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## Diversity of Vertebrate Feeding Systems

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### SYNOPSIS

The vertebrate gut tube can be divided into “front-end” and “back-end” components according to topology, function, and research tradition. The purpose of front-end feeding systems is to acquire food to be delivered to the back-end for chemical digestion and assimilation. In accomplishing this, the feeding system faces as many as five separate mechanical tasks recognized as “feeding stages:” capture/subjugation, ingestion, transport, processing, and swallowing. In general, aquatic species exploit the high density of water to manipulate food items by modulating water flow through the mouth and pharynx. In contrast, terrestrial vertebrates typically employ some form of hyolingual feeding in which movements of the tongue and hyobranchial apparatus take the place of water flow in capturing, supporting and manipulating food. The condition of the bolus, when swallowed, varies markedly among taxa. Most ectotherms process their food little, if at all, whereas mammals and birds typically reduce their food to small particles (in mammals, by oral mastication; in birds, within the “gastric mill” of the gizzard). This fundamental difference probably relates to the need of endotherms to increase gut passage rates.

### INTRODUCTION

The study of vertebrate feeding proceeded historically along two lines. On the one hand, functional morphologists examined the myriad mechanisms by which vertebrates procure, process and swallow food. On the other, physiologists studied the structure and function of the gut during digestion and absorption of the food swallowed. These distinct fields of endeavor reflect not only different topological foci (“front end” vs “back end” of the gut tube),

but a long-standing division of the life sciences into morphology and physiology (Owen, 1866; Gegenbauer, 1878; Woodger, 1929; Russell, 1916; see Schwenk, 2000d for discussion).

Although the modern separation of physiological and morphological approaches in the study of vertebrate feeding is justified to some extent by differences in research methodology, their continued isolation seems to be more a manifestation of historical inertia than of biological reality. It is clear that form and function of the gut's front end and back end are inseparately related and that evolutionary changes in one are likely to have consequences for the other. This statement is so obvious as to be nearly superfluous. Nonetheless, it is worth emphasizing that the traditional partitioning of the field obscures the reality of feeding system evolution. Feeding function *Sensu Lato* requires the functional and anatomical integration of many separate components. The evolution of such integrated systems poses a major challenge in current evolutionary theory and is poorly understood in the context of traditional atomistic or reductionist approaches (Wagner and Schwenk, 2000; Schwenk, 2001b; Schwenk and Wagner, 2001). While some kind of rapprochement in the study of vertebrate feeding systems is widely acknowledged—indeed, it is a theme central to this volume—a truly synthetic understanding of the evolution of the feeding system still eludes us.

Given the functional and evolutionary integration that necessarily exists between front and back ends of the gut, it is not surprising that many common factors can be found to have influenced their phenotypes—ectothermy vs endothermy, and diet. Nonetheless, it is apparent that common environmental “problems” (e.g. herbivory) have often resulted in clade-specific solutions and that similarities among taxa in one end of the system (e.g. longer relative gut length) are not always paralleled in the other (e.g. different mechanisms of reduction). Thus, integration does not imply that front and back ends must always evolve in lock step—only that evolutionary changes in one are likely to have consequences for the other. Indeed, the extent to which feeding mechanisms and gut physiology are deterministically coupled remains an open and important question.

In this chapter we provide an overview of the mechanical tasks faced by vertebrates when they feed and consider some of the diverse ways these tasks are executed in different taxa. The feeding systems of larvae are not considered in this review due to limited space and the fact that many larval forms are exceptionally small, particularly in fishes, and operate within the different physical paradigm of low Reynolds numbers where viscous forces predominate. Clearly the question of how such organisms feed and metamorphose into a high Reynolds number world is of great interest, but one we cannot treat here. Readers are referred to reviews provided by Sanderson and Kupferberg (1999) and Wassersug and Yamashita (2001).

## MORPHOLOGY OF THE FEEDING APPARATUS

A complete account of feeding system morphology is beyond the scope of this chapter but an introduction to relevant structures and terminology will help to clarify the following sections. Overviews of trophic morphology in fishes can be found in Lauder (1985a), Vandewalle et al. (1994), and Motta and Wilga (2001), and for tetrapods in Bramble and Wake (1985), Hiiemae and Crompton (1985), Schwenk (2000a), and in the taxon-specific chapters within Schwenk (2000b). General references that include excellent sections on feeding structure include Liem et al. (2001) and Hildebrand and Goslow (2001). As discussed, a traditional consideration of feeding form and function begins at the head and ends at the esophagus, so we confine our discussion to front-end components of the feeding system.

The anterior end of the gut tube in deuterostome embryos opens through the stomadeum to form the mouth. Between the opening of the mouth and the entrance to the esophagus lies a cavity somewhat arbitrarily divided into an anterior buccal cavity and a posterior pharynx. A hallmark of vertebrate evolution was the origin of a series of U-shaped skeletal arches supporting the pharynx. These so-called visceral arches form from a novel embryonic tissue, the neural crest (e.g. Thorogood, 1993). Ancestrally the pharyngeal skeleton formed a kind of "basket" that functioned as a filter to trap suspended food particles brought into the mouth by ciliary currents. The evolution of joints and associated branchiomic musculature led to flexion of the skeletal elements and active pumping of water for feeding and respiratory function (Mallatt, 1996). This system is retained more or less unchanged in larval lampreys.

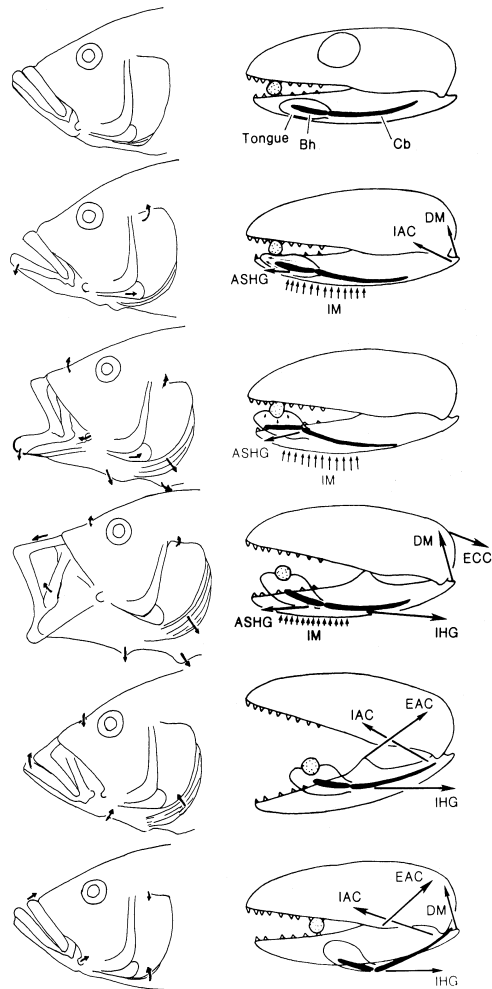
The origin of jaws from an anterior visceral arch was probably associated with increasingly active and predaceous behavior (Northcutt and Gans, 1983) and a transition from suspension feeding to prehension of individual food particles (Mallatt, 1984). Arguably, jaws were a key innovation in the vertebrate lineage, leading to an explosion of gnathostome (jawed vertebrate) diversity and ultimately the demise of most jawless clades. We can reasonably infer that a great deal of this diversity was engendered by the trophic flexibility of jaw-based feeding systems, which permitted the invasion of new adaptive zones. Thus the jaws and their associated teeth and musculature, were established early in vertebrate evolution as the central elements of vertebrate feeding system evolution. They are the focus of most feeding studies.

Vertebrate jaws are complex structures with multiple evolutionary and developmental sources. They develop from cartilages of the first visceral arch, i.e. the palatoquadrate in the upper jaw and the mandibular (or Meckel's) cartilage in the lower jaw. In most adult vertebrates the jaws are primarily composed of dermal (membrane) bones that invest the cartilages during later development. A few parts ossify directly as endochondral bones, notably at

the jaw joint, to form an upper quadrate bone and a lower articular, but the cartilages usually atrophy and in many species disappear. In basal bony fishes and tetrapods, the upper jaw fuses to other dermal bones of the facial skeleton, but retains independence, or at least limited mobility, in many taxa, especially fishes (e.g. Lauder, 1985a; Motta and Wilga, 2001). Indeed, the ability to protrude the jaws is an essential component of feeding in many fishes, particularly in suction feeders (Fig. 1.1) (Lauder, 1985a; Westneat, 1990; Motta and Wilga, 2001; Wilga et al., 2001). In tetrapods, the jaws are never protrusible; however, several lineages, notably birds and squamate reptiles, have evolved kinetic joints in the dermal skull so that the upper jaws and other skull elements can flex relative to the braincase (Beecher, 1962; Frazzetta, 1962; Bock, 1964; Zusi, 1993; Herrel et al., 1999; Hoese and Westneat, 1996; Arnold, 1998; Bout and Zweers, 2001; Metzger, 2002). Such “cranial kinesis” is most highly developed in advanced (macrostomatan) snakes, in which upper and lower jaw and palatal bones are independently and unilaterally mobile (Gans, 1961; Cundall and Greene, 2000). This increases gape and generates ratchet movements of the toothed elements, one side at a time, to pull the snake’s head and body over a prey item.

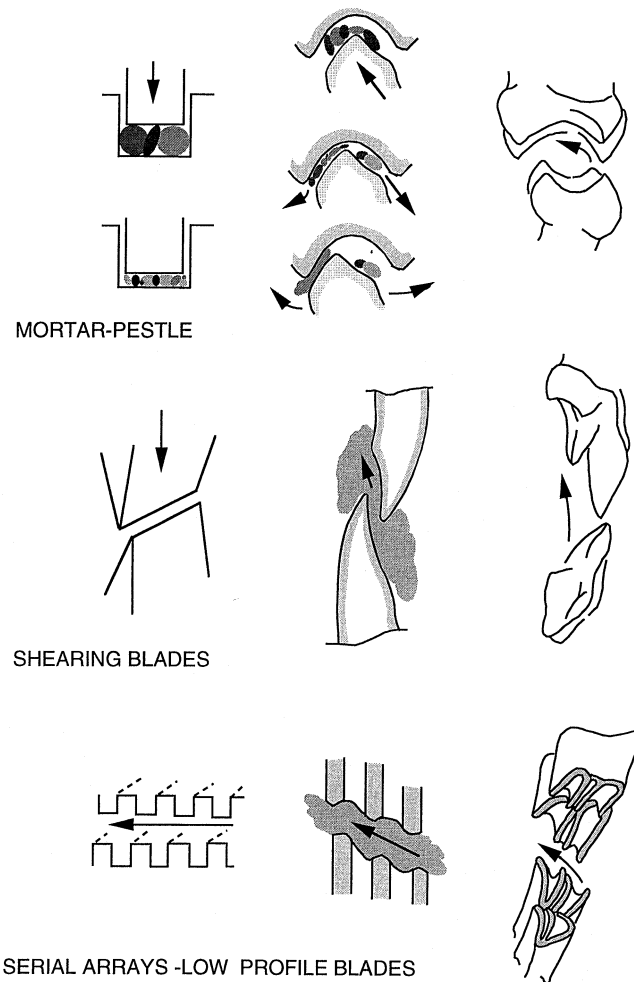
Mammals are distinguished by an akinetic and generally robust skull (Davis, 1961). The endochondral jaw joint bones of other vertebrates have been miniaturized and displaced to the middle ear in mammals, where they contribute to the auditory apparatus (Allin, 1975; Novacek, 1993; Rowe, 1996). A new jaw joint has evolved between two dermal bones, the dentary of the lower jaw and squamosal of the upper (the latter element is usually fused with others to form the temporal bone). A diagnostic feature of living mammals and closely related fossil taxa is the presence of only a single bone, the dentary, in the lower jaw. The dentary is, itself, a developmental composite, comprising the fusion of six separate *Anlage* (Atchley, 1993). The dentary bones of each side are joined anteriorly by a fibrous symphysis to form the mandible. The strength of the symphysis and the extent to which it transmits forces from one half of the mandible to the other varies among species (e.g. Beecher, 1979; Lieberman and Crompton, 2000).

Teeth evolved in association with jaws. They are composed primarily of dentine and enamel, ancient hard tissues that invested the armor plates of ancestral jawless fishes (Butler and Joysey, 1978; Reif, 1982). Primitively, teeth were found throughout the buccal cavity and pharynx on various elements of the palate and pharyngeal skeleton, but palatal and pharyngeal teeth are often lost, especially in tetrapods. The marginal teeth of the jaws are restricted to the dentary of the lower jaw, and the maxilla and premaxilla of the upper jaw in bony vertebrates. In mammals and crocodylians, the teeth are rooted in deep sockets within the bone, but in most vertebrates they are cemented to the apical or medial jaw surfaces. The exposed, or crown portion of the tooth varies extensively in form, even among closely related species in some cases, variation that may be functionally related to



**Fig. 1.1.** Feeding in aquatic vertebrates usually involves manipulation of food particles indirectly through the modulation of water flow (left), whereas in tetrapods, the tongue and hyobranchial apparatus take over this role (right). Suction feeding in bony fishes (left) results from an explosive expansion of the mouth and pharynx caused by protrusion of the jaws, hyoid retraction, and opercular abduction. The negative pressure generated within the mouth causes an inrush of water that drags prey in. Tetrapods often capture food with the tongue which also supports and manipulates it within the mouth (right). Cyclical movements of the hyolingual apparatus transport the food item back to the pharynx for swallowing. ASHG: anterior suprahyoid muscle group; Bh: basihyal element of hyobranchium; Cb: ceratobranchial element of hyobranchium; DM: depressor mandibulae muscle; EAC: external adductor muscles; ECC: epaxial cervical muscles; IAC: internal adductor muscles; IHG: infrahyoid muscle group; IM: intermandibularis muscle. Left side figures from Karel F. Liem (1979). Reprinted by permission of Wiley-Liss, Inc., a subsidiary of John Wiley and Sons, Inc. Right side figures from Bramble and Wake (1985), reprinted by permission of the publisher and President and Fellows of Harvard College.

the types of food eaten and the manner in which it is procured and processed in the mouth (Fig. 1.2). This is especially true for mammals because they masticate their food (see later). The pharyngeal teeth of some derived teleost fishes show similar, diet-based adaptations in crown form (e.g. Liem, 1973; Sibbing, 1991). Tooth reduction or loss is relatively commonplace among many clades. Turtles and birds have lost their teeth altogether and replaced them with a horny (keratinous) investment of the jaws called a beak or bill.



*Fig. 1.2.* Crown form in mammalian teeth is closely tied to the nature of the food eaten. Functional specialization of teeth is part of a suite of derived mammalian traits associated with the evolution of mastication. Mastication results in comminution of food, i.e. its reduction to a slurry of fine particles mixed with saliva. From Hiemae (2000), reproduced with permission of Elsevier Science.

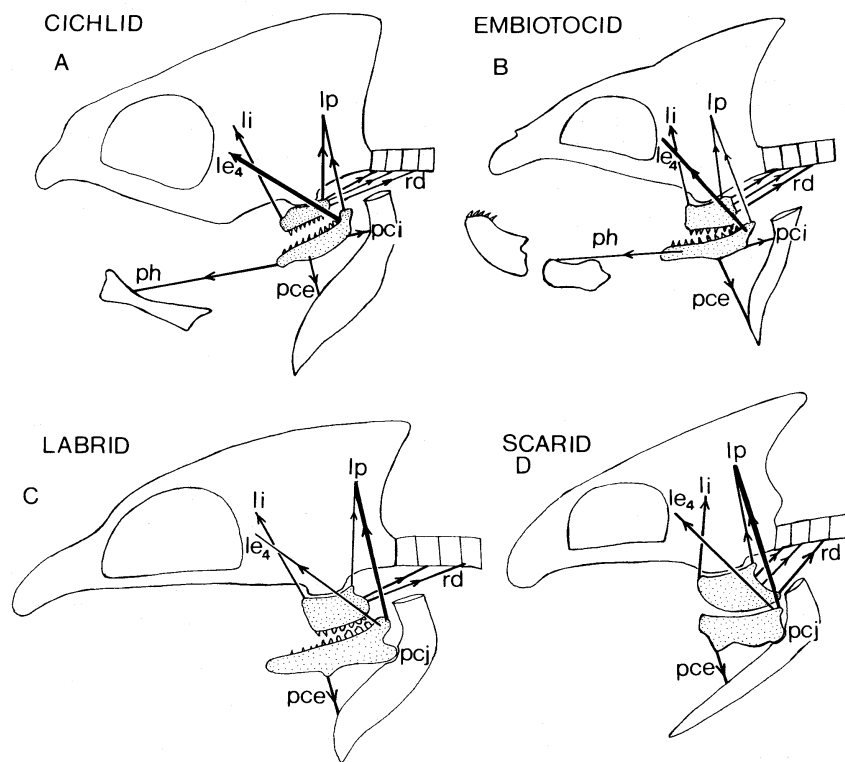
In most vertebrates, lower jaw motion is mostly limited to dorsoventral movements. Jaw closing is effected by adductor mandibulae musculature that is variously subdivided in different taxa. Adductor muscles run from the cranium to the lower jaw and are innervated by the trigeminal nerve (cranial nerve V). In most fishes, jaw opening is caused by the action of ventromedial hypobranchial muscles that run anteriorly from the pectoral girdle to the lower jaw (Wilga et al., 2000). These are innervated by spino-occipital nerves and/or the hypoglossal (c.n. XII). In nonmammalian tetrapods, a depressor mandibulae takes over jaw opening. It runs from the back of the cranium and neck to the retroarticular process of the mandible, depressing it by pulling up behind the jaw joint. Since this muscle is developmentally and evolutionarily derived from the superficial constrictor musculature of the throat, it is innervated by the facial nerve (c. n. VII). Jaw opening is often accompanied by elevation of the cranium caused by contraction of the epaxial neck musculature. Mammals use a novel muscle, the digastric, to depress the lower jaw. Its name derives from the fact that in many species it comprises two distinct bellies separated by a short tendon, each innervated by a different nerve (c.n. V and VII). It runs from the paroccipital process of the skull base to the anterior end of the mandible.

During the evolution of mastication (see below) mandibular movements in most mammals became complex. They are mostly dorsoventral in carnivorous species but in herbivores include dramatic mediolateral and/or antero-posterior movements. The jaw joint is variously modified to accommodate such mobility. Mastication in mammals is associated with the evolution of a novel adductor muscle, the masseter, running from the zygomatic arch (cheek bone) to the lateral surface of the mandible. The masseter adds lateral and anterior components to jaw movement that are balanced by the dorsal and medial components of pterygoideus and temporalis adductors.

The pharyngeal skeleton is an essential part of the feeding apparatus in both fishes and tetrapods. Ancestrally, there were seven visceral arches constituting the pharyngeal skeleton (splanchnocranium) of gnathostomes. Each arch is composed of several jointed elements joined in the ventral midline. The first, most anterior arch is the mandibular, comprising upper and lower jaws. The second is the hyoid arch and the remaining five the branchial (or gill) arches. The upper part of the hyoid arch in fishes (hyomandibula) runs from the jaw joint to the neurocranium and variously supports, braces or suspends the jaws. It is homologous to the columella (stapes), a middle ear ossicle, in tetrapods. The lower part (ceratohyal) is usually highly mobile. When at rest, the paired ceratohyals lie within the arc of the lower jaw, but when pulled back by hypobranchial muscles, the hyoid arch swings posteroventrally, depressing the floor of the pharynx and increasing its volume. Rapid hyoid retraction, along with elevation of the neurocranium and lateral movement of the opercular bones, are used by many fishes to generate suction within the mouth and pharynx to create currents for suspension

feeding, prey capture, and/or prey manipulation (see below). Many elements of the pharyngeal skeleton in bony fishes bear teeth (as do palatal and neurocranial bones) which are used to hold, grasp, manipulate, transport, and process food. In some teleosts, upper and lower tooth-bearing elements of the pharyngeal arches interact to form an internal set of "pharyngeal jaws" used in elaborate manipulatory and processing behavior (Liem, 1973; Liem and Osse, 1975; Liem and Greenwood, 1981; Lauder, 1983b, 1985a; Sanford and Lauder, 1989; Sibbing, 1991; Vandewalle et al., 1994; Galis and Drucker, 1996), a condition known as "pharyngognathy" (Liem and Greenwood, 1981; Fig. 1.3).

Fish use the pharyngeal skeleton, in particular the hyoid arch, to create feeding currents through volumetric changes of the pharynx. This is only possible in water because the density of prey is closely matched by the surrounding density of the medium. Rapid water flow is thus able to overcome



*Fig. 1.3.* Schematic representation of the pharyngeal jaw apparatus in four families of teleostean fish. The pharyngeal jaws are lightly stippled. Letters refer to muscle groups that act on the jaws to produce complex crushing, grinding, and transport movements. From Liem and Greenwood (1981), reproduced with permission of the Society for Integrative and Comparative Biology.

the prey's inertia. Tetrapods could not employ such inertial suction when they first began to feed in the terrestrial environment, but they nonetheless exploited the hyoid mobility inherited from their piscine ancestors when feeding on land (Shaffer and Lauder, 1988; Gillis and Lauder, 1994, 1995; Reilly, 1996). They accomplished this primarily through the evolution of a novel structure, the mobile, muscular tongue. The tongue evolved by elaboration of hypoglossal muscles associated with the hyoid and the first two or three branchial arches (Kallius, 1901). The reduced (compared to fishes) pharyngeal skeleton of tetrapods is called the hyobranchial apparatus or hyobranchium, and it supports the tongue and throat musculature (e.g. Fürbringer, 1922; Weissengruber et al., 2003). The hyobranchium of nonmammalian tetrapods is often inaccurately referred to as the "hyoid apparatus," a term appropriately applied only to mammals in which the branchial arch contribution is lost or greatly reduced (Schwenk, 2000a). In combination, the tongue and hyobranchium are called the hyolingual apparatus. Instead of modulating water flow, movements of the tetrapod hyobranchium move the tongue which, in effect, takes the place of water in capturing, supporting, and manipulating food particles (Fig. 1.1). Tongue movement that is extrinsically generated by hyobranchial movement is enhanced in many tetrapods by intrinsically generated shape changes of the tongue's soft tissues (see below). In secondarily aquatic tetrapods that revert to suction feeding, the hyobranchial apparatus is once again used to modulate the flow of water by changing pharyngeal volume (Lauder, 1985a; Van Damme and Aerts, 1997; Deban and Wake, 2000; Aerts et al., 2001; Lemell et al., 2002). It is noteworthy that in these species the tongue is almost always reduced or even lost — an indication of its uniquely terrestrial role in feeding (Bramble and Wake, 1985).

The tongue is a critical element of the tetrapod feeding system, largely overlooked in earlier studies of feeding. In many taxa, it participates in all stages of feeding, from prey capture to swallowing. Its morphology is diverse, ranging from little more than an epithelium covered part of the hyobranchium, to an astoundingly complex muscular organ capable of extreme changes in length and shape. The protean nature of tongue form in some taxa (notably mammals and some squamate reptiles) arises from its unusual biomechanical properties. The tongue is one of the very few vertebrate organs capable of hydrostatic deformation (Owen, 1868; Kier and Smith, 1985; Smith and Kier, 1989). Such so-called "muscular hydrostats" comprise solid muscle masses with a complex histology in which fiber systems are arrayed orthogonally, sometimes including helical systems as well (Kier and Smith, 1985; Smith and Kier, 1989; Schwenk, 2001a). Because the organ retains a constant volume and the intracellular fluid within it is incompressible, local or global reductions in diameter cause elongation and/or shape change. For example, myrmecophagous mammals use extreme length changes in their serpentine tongues to probe ant and termite nests (Reiss,

2000); generation of intraoral suction within the buccal cavity during suckling in infant mammals is made possible by an oropharyngeal seal at the back of the mouth created by shape changes in the tongue (German and Crompton, 2000); lizards, terrestrial turtles and mammals form humps and cup-shaped depressions in the tongue to hold and push the bolus during hyolingual transport through the mouth (Bramble and Wake, 1985; Hiiemae, 2000; Schwenk, 2000c); and hydrostatic elongation of the tongue in combination with a uniquely shaped hyobranchium, provides the explosive trigger that projects the chameleon's tongue out of its mouth (Wainwright and Bennett, 1992).

## OVERVIEW OF VERTEBRATE FEEDING

### Feeding Mode, Sensory Biology and Foraging Strategy

Before a feeding bout can begin, it is necessary for an animal to find a potential food item and to identify it as appropriate. This requires the use of various sensory systems and some kind of foraging strategy. The evolutionary interplay of sensory function, foraging, and feeding mode has rarely been explored in detail, but the need for their coordinated function is obvious. Vitt et al. (2003), for example, provide a case study of squamate reptiles showing that historical changes in the feeding system have had cascading effects on the evolution of sensory systems and ultimately, community ecology and geographic distribution. The study illustrates that an understanding of the integration of feeding mode, sensory biology, and foraging mode can potentially lead to compelling explanations for higher level patterns, in this case, the structuring of squamate communities on a global scale (Vitt et al., 2003). These patterns are necessarily taxon specific but the important role other systems and behavior play in feeding biology is noteworthy.

The remainder of this chapter primarily concerns feeding function from the moment an appropriate prey item is within striking distance until it passes into the esophagus. In studying this behavior, several stages of feeding are formally recognized.

### Vertebrate Feeding Stages

In order to acquire and digest food successfully, it is necessary for an animal to proceed through a series of different mechanical tasks, concluding with passage of the food bolus into the esophagus. These tasks are identified technically as "feeding stages" to highlight their different functions and to facilitate description and comparisons of feeding across taxa (Bramble and Wake, 1985; Hiiemae and Crompton, 1985; Schwenk and Throckmorton, 1989; Schwenk, 2000a). However, it is necessary to state several caveats about

feeding stages before describing them. First, as noted, their recognition is based on the differing functional roles they play during a feeding bout. As such, feeding stages can be thought of as phenotypic “solutions” to a series of mechanical “problems” encountered during the course of getting food from the environment into the esophagus. There is potentially more than one solution to any given mechanical problem, so different taxa sometimes carry out the same feeding stage in mechanistically different ways. This leads to the second point, namely that use of a common name for the “same” feeding stage in different species should not be taken as an assertion of evolutionary homology. The homology of feeding stages among taxa is an open and critical research question, as is, for that matter, the extent to which the stages can be considered evolutionary “characters” at all (Reilly and Lauder, 1990; Smith, 1994; Schwenk, 2000a; Wainwright and Friel, 2001; McBrayer and Reilly, 2002b). Third, any given species or individual might exhibit only a subset of all possible feeding stages (described below). Individuals might also vary in the particular feeding stages manifested during one feeding bout compared to another, or might vary the mechanism employed during a particular feeding stage depending on the nature of the food eaten or other local circumstances. Finally, although some stages must necessarily precede other stages (e.g. capture must precede swallowing), some do not always occur sequentially. For example, capture/subjugation and ingestion are often combined into a single stage (ingestion), whereas processing and transport cycles are occasionally alternated or interspersed (e.g. Hiiemae and Crompton, 1985; Schwenk and Throckmorton, 1989; Hiiemae, 2000; Schwenk, 2000c; McBrayer and Reilly, 2002a).

In all vertebrates, feeding emerges from the complex coordination of skull, jaw, tongue, and hyobranchial movements. In tetrapods especially, these movements are rhythmic and cyclic, leading to the suggestion that they are controlled by pattern generators in the central nervous system (Dellow and Lund, 1971; Thexton, 1973; Hiiemae, 2000). Bramble and Wake (1985) proposed that there is a basic or “model” feeding cycle that we might infer represents the ancestral or primitive pattern of coordinated movements and motor patterns in tetrapod feeding. There has been a great deal of discussion regarding the utility of the Bramble-Wake model in predicting the feeding kinematics of different taxa and during different feeding stages (e.g. Schwenk and Throckmorton, 1989; Reilly and Lauder, 1990; Delheusy and Bels, 1992; Bels et al., 1994; Lauder and Gillis, 1997; Schwenk, 2000c; Herrel et al., 2001), with no consensus emerging. Regardless, the critical point is that tetrapod feeding, at least, results from rhythmic, cyclical, and coordinated movements of the aforementioned parts. The fundamental unit of this behavior is the “gape cycle,” representing a single excursion of the jaws from closed to open and back to closed (Bramble and Wake, 1985; Hiiemae and Crompton, 1985; Schwenk, 2000a). Movements of all other components of the feeding system are usually described relative to the gape cycle to facilitate comparisons,

although in some cases jaw movements are relatively trivial compared to movements of other parts, such as the hyobranchial apparatus. A single feeding bout represents a variable number of sequential gape cycles, with modulation of kinematic patterns occurring throughout, depending on the mechanical task at hand (the feeding stage) and the position and condition of the bolus. Although the different feeding stages outlined below can sometimes be differentiated qualitatively as well as quantitatively, only rarely are the kinematic transitions between them sharply defined.

### **Capture/Subjugation**

Active prey must first be captured and subjugated before it can be eaten. Once subdued, it can be brought into the mouth (ingestion). These actions represent nominally the first and second stages of feeding. However, in most vertebrates food is captured with the mouth so that capture and subjugation of prey occurs at the same time that it is moved into the oral cavity. Thus, in most vertebrates the single stage of ingestion accomplishes all three functions. However, in many species, particularly mammalian predators that feed on relatively large prey, a separate capture/subjugation stage is necessary before the food can be ingested. Such mammals typically run down and attack prey with the forelimbs and jaws to subdue and kill them (Ewer, 1973; Van Valkenburgh, 1996). Once quiescent, the prey can be consumed and ingestion initiated. Primates also typically use the forelimbs to grab, manipulate and sometimes kill a food item before placing it in the mouth. Although less common, a separate capture/subjugation stage occasionally occurs in nonmammalian taxa, such as fish-spearing with the bill in some wading birds, or raptorial capture and killing with the feet in other birds. The venomous crotalid snakes (rattlesnakes and kin) are particularly illustrative because after an envenomating bite they release their prey and allow it to die before ingesting it (Cundall and Greene, 2000). Rarely, capture and subjugation are performed as separate tasks, as in constricting snakes that capture a prey item with the jaws, but hold and subjugate it in coils of the body until it can be transported (Cundall and Greene, 2000).

### **Ingestion**

Ingestion refers to the transfer of a food item from the environment into the oral cavity. As noted, in most vertebrates this is accomplished with the mouth so that capture/subjugation and ingestion are combined into a single ingestion stage.

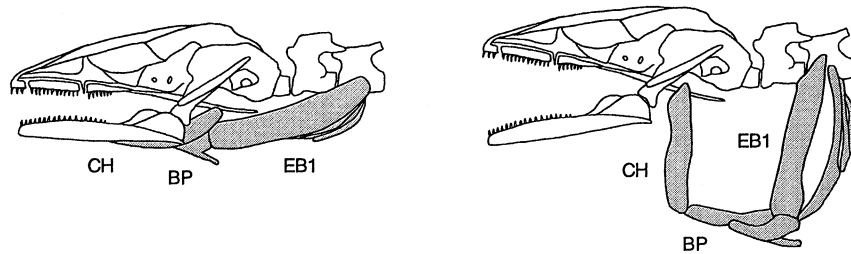
In aquatic vertebrates, ingestion occurs in one of three ways: suspension feeding (sometimes inaccurately called "filter feeding"), suction feeding or jaw prehension. In suspension feeding, small food particles are collected from the water surface, water column or the benthos when water is passed through a porous structure, such as the gill rakers of the pharyngeal skeleton in many fishes or the baleen plates of mysticete whales (e.g. Northcott and

Beveridge, 1988; Sanderson and Wassersug, 1993; Goodrich et al., 2000; Werth, 2000b). Many aquatic birds use elaborations at the margins of the bill to filter algae and other suspended food particles from the water (Zweers et al., 1977, 1995; Kooloos et al., 1989). Some freshwater turtles draw small, floating food particles into the mouth (Belkin and Gans, 1968), trapping them in esophageal papillae when the water is expelled (Vogt et al., 1998).

Suspension feeders either actively pump water into the mouth and pharynx, or engulf suspended food particles as they move their bodies forward with mouth agape. Many fishes can shift between these two modes of suspension feeding. However, drawing larger food items into the mouth requires the rapid generation of substantial negative pressure within the mouth and pharynx. This is referred to as suction feeding. As water is accelerated into the mouth, its rapid flow draws the prey along with it. There is a continuum among taxa in the amount of suction used and the extent to which the prey moves into the mouth versus the mouth over the prey (Norton and Brainerd, 1993; Liem, 1993; Nemeth, 1997; Van Damme and Aerts, 1997; Summers et al., 1998; Wainwright et al., 2001). In "inertial suction" the prey item is accelerated relative to a fixed point and moved into the mouth along with the water, whereas in "compensatory suction" the negative pressure generated by the predator is only enough to overcome the effects of its own bow wave as it moves forward, engulfing a stationary prey item. Such "ram feeders" attempt to mitigate the pressure wave by means of a large gape, capacious pharynx and unilateral flow of water.

In bony fishes, suction is generated by an explosive expansion of the mouth and pharynx caused by expansive movements of the jaws, neurocranium, opercular bones and pharyngeal skeleton, especially retraction and depression of the hyoid arch (e.g. Lauder, 1983a, b, 1985a, b; Müller and Osse, 1984; Bemis and Lauder, 1986; Bemis, 1987; Lauder and Shaffer, 1993; Liem, 1993; Gillis and Lauder, 1995; De Visser and Barel, 1998; Ferry-Graham and Lauder, 2001; Grubich, 2001; Westneat, 2001; Sanford and Wainwright, 2002). Upper jaw protrusion and kinesis create a small, round, anteriorly directed gape that increases water velocity and targets prey directly in front of the fish (Fig. 1.1). The cartilaginous elasmobranchs obviously lack the opercular apparatus and other elements of the bony fish skull and rely primarily on retraction of the hyoid arch to generate suction (Wu, 1994; Wilga and Motta, 1998; Edmonds et al., 2001; Motta and Wilga, 2001). A labial cartilage functions to restrict gape and accelerate flow.

Many aquatic tetrapods, especially salamanders and turtles, have secondarily reverted to suction feeding (Erdman and Cundall, 1984; Lauder, 1985; Lauder and Shaffer, 1985; Elwood and Cundall, 1994; Lauder and Reilly, 1994; Van Damme and Aerts, 1997; Deban and Wake, 2000; Aerts et al., 2001; Deban and Marks, 2002; Lemell et al., 2002). As in fish, suction is generated by rapid expansion of the pharynx (Fig. 1.4). These taxa typically have an elaborate and robust hyobranchial apparatus that is articulated in



*Fig. 1.4.* Skull (white) and hyobranchial apparatus (gray) of a larval aquatic salamander in lateral view. At left, the hyobranchium is at rest, lying flat within the throat. When retracted, at right, the downward pivoting of the ceratohyal and the rest of the hyobranchial apparatus causes a massive expansion of buccal and pharyngeal cavities to generate suction for the modulation of water flow. BP: branchial plate; CH: ceratohyal; EB1: first epibranchial. From Deban and Wake (2000), reproduced with permission of Elsevier Science.

such a way that at rest it lies flat in the floor of the mouth and throat, but when retracted it unfolds, dropping dramatically to vastly increase pharyngeal volume (e.g. Van Damme and Aerts, 1997; Deban and Wake, 2000). Esophageal expansion during the strike in some turtles helps prevent back pressure, suggesting that suction may be compensatory rather than inertial in these species (Lauder and Prendergast, 1992; Lemell et al., 2000). Long-necked turtles use a snake-like strike to propel the head toward the prey (Weisgram and Splechtina, 1992; Van Damme and Aerts, 1997, 2002; Aerts et al., 2001).

Patent gill slits allow fish and larval salamanders to draw water through the pharynx in one direction during suction feeding (unidirectional flow), whereas in metamorphosed salamanders, turtles, and mammals the water must exit the mouth during the compressive stage immediately following capture (bidirectional flow), leading to a putative mechanical inefficiency (Lauder and Shaffer, 1986). Nonetheless, feeding performance in some highly aquatic adult salamanders is superior to larval forms with unidirectional flow, suggesting that morphological and behavioral adaptations can overcome this potential handicap (Miller and Larsen, 1989). A very few salamanders feed underwater using the terrestrial mechanism of tongue prehension (Deban and Wake, 2000).

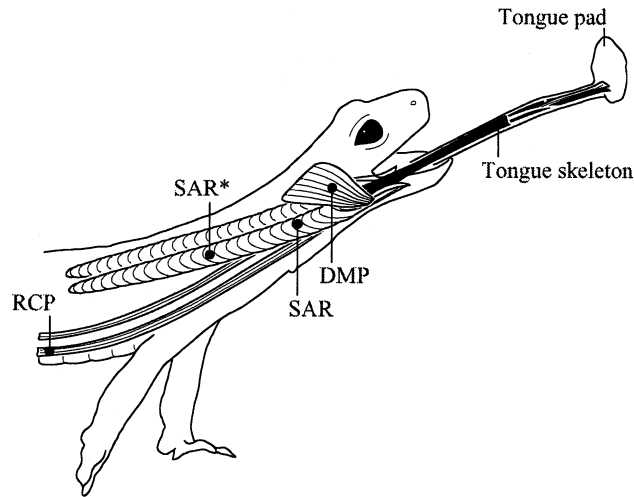
All neonate mammals (with the possible exception of some monotremes) use suction for ingestion of milk (e.g. German and Crompton, 2000) but suction feeding is uncommon in adult mammals. Walrus use suction to suck molluscs from the substrate (Kastelein et al., 1994) and several other pinnipeds may also use suction (Werth, 2000b). Some blunt-headed cetaceans, such as pilot whales, probably use suction for ingestion of food items such as squid (Werth, 2000a, b).

Jaw prehension of prey during ingestion is less common in aquatic vertebrates than suction and suspension feeding. Large, predaceous sharks, such as lamniforms and carchariniforms tend to overcome a prey item by

rapidly overtaking it, either engulfing it within the mouth or biting it. Some specialized biters, however, remove mouth-sized chunks of flesh from their prey using protrusible jaws and rows of sharp, serrated teeth (Frazzetta and Prange, 1987; Frazzetta, 1988, 1994; Motta and Wilga, 2001; Wilga et al., 2001). Some bony fish use the jaws and marginal teeth to grasp prey directly or to scrape food, such as algae, off the substrate (e.g. Liem, 1980; Turingan and Wainwright, 1993; Wainwright and Turingan, 1993; Alfaro and Westneat, 1999; Wainwright et al., 2000; Alfaro et al., 2001). Many species bite pieces from large prey in much the way some sharks do (Liem, 1980; Alfaro et al., 2001). Jaw feeding fish typically retain the use of suction to manipulate and transport prey within the pharynx. Crocodylians use the jaws to capture prey in water, typically with a rapid, sideways jerk of the head (Busbey, 1989; Davenport et al., 1990; Cleuren and De Vree, 2000). Some species, such as gavials, have long, narrow snouts lined with needle-like teeth specialized for the prehension of fish in water (Cleuren and De Vree, 2000).

Either the tongue or the jaws are used as prehensile organs during ingestion in the vast majority of terrestrial vertebrates (Schwenk, 2000b). During metamorphosis, salamanders with aquatic larvae shift from suction feeding to lingual prehension (Lauder and Shaffer, 1988; Shaffer and Lauder, 1988; Reilly, 1996; Deban and Marks, 2002), a transition associated with remodeling of the hyobranchial apparatus, closure of the gill slits and development of the tongue (Wake, 1982; Wake and Deban, 2000). Some aquatic salamanders remain specialized suction feeders as adults, but postmetamorphic terrestrial species feed in water only infrequently and inefficiently. Tongue protrusion during lingual prehension is coupled to hyobranchial protraction, which varies from modest to extreme (e.g. Larsen et al., 1989; Findeis and Bemis, 1990; Lauder and Reilly, 1994; Wake and Deban, 2000; Deban et al., 2001). In plethodontids the hyobranchial apparatus is folded into a cylinder and protruded or projected out of the mouth along with the tongue (Fig. 1.5; Lombard and Wake, 1976; Deban et al., 1997; Wake and Deban, 2000). Prey items adhere to the sticky tongue pad. Virtually all terrestrial salamanders ingest prey with lingual prehension, but some, in particular larger species, resort to jaw prehension for large prey (Wake and Deban, 2000).

Most frogs are also obligate lingual feeders, although some species occasionally approach large or difficult to capture prey closely enough to use the jaws (Anderson, 1993; Nishikawa, 2000). Frogs use three different mechanisms of tongue protrusion, i.e. mechanical pulling, inertial elongation, and hydrostatic elongation, each manifesting a characteristic suite of functional traits. Although hydrostatic elongation of the tongue is commonplace in mammals and some lizards, it is exceptional in frogs and restricted to species in two families with unusual tongue morphology (Ritter and Nishikawa, 1995; Nishikawa et al., 1999; Nishikawa, 2000). Unlike



*Fig. 1.5.* Schematic representation of tongue projection during lingual prey capture (ingestion) in a plethodontid salamander. Note that the hyobranchial apparatus (tongue skeleton) is folded and projected from the mouth along with the tongue. DMP: depressor mandibulae muscle; RCP: rectus cervicis profundus muscle; SAR: subarcualis rectus muscle. From Deban and Dicke (1999), reproduced with permission of The Company of Biologists.

salamanders and lizards, the hyobranchial apparatus in these frogs participates only indirectly in tongue protrusion.

Among lepidosaurian reptiles, tuatara and iguanian lizards rely on lingual prehension (Schwenk and Throckmorton, 1989; Bels et al., 1994; Schwenk, 2000c). A few species are obligate tongue feeders but most decrease tongue protrusion distance as prey become larger, eventually shifting to jaw prehension (Gorniak et al., 1982; Schwenk and Throckmorton, 1989; Schwenk, 2000c; Kardong and Bels, 2001). Tongue protrusion during feeding is coupled to hyobranchial protraction, as in salamanders, but movement is much more limited and the hyobranchium never leaves the mouth. The tongue curls around the margin of the lower jaw and prey adhere to its sticky, papillose surface. Chameleons have modified this basic system by inserting a ballistic, projection phase in which the tongue is launched off a supporting process of the hyobranchium out of the mouth (Schwenk and Bell, 1988; Wainwright and Bennett, 1992; Schwenk, 2000c). The tongue surface is actively dimpled during prey prehension, generating suction to provide extra adhesion for relatively large prey (Herrel et al., 2000). With very few exceptions, the remaining lizards are obligate jaw feeders. Many of these have kinetic skulls that improve the speed and precision of jaw capture by allowing simultaneous movement of upper and lower jaws in a pincer-like action (Frazzetta, 1983; Schwenk, 2000c; Metzger, 2002). Snakes have taken jaw prehension and cranial kinesis to its most extreme form (Cundall and Greene, 2000).

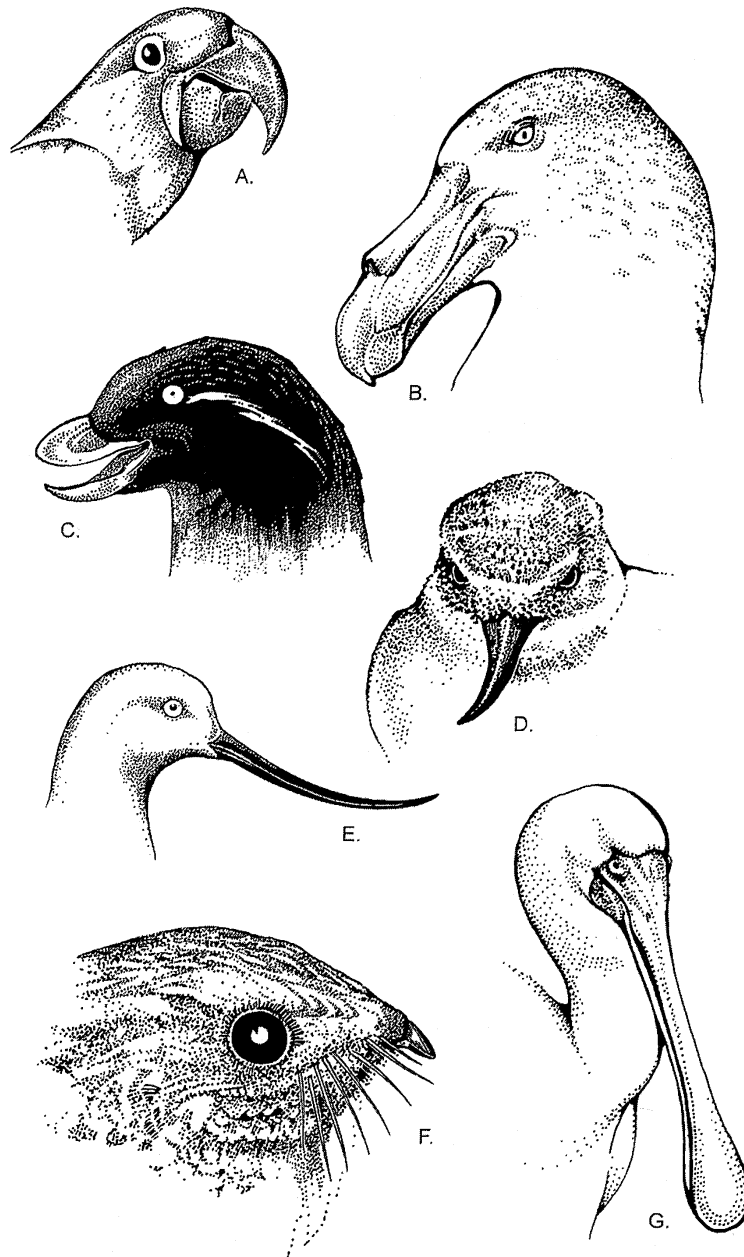
Lingual ingestion in turtles is restricted to terrestrial species (Summers et al., 1998; Wochesländer et al., 1999). Tongue protrusion is limited, with the tongue usually making contact with the food item at or near the jaw margins, almost within the mouth. Tongue retraction is typically accompanied by a bite. Semiaquatic species feeding on land use the jaws for prehension.

The highly reduced tongue of most birds makes lingual ingestion impracticable for many species. Nectivores, however, are specialized lingual feeders. Hummingbirds, for example, probe flower nectaries with their very long tongues, using narrow channels in the tongue to acquire nectar by capillarity. Other nectivorous species, such as lorries, have keratinous, brush-like tongue tips to increase surface area for nectar retrieval (McLelland, 1979). Woodpeckers use exceptionally long tongues to probe holes and crevices, using them to ingest larval insects (McLelland, 1979; Zweers and Berkhoudt, 2001) and crossbills pull seeds from cones using the tongue (Benkman, 1987).

The extent to which mammals use lingual ingestion is relatively unstudied, but we suspect it is more common than supposed. Certainly specialized myrmecophages are well known to use their long, extensible tongues to probe ant and termite nests for prey (Reiss, 2000). Many nectar- and fruit-eating bats ingest liquid or soft food by lapping, often evincing brush-like tongue tips (like some nectar-feeding birds) to maximize adherent food (Griffiths, 1982). Giraffes and related okapi use exceptionally protrusible tongues to strip leaves off trees (Owen, 1868; Kingdon, 1979) and some grazing bovids pull grass into the mouth for cropping using a prehensile tongue (KS, pers. obs.).

Jaw prehension of food is common and general among tetrapods. Crocodylians lack a protrusible tongue and are obligate jaw feeders (see above). Similarly, gymnophione amphibians (caecilians) lack protrusible tongues and use the jaws to capture prey (Bemis et al., 1983; O'Reilly, 2000). The majority of birds are specialized for jaw prehension. They have modified the bill and rhamphotheca (the keratinous part) in myriad ways for this purpose (Fig. 1.6; Zweers, 1985; Zweers et al., 1994, 1997; Rubega, 2000; Zweers and Berkhoudt, 2001). Scleroglossan lizards and snakes have modified the tongue for chemoreception and, with very few exceptions, rely on the jaws for ingestion (Cundall and Greene, 2000; Schwenk, 2000c; Kley, 2001). Most mammals are jaw feeders as well. Except for mammals, most jaw-feeding vertebrates have reduced, simplified or immobile tongues.

Infrequently, structures other than the jaws and tongue are used for ingestion in tetrapods. The forelimbs are used in some mammals, such as primates and rodents, and in some frogs (Gray et al., 1997). Rarely, the hind limbs are used (as in some birds such as raptors), or other structures, such as an elephant's mobile trunk or the prehensile lips of black rhinoceroses and some other mammals (Kingdon, 1979). Whatever specific mechanism is used, ingestion results in the placement of the food item in the mouth where it is



*Fig. 1.6.* Diversity of the jaws and beak in birds. Birds lack teeth and do little oral food processing, but the beak is specialized in various ways for food acquisition. (A) hyacinth macaw; (B) southern giant petrel; (C) parakeet auklet; (D) wrybill; (E) Andean avocet; (F) whippoorwill; (G) African spoonbill. From Rubega (2000), reproduced with permission of Elsevier Science.

positioned for processing or for immediate transport to the pharynx for swallowing. In some cases, a killing bite and/or head shake is interposed here (see processing, below).

### **Intraoral Transport**

Intraoral transport (or simply transport) usually refers to posterior movement of the food item through the oral cavity to the pharynx where it can be swallowed, but more generally it can be taken to mean any intraoral movement and manipulation of the food item once held in the mouth. For example, food that is chewed is often laterally repositioned so that it lies between upper and lower tooth rows. Side-switching during chewing is common in mammals and in many lizards (Hiemae and Crompton, 1985; Hiemae, 2000; Schwenk, 2000c; Reilly et al., 2001; McBrayer and Reilly, 2002a). A food item is sometimes transported anteriorly if, after ingestion, it comes to lie too far back in the mouth for processing (Schwenk and Wake, 1993; Schwenk, 2000a, c). In mammalian studies, two discrete types of transport are often distinguished (Hiemae et al., 1978; Hiemae and Crompton, 1985; Hiemae, 2000). In stage I transport, food is moved from the incisive area at the front of the mouth to the postcanine region for processing. In stage II transport, liquids and reduced food are moved posteriorly through the fauces (the posterior border of the oral cavity demarcated by the vertical columns of the palatoglossal muscles), either for bolus formation or for immediate swallowing.

In aquatic vertebrates, transport is usually accomplished hydrodynamically (hydraulically) by creating pressure gradients within the oropharyngeal (and opercular) cavities (e.g. Lauder, 1985a; Bemis, 1987; Liem, 1990; Gillis and Lauder, 1994, 1995; Lauder and Gillis, 1997). In some teleost fishes, tooth-bearing pharyngeal jaws are used to manipulate prey, moving it toward the esophagus (e.g. Liem and Greenwood, 1981; Sibbing, 1982; Lauder, 1983, 1985a; Sibbing et al., 1986; Vandewalle et al., 1994). Many cetaceans and pinnipeds also use hydrodynamic transport of captured food (Werth, 2000a, b).

In terrestrial vertebrates, most transport and manipulation of food is hyolingual (Bramble and Wake, 1985; Hiemae and Crompton, 1985; Schwenk, 2000a), meaning that it is mediated by coordinated, cyclical movements of the tongue and the hyobranchial skeleton (Fig. 1.1). During transport the food item sits on the tongue while cyclical motions of the tongue and hyobranchium move it toward the pharynx for swallowing, or reposition it in the mouth for processing (see next section). In taxa with muscular or fleshy tongues (mammals, many lizards, some turtles, parrots, possibly waterfowl), the tongue forms itself around the food item during transport, cupping it, or humps up in front of it, pushing it. In one bird lacking a fleshy tongue (and probably others), the tongue is bent sharply downward at an intrinsic hyobranchial joint and the food item is transported on the tongue

behind the peak (Rubega et al., submitted manuscript). Among various tetrapods, palatal teeth, palatal rugae, or other keratinous projections on the palate prevent the bolus from moving forward while the hyolingual apparatus protracts beneath it in preparation for the next transport cycle (Bramble and Wake, 1985; Hiiemae and Crompton, 1985; Zweers, 1985; Hiiemae, 2000). In frogs, hyolingual transport may be unnecessary due to the brevity of the pharynx in this virtually neckless group. Except in a few species that use hydrostatic tongue elongation, the frog tongue is attached at the front of the mandible so that when it flips back into the mouth during ingestion, the adherent prey item is placed at the rear of the throat in position for immediate swallowing.

Many tetrapods sometimes replace hyolingual transport with inertial transport, in which the food item is released or tossed by the jaws (and the head repositioned over it) so that it comes to lie farther back in the mouth (Gans, 1969). Inