Neither the tadpole's branchial food traps nor its gill filters are themselves ciliated. How particulate matter is cleared from the gill rakers of suspension-feeding fishes is essentially the same unsolved problem. From whale to tadpole, and for most suspension feeders in between, this part of the suspension-feeding process remains a mystery.

Another area of major ignorance is the flow regime at the collecting surfaces. The works of Rubenstein and Koehl (1977), Jørgensen (1983), LaBarbera (1984), Shimeta and Jumars (1991), and others on invertebrate suspension feeding have emphasized the complexity of the suspension-feeding process. There are scale effects involved which have rarely been appreciated by biologists studying vertebrate suspension feeding. The entrapment properties of biological filters are affected by flow velocity, pore size, amount of material already collected on the surfaces, etc. All of these factors affect each other and can vary instantaneously in flexible biological filters, like those of vertebrates. Suspension feeding for these animals has a dynamic responsiveness which makes the kinematics and mechanics of the process far more complex than the ballistic capture systems of their toothed, macrophagous relatives. We now know that it is naive to equate suspension feeding with simple sieving, nor can we expect to understand the feeding capability of a suspension feeder by measuring the gross static dimensions of its filters alone. To discover what suspension-feeding mechanisms are operative requires precise hydrodynamic data that are currently lacking.

Our review of the morphology of vertebrate suspension feeders suggests that these data will be difficult to collect. Flow through suspension-feeding structures is not constant for even a few seconds, except possibly for the larger continuous ram feeders, and even there it is altered by the

process of entrapment itself. Intermittent ram feeders and both types of suction feeders create a flow of varying velocity. It will be extremely difficult to measure water velocities in these animals to establish the flow regime when and where particle entrapment takes place. Yet such data will be essential, if we are to know even how most vertebrate suspension feeders actually manage to extract particulate matter from the water.

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