

**MORPHOLOGICAL CONSTRAINTS ON
TETRAPOD FEEDING MECHANISMS:
WHY WERE THERE NO
SUSPENSION-FEEDING MARINE REPTILES?**

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INTRODUCTION

Although tetrapods are primarily designed for a terrestrial existence, tetrapod history is rife with secondarily aquatic forms. Semiaquatic taxa are usually freshwater, and more fully aquatic taxa are usually marine. With the reinvasion of the aquatic environment, modification of the tetrapod body plan originally designed for feeding and locomotion on land would be necessary to accommodate these functions in the very different medium of water. Both the diversity of living marine tetrapods and the additional diversity afforded by the fossil record demonstrate numerous examples of parallelisms and convergences in the various lineages (Massare, 1987, 1988; Carroll, 1985). Yet aquatic suspension feeding, common among fish, is conspicuously absent in marine nonmammalian tetrapods: baleen whales appear to be the only group that has adopted this form of feeding in past or present marine environments. The notion of morphological or phylogenetic constraint is often invoked when evolutionary patterns differ between groups of organisms (McKittrick, 1993; Carroll, 1985). In this chapter we review the morphological requirements for suspension feeding, and address the issue of whether differences in design between mammals and other tetrapods have resulted in morphological constraints that can explain the apparent absence of suspension-feeding marine reptiles.

During the Paleozoic, when oceanic productivity is thought to have been comparatively low (Bambach, 1993 and personal communication), marine tetrapods were rare. Those tetrapods that did venture into the water, such as the Permian

mesosaurs, were small (1 m or so in length) and limited to inland saltwater basins (Carroll, 1988). As productivity increased, more groups of tetrapods diversified in the oceans. During the Mesozoic there were invasions and significant marine radiations of at least 16 diapsid lines (Carroll, 1985), as well as radiations of several groups of turtles, birds, and amphibians. Benton (in Cruickshank, 1993) estimates that as many as 31 groups of tetrapods have undergone marine radiations during the Mesozoic and Cenozoic combined (including three Cenozoic episodes of mammalian invasion: whales, sea cows, and pinnipeds). Radiations within these groups produced an array of high-level marine carnivores preying on a variety of other marine reptiles, fish, and invertebrates.

All Mesozoic marine tetrapods, except turtles, became extinct at or before the end of the Cretaceous. Turtles, sea snakes, and marine iguanas are reptiles found in today's oceans, but birds and mammals have been the dominant marine tetrapods throughout the Cenozoic. Whales represent the only radiation of marine tetrapods that includes suspension feeders. The crabeater seal, *Lobodon carcinophagus*, is sometimes considered to be a suspension feeder: however, it probably captures macroplanktonic food items individually (Sanderson and Wassersug, 1993).

MARINE TETRAPOD PREDATORY GUILDS

With the exception of sea cows, marine iguanas, and a few species of turtles, all of which have limited coastal distributions, marine tetrapods are, or were, carnivorous. The prey preference and predatory mode of extinct marine tetrapods can be inferred from tooth morphology and swimming capabilities. Most fossil and Recent marine tetrapods can be assigned to one of the predatory guilds Massare (1987) described for Mesozoic marine reptiles. All of these guilds are generally applicable to, and include, members from several radiations of marine reptiles and mammals, but do not include a suspension-feeding mode of life.

Suspension feeding, defined as the "capture (of) planktonic prey as water flows past the feeding apparatus" (Sanderson and Wassersug, 1993), implies microphagy and nonselectivity. Among tetrapods in today's oceans this feeding method is used only by baleen whales. However, suspension feeding is not particularly unusual in fish. It has evolved multiple times in actinopterygians (e.g., in the paddlefish, family Polydontidae, and within many teleost families, especially in the Clupeidae, Cyprinidae, and Cichlidae) and elasmobranchs (in the manta ray, the whale shark, the basking shark, and the megamouth shark) (Sanderson and Wassersug, 1993). Suspension feeding is also practiced by amphibian tadpoles, which possess gills and are thus not subject to typical tetrapod constraints on aquatic feeding (Sanderson and Wassersug, 1993).

Given the diversity of predatory guilds represented by the Mesozoic marine reptiles, and their prominence in the oceans for at least 150 million years, it is surprising that there is no evidence of suspension-feeding marine reptiles. A few fossil reptiles have been claimed to be suspension feeders, but on closer examination these interpretations are dubious at best. The Permian mesosaurs in the genus *Mesosaurus* are sometimes described as suspension feeders (Carroll, 1988). However, this reconstruction depends on an erroneous interpretation of the mandibular teeth as small marginal upper teeth, and a more detailed examination of mesosaur functional morphology suggests that they probably captured individual prey selectively rather than processing large volumes of water nonselectively as do true suspension feeders (S. Modesto, personal communication). The plesiosaur *Kimmerosaurus* has also been proposed to be a suspension feeder (Brown, 1981), but Sanderson and Wassersug (1993) consider its teeth to be too short and too widely spaced for this interpretation to be plausible. Based on its lack of teeth, Carroll and Zhi-Ming (1991) suggest the Triassic reptile *Hupehsuchus* may have been a suspension feeder. Not only is there no positive evidence to support this interpretation of its feeding biology, but the authors themselves point out that the small narrow skull and relatively long neck make suspension feeding unlikely (Carroll and Zhi-Ming, 1991).

Why is there no evidence of suspension-feeding marine reptiles in the Mesozoic? The fossil record of Mesozoic marine reptiles and large Cenozoic marine vertebrates, such as whales and seals, is by no means complete. However, we think it highly unlikely that preservational bias could account for the absence of suspension-feeding marine reptiles from the record. Fossils of other marine tetrapods show considerable diversity in feeding mechanisms (Massare, 1987; Carroll, 1988), and baleen whales and suspension-feeding sharks and rays from the Cenozoic have been preserved (Carroll, 1988).

The size attained by some baleen whales might suggest that suspension feeding is restricted to very large animals. However, suspension-feeding fish range from a few centimeters to several meters in length. Many early baleen whales were only 3 or 4 m long (Pivorunas, 1979), and modern baleen whales range in length from 6 m (the pygmy right whale, *Caperea marginata*) to 30 m (the blue whale, *Balaenoptera musculus*) (Leatherwood et al., 1983). This size range easily includes many marine reptiles, although at small body sizes suspension feeding is apparently limited to animals that possess gills (Sanderson and Wassersug, 1993).

We propose instead that neomorphies of the mammalian mouth and pharynx, especially those that allowed for a seal to be formed between the nasopharynx and the buccal cavity, were the key adaptive features in the origination and diversification of suspension-feeding mammals. All other fully marine tetrapods were constrained to feed on larger prey items. We first review the feeding methods

employed by modern suspension-feeding vertebrates, and then discuss the morphological constraints that prevent nonmammalian tetrapods from feeding in these ways.

PLANKTON AVAILABILITY AND UPWELLING ZONES

High productivity of nearshore waters during times of intense upwelling are assumed to have played an important role in the multiple origins and diversifications of marine tetrapods since the Permian (Lipps and Mitchell, 1976). Upwelling supplies surface waters with enough nutrients to support high densities of phytoplankton that, in turn, support high standing crops of zooplankton. Aquatic planktivores depend on the dense swarms of zooplankton that commonly occur near areas of high primary productivity, as capture rates of suspension-feeding organisms are closely related to prey density. Huge numbers of small suspension-feeding fish, or smaller numbers of large suspension feeders like whales and whale sharks, feed on these zooplankton. Although Mesozoic plankton communities were undoubtedly taxonomically different from those in Recent oceans (Tappan, 1969), there is no evidence that their productivity would not result in enough zooplankton to support large suspension feeders. In fact, areas of high productivity produced by upwelling and current divergences seem to have been present throughout the Mesozoic (Lipps and Mitchell, 1976). Parrish and Curtis (1982) used a paleoclimatological model to retrodict areas of upwelling from the deposition of organic-rich sediments, and showed that upwelling was especially prominent during the Triassic and Cretaceous, coinciding with the periods of greatest diversifications of marine reptiles (Bardet, 1994). Similarly, high levels of Cenozoic upwelling coincide with radiations of marine mammals (Lipps and Mitchell, 1976).

Although the physical conditions conducive to high primary productivity and large standing crops of zooplankton were probably common at some time during the Mesozoic, the absolute intensity and productivity of these areas cannot be measured. However, despite a sparse fossil record, the diversity and abundance of zooplankton can be inferred from fossilized phytoplankton and the maturity of the ecosystem. Tappan (1969) traced the stages of oceanic ecosystems through the Mesozoic and found that high phytoplankton diversity and productivity began during the Early Jurassic. The abundance of fossil coccolithophorids and dinoflagellates from this time, as well as radiations of herbivorous pelagic animals that rely on high levels of phytoplankton, implies high oceanic productivity. The fossil evidence indicates that Mesozoic oceanic productivity was able to support a diversity of trophic groups similar to that found during the Cenozoic. Therefore, limited ecological opportunity cannot account for the absence of suspension-feeding marine reptiles, especially as

suspension-feeding actinopterygians were common during the Mesozoic (B. Chernoff, personal communication).

PREY CAPTURE IN SUSPENSION FEEDERS

Aquatic suspension feeders can collect zooplankton either by creating suction to draw prey into their mouths (suction feeding) or by relying on their momentum to force water into their mouths (ram feeding) (Sanderson and Wassersug, 1993). Suction feeding is used primarily by some suspension-feeding fish, which take advantage of opercular movements to draw water into the mouth and through the gill slits. Tadpoles and some birds may use other buccal structures to create suction. Although suspension-feeding birds may seem relevant to this discussion, only a bird that fed while fully submerged would be confronted with the same functional problems as other marine tetrapods, and none are known to have existed (Feduccia, 1980). Ducks and flamingos, which feed with their heads out of the water or only partially submerged, use their tongue in a suction-feeding fashion to pump small amounts of water through their mouth, where they collect algal cells on the lamellae of their partially submerged beak (Sanderson and Wassersug, 1993). The fringe-billed pterosaur *Pterodaustro* may have fed in an analogous fashion (Bakker, 1986). This use of the tongue to strain food may only be possible if the action is essentially performed out of the water, where large amounts of water will not be forced into the mouth and where presumably the action of gravity can also aid in expelling the water from the mouth. The bird mode of suspension feeding is a very different functional issue from engulfing a mouthful of water and expelling it in a completely submerged situation.

Suction is not usually employed by large suspension-feeding vertebrates: most whales and large chondrichthyans obtain food by ram feeding (Sanderson and Wassersug, 1993). However, suction feeding involving the capture of large prey items has been reported for a number of aquatic tetrapods, including salamanders, turtles, walruses, seals, and toothed (odontocete) whales (Werth, 1992), and intermittent suction feeding may be the mode of suspension feeding in the megamouth shark (Sanderson and Wassersug, 1993). The only baleen (mysticete) whales that use suction to feed are the gray whales (family Eschrichtidae), which are not planktonic suspension feeders, but instead suck up mud and water from the sea floor, and then strain it through the baleen, entrapping small food items (Nowak, 1991).

The majority of baleen whales are suspension feeders that feed by continuous or intermittent ram feeding. Continuous ram feeders, also known as skimmers or tow-net feeders (including large animals such as whale sharks and right whales as

well as some small fish such as menhaden and anchovies), take advantage of the unidirectional flow produced by their movement through the water. Swimming with the mouth open, they continually force water into the mouth anteriorly; the water then flows out of the buccal cavity laterally through the baleen (in the case of the whales), or exits through the gill slits in fish (where the particles are either trapped on gill rakers or entrained in mucus on the roof of the mouth) (Sanderson et al., 1991). Several species of whales in the genus *Balaena* (right or bowhead whales) feed continuously by trapping particles as water exits through baleen filters along the side of the mouth.

Rorqual whales (Balaenopteridae), the only known intermittent ram feeders, collect food by engulfing plankton-laden water. To begin the feeding process, the animal swims forward with its mouth open, engulfing a tremendous amount of water. The mouth is subsequently closed until the baleen covers the gape between the upper and lower jaws; water is then forcefully expelled, trapping plankton on the baleen. The expulsion of water is possibly by the compression of the buccal cavity and the protrusion of the tongue, although the precise mechanism is unknown (Sanderson and Wassersug, 1993). In order to generate enough momentum to feed in this way, intermittent ram feeders must be of large body size (Sanderson and Wassersug, 1993); the smallest rorqual is the Minke whale (*Balaenoptera acutorostrata*) of around 10,000 kg, and the other four species are considerably larger than this, with the blue whale (*Balaenoptera musculus*) attaining body masses of up to 190,000 kg (Nowak, 1991). Note that there is no biomechanical reason for a similar size constraint on continuous ram feeders or on suction feeders.

RECOGNIZING A FOSSIL SUSPENSION-FEEDING TETRAPOD

How might one identify a suspension-feeding marine reptile from its fossil remains? Sanderson and Wassersug (1993) have identified a number of morphological features, many of which could be preserved in fossil specimens, that are functionally correlated with various modes of suspension feeding, and the discussion below is modified from their work.

First, the head is large, from a quarter to a third of the total length, with the elongation of the rostrum to allow for a large buccal volume. The dentition is reduced: chondrichthyans have many rows of small, reduced teeth, and baleen whales have lost the teeth entirely and replaced them with baleen. The eyes are small, and the orbits are reduced in all large living suspension feeders, presumably because vision is not an important sense for this mode of feeding.

Baleen whales have a large, anteriorly sloping, occipital area for the expansion of the area of attachment of the epaxial muscles. These muscles probably act to

resist the downward torque on the head produced when the mouth is opened and to resist sideways movement of the head. They also have a very short cervical region, to stabilize the head by limiting the movement of the head on the body. The jaw bones are elongated and broadened, but are not heavily ossified, as they function as regulators of water flow rather than organs of prey capture. In the intermittent ram-feeding rorquals, there are additional morphological features that allow the jaws to be rapidly closed around a mouthful of water, such as a small coronoid process reflecting the presence of somewhat more powerful jaw adductor muscles than in right whales.

How might these criteria be applied to a marine tetrapod of unknown feeding mode? A possible candidate is *Shonisaurus* from the Late Triassic of Nevada (Camp, 1980), an animal not discussed by Massare (1987). This is the largest known ichthyosaur, with a total length of up to 15 m (Camp, 1980; Kosch, 1990), and is thus of comparable size to many baleen whales. It has a relatively large head, long slender jaws with a reduced dentition, and a peculiarly deep body. Its limbs are unusual in being greatly elongated through the manus and the pes, with the hindlimb of equal size to the forelimb. Carroll (1988) points out that the limbs are unusual in only having three rows of phalanges, where hyperphalangy is the norm for ichthyosaurs, and suggests that the limbs functioned more like paddles than like fins. *Shonisaurus* certainly presents the appearance of an animal that gently skulled through the water, rather than one that actively pursued its prey. But might this animal have been a suspension feeder?

Although the head of *Shonisaurus* is relatively large and slender-jawed, its head is only about 20% of its total length (Kosch, 1990), which is somewhat smaller than the proportions of living large suspension feeders. The orbit is large, suggesting a large eye which is not typical of present-day suspension feeders. However, most importantly, *Shonisaurus* does not possess any morphological features that could be interpreted as a straining device, or as supporting a soft-tissue straining device. Although the teeth are small, they are fairly widely spaced, and are certainly not closely packed in any fashion that might act as a sieve to strain plankton. The upper and lower jaws are appressed against each other: there is no arching of the upper jaw to accommodate a soft-tissue filtering device, as in continuous-feeding right whales. An intermediate-feeding mode (as in rorquals), where the filtering tissue might be less extensive and not evidenced by a profound arching of the jaws, is precluded by the small coronoid bone, suggesting the lack of sufficient jaw adductor musculature to rapidly close the jaws around a mouthful of water.

The form of the teeth best seem to approximate to the type that Massare (1987) interpreted as generalized grasping organs, possibly indicative of a diet of soft-bodied prey items such as cephalopods. The reduced dentition is reminiscent of that of present-day beaked whales (Ziphiidae) which employ suction to ingest

squid and small fish (Nowak, 1991; Werth, 1992): perhaps *Shonisaurus* had developed some analogous mode of feeding, a dietary interpretation that would be consistent with the skeleton which suggests slow swimming rather than active pursuit. However, the available evidence does not indicate that *Shonisaurus* was a suspension feeder.

NEOMORPHIES OF THE MAMMALIAN PHARYNX

We suggest that the loss of gills in adult tetrapods and the design of the tetrapod oropharyngeal region severely constrains possible aquatic feeding mechanisms. However, neomorphies associated with the evolution of mastication and suckling may have allowed mammals to develop suspension feeding. These features include the ability to separate different portions of the oropharyngeal cavity from each other by the means of muscular seals acting against the posterior soft palate (Smith, 1992; Crompton, 1995) (see Figure 1B). These seals can act to contain food being masticated in the oral cavity from the pharyngeal region until swallowing occurs, and can also allow liquids to be swallowed while maintaining a patent airway.

These seals are formed in the following fashion (Crompton, 1995). The anterior seal (seal #1) is formed between the oral cavity and the oropharynx by the tensing of the tensor veli palatini muscle, and the drawing of the tongue dorsally by the palatoglossus muscle. The intrinsic tongue musculature can then shape the tongue so that its dorsal surface is forced up against the anterior portion of the soft palate. The posterior seal (seal #2), separating the oropharynx from the nasopharynx, results from the contraction of the palatopharyngeal muscle within the posterior portion of the soft palate, which grips the epiglottis and the larynx so that they form a seal against the back of the soft palate. The typical mammalian pharyngeal elevator and constrictor muscles, which include the palatoglossus and the palatopharyngeus, represent a differentiation of the branchiomic musculature unique to mammals, especially in the fact that they are largely innervated by cranial nerve X (as opposed to the muscles used in swallowing in nonmammalian amniotes, which are primarily innervated by nerve VII) (Smith, 1992).

The action of these two seals can best be seen in suckling: first, with seal #1 applied, depression of the tongue behind the nipple allows milk to accumulate in the oral cavity; next, seal #1 is broken by lowering the tongue and releasing the tension on the anterior soft palate, and milk accumulates in the oropharynx, where seal #2 prevents it from entering the nasopharynx; finally, with the reapplication of seal #1 and the drawing backward of the tongue, milk is forced backward around the epiglottis into the esophagus. The continued application of seal #2 as the milk is

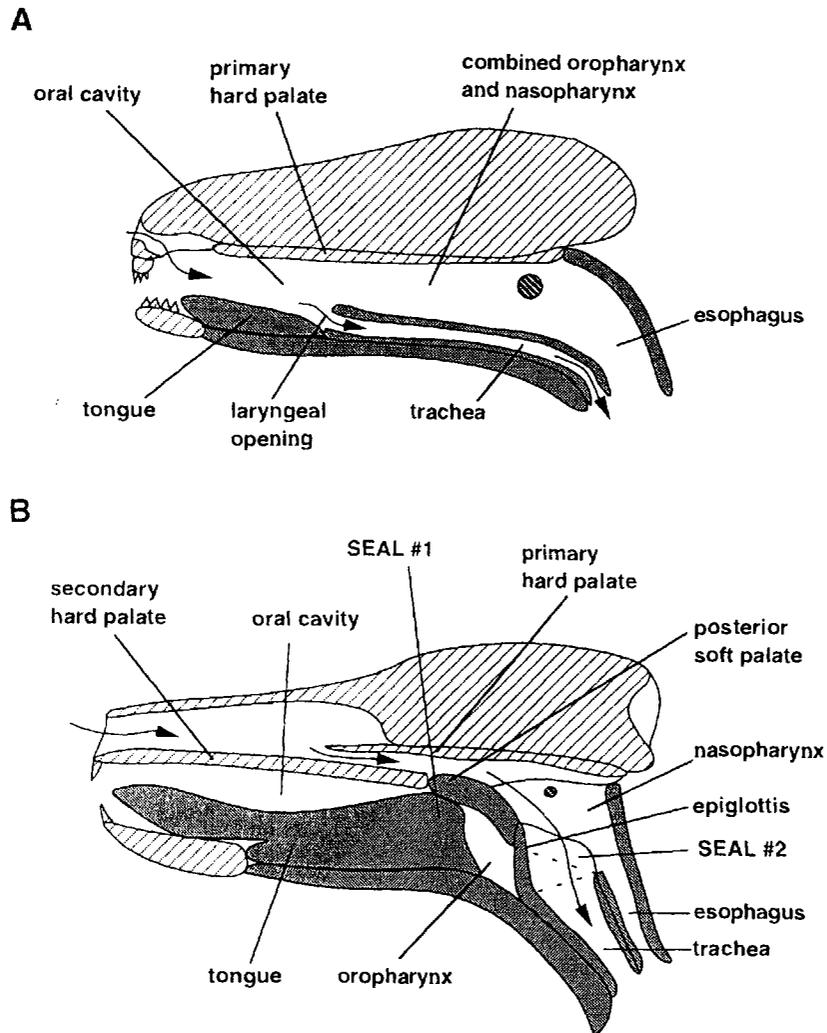


Figure 1. Schematic cutaway views of tetrapod oropharyngeal cavities: **A)** Condition in a nonmammalian amniote (modified from Smith, 1992, based on *Ctenosaura similis*, and from Kardong, 1995). **B)** Condition in mammal (modified from Crompton, 1995, based on *Didelphis virginianus*). Explanation: **arrows** = passage of air, **lightly hatched areas** = bone, **darkly hatched areas** = middle ear opening, **shaded areas** = soft tissue.

swallowed allows for a patent airway to be maintained during swallowing, so that suckling and breathing can occur at the same time. However, when mammals swallow solid food, seal #2 is invariably broken to allow its passage into the esophagus.

In adult mammals seal #1 acts to retain the food in the oral cavity until it has been masticated to a suitable consistency. The food then moves past seal #1 into the oropharynx, where a bolus is formed, and the bolus subsequently moves over the epiglottis, across the lower part of the nasopharynx, into the esophagus. During the swallowing of the food bolus seal #2 prevents the passage of food into the trachea. Note that in adult humans the larynx is moved posteriorly; the oropharynx and nasopharynx are confluent, and seal #2 is absent. Humans are the only mammals that are at risk of choking by accidentally inhaling food into the trachea, and are also the only ones that can voluntarily breathe through the mouth (see Lieberman, 1984).

Baleen whales invert the tongue to form a large pocket during feeding, presumably allowing the confluence of the oral cavity and oropharynx for the collection of plankton-laden water with the loss of seal #1 (F. W. Crompton, personal communication, following illustrations in Lambertsen, 1983). In this case the tight application of seal #2, preventing the mass of water from entering the trachea or esophagus, is clearly essential.

Despite the obvious utility of these seals in suckling, they probably originally evolved as a component of the mammalian swallowing reflex (Smith, 1992; F. W. Crompton, personal communication), where mastication reduces food to a bolus of small particles that is then swallowed in a single action down a relatively narrow food passageway. The morphology of the hard palate of derived cynodonts such as *Pachygenelus* suggests that it had a tensor veli palatini muscle (essential for forming seal #1) (Crompton, 1995). Presumably seal #2 was also present; the presence of seal #1 suggests that suckling may have occurred (Crompton, 1995), and the mammalian suckling reflex requires the interaction of the two seals. The inferred presence of these pharyngeal seals in derived cynodonts implies that they are mammalian sympleiomorphies.

SUSPENSION FEEDING IN MARINE TETRAPODS

Although the detailed mechanisms of prey capture in modern suspension feeders are poorly understood (Sanderson and Wassersug, 1993), a few general constraints may be inferred from the process. To be a successful suspension feeder without gill slits, an animal must be able to seal the back of the oral cavity to prevent engulfed water from entering the pharynx. It must also possess the appropriate facial musculature (lips and cheeks in at least the primitive mammal condition) that can resist the intraoral water pressure produced during feeding, and a way to collect and swallow small particulate food items. Unfortunately, many of the structures that confer these abilities on modern suspension feeders are composed of soft tissues that

are not easily characterized in the fossil record. In the absence of contradictory evidence, we consider the characteristics of modern nonavian diapsids representative of diapsid marine reptiles. All modern nonmammalian amniotes and adult terrestrial amphibians lack the features that would facilitate the transition from a carnivorous to a nonselective microphagous way of life.

When water is forced into the oral cavity during any type of suspension feeding, food particles must be retained and directed toward the pharynx while water is expelled from the oral cavity. Food may be caught in mucus or trapped in strainers that cover the area through which water exits the mouth (gills in fish and the sides and/or front of the mouth in whales). In animals without gills, a primary alternate route of escape for water is through the rear of the oral cavity. Separation of the oral and nasal cavities by hard and soft palates and the associated pharyngeal musculature are mammalian neomorphies that allow the formation of seals at the back of the mouth. The critical feature for suspension-feeding mammals is seal #2, which grips the epiglottis and larynx against the posterior pharynx, preventing the animal from inhaling or ingesting large volumes of water, and allowing it to collect and swallow food without disrupting the airway.

Among modern aquatic reptiles, turtles have been reported to suction feed, although they cannot seal the back of their oral cavity. Turtles apparently swallow water together with the food (D. Bramble, personal communication), and it seems unlikely that they could evolve suspension feeding from this mode of food intake. Thus, it is clear that nonmammalian amniotes are not incapable of suction feeding of some sort, although the separation of the oropharynx from the trachea by seal #2 appears to be a critical feature in suction feeding toothed whales (Werth, 1992). As ectotherms only require about one tenth the amount of food per day as endotherms, the actual amounts of water that might be accidentally ingested or inspired along with engulfed food would similarly be less.

Crocodiles might be potential candidates for developing a form of suspension feeding analogous to that seen in mammals. Crocodiles alone among modern reptiles can elevate the base of the tongue to form a seal between a hard palate and the tongue, and have a separation of the oral, nasal, and tympanic cavities, paralleling the mammalian condition (Smith, 1992). Although an anterior hard palate consisting of the maxilla and vomer is primitive for crocodiles, a posterior hard palate, including extensions of the pterygoids, is an apomorphy of the Eusuchia, the Cenozoic clade of primarily freshwater crocodiles (Benton and Clark, 1988). The oral, nasal, and pharyngeal cavities are continuous with each other in all other modern tetrapods, except some lacertilians (Smith, 1992) (see Figure 1A). In these groups, water pushed toward the back of the mouth could easily be forced through the pharynx and into the esophagus. Large volumes of accidentally ingested seawater could potentially cause serious osmotic stress to an animal, although living

marine diapsids do possess extrarenal salt glands which can excrete excess salt. Ingested salt might especially be a problem for suspension feeders, as they must process a greater number of mouthfuls containing a greater volume of water than a macrophagous animal.

Water may also be forced from the oropharyngeal cavity into the lungs. In modern baleen whales the epiglottis is permanently positioned to separate the entrance to the trachea completely from the oropharynx (Werth, 1992), but in the typical reptilian condition the larynx opens directly into the oral cavity at the base of the tongue. The laryngeal constrictor muscles may help guard against accidental inhalations; however, they are probably not as effective as complete separation of the two passages. The oropharyngeal cavity is also continuous with the choana and the tympanic area (Smith, 1992), both of which could be stressed by high internal water pressure associated with suspension feeding. Thus, the divisions of the mammalian oropharyngeal region may be vital to successful suspension feeding.

Facial muscles may also be needed for efficient plankton capture in the absence of gills. During continuous ram feeding, the sides of the face must resist the lateral component of the water pressure to prevent disruption of the flow past the straining devices. During intermittent ram feeding, contraction of facial muscles may be necessary to complete expulsion of water from the mouth. In whales, expulsion may be brought about by contraction of a sheet of muscles surrounding the buccal area and face (Lambertsen, 1983). Since facial muscles are not present in nonmammalian tetrapods, they lack convenient precursors to be modified for this function. Lips, which form a seal at the front of the mouth, allowing mammals to exclude water from the oral cavity, are also a uniquely mammalian character. Although whales do not have typically mammalian "lips" or "cheeks," their sheet of facial musculature is presumably homologous with the more generalized mammalian condition of facial muscles. Again, both cheeks and lips probably evolved in association with mastication and suckling.

After water is expelled from the mouth, the food must be collected and swallowed. In contrast with the mammalian condition, the primitive tetrapod buccal apparatus is not well suited for ingesting small particles. The unmodified tetrapod tongue does not have a mobile fleshy tip and can produce less movement independent of the hyoid than can a mammalian tongue (Smith, 1992). This may severely hinder an animal's ability to collect many small, widely distributed particles, and to form a bolus from them. Furthermore, nonmammalian tetrapods are poorly equipped to swallow small particulate food items; they generally ingest large lumps of food that they slowly force from the buccal cavity to the esophagus. Rather than swallowing their food with a quick swallowing reflex, as do mammals, nonmammalian tetrapods rely on the slow squeezing of the constrictor coli muscle, and often on head movements and gravity, to force food from the back of the mouth

into the esophagus, and swallowing is a more gradual process (Smith, 1992). This method of swallowing would not work well for collections of small particles: the action of the constrictor coli would simply squash such a food bolus, effectively redistributing the food throughout the mouth. Since the nonmammalian nasal and auditory cavities are continuous with the oropharyngeal cavity, they could also potentially become coated with food particles (Smith, 1992). Mammals do not encounter any of these problems when processing small particulate food since the oropharyngeal cavity is well divided and they have a sophisticated swallowing reflex ideally suited to the ingestion of small particles. The mammalian swallowing reflex probably arose in conjunction with teeth suitable for chewing (Smith, 1992).

CONCLUSION

In the absence of gill slits, the primitive tetrapod characters of an undivided oropharyngeal cavity, the absence of muscular lips and cheeks, a relatively immobile tongue, and lack of a coordinated swallowing reflex were not conducive to the evolution of suspension feeding. However, it is not inconceivable that a nonmammalian tetrapod could have evolved mammal-like features of the orobuccal region in a convergent fashion. For example, a posterior secondary palate could have developed earlier within the crocodylian line, in which case it might have been a feature of the Mesozoic marine crocodiles. Additionally, large, scaly plates could have acted in an analogous fashion to facial muscles in adding the necessary resistance to the cheeks of a potential continuous ram feeder. Certain birds and amphibians have also evolved a more mobile tongue (Smith, 1992; Bramble and Wake, 1985), and ornithischian dinosaurs probably had muscular cheeks (Norman and Weishampel, 1985). However, it would require the modification of a whole complex of primitive tetrapod characters, rather than any one key morphological feature, to permit the capture and ingestion of small particulate food items necessary for successful suspension feeding in a nonmammalian tetrapod.

Mammals, on the other hand, are already equipped with a suite of characters that allow them to perform many of the steps associated with successful suspension feeding. The ability to form a seal between the nasopharynx and the buccal cavity, and the possession of a fleshy mobile tongue and muscular lips and cheeks, are all part of the complex morphological changes associated with the evolution of mammalian mastication, swallowing, and suckling (Smith, 1992; Crompton, 1995). These features are ideally suited to the demands of suspension feeding, and they probably needed little modification to function effectively in this new context.

Marine reptiles also show a diversity of body sizes that overlap with modern vertebrate suspension feeders, so it is unlikely that their diet was constrained by

size. However, it is also true that there are no known aquatic reptiles that attained the very large body sizes seen in some present-day baleen whales, especially of those that feed by intermittent ram feeding, for which large size is a requirement (Sanderson and Wassersug, 1993). The largest Mesozoic marine reptiles include the pliosaur (short-necked plesiosaur) *Kronosaurus* and the ichthyosaur *Shonisaurus*, which both reached lengths of around 15 m (Carroll, 1988). Coincidentally, this is a similar size to that of the largest living toothed whale, the sperm whale (Nowak, 1991), so perhaps the lack of a suspension-feeding mode among Mesozoic marine reptiles may also explain why they did not reach sizes attained by the largest of the present-day baleen whales.

We believe that ecological constraints do not adequately account for the absence of suspension-feeding marine reptiles. Although the planktonic communities were different from those in Recent oceans, it is unlikely that there was too little productivity to support large-bodied suspension feeders at any time during the Mesozoic. In conclusion, we believe that morphological phylogenetic constraints and not ecological conditions may have been insurmountable obstacles in the evolution of nonmammalian tetrapod suspension feeders.

SUMMARY

Diapsid reptiles were common free-swimming marine predators during the Mesozoic. Although there was considerable diversity in their modes of predation, there were no suspension-feeding species. We suggest a morphological constraint prevented the evolution of this feeding type among Mesozoic marine reptiles, rather than scarcity of suitable planktonic prey. Aquatic tetrapod suspension feeders cannot use gill slits to create a unidirectional current through the buccal cavity, as do suspension-feeding fish. Instead they must feed by engulfing water containing many small planktonic animals and expelling water from the oral cavity via the mouth. The characters that enable baleen whales to feed in this way are all mammal neomorphies. Without the mammalian ability to form a tight seal at the back of the mouth, and to collect and swallow small particulate food, nonmammalian tetrapods, including Mesozoic marine reptiles, may have been limited to capturing larger individual prey items.

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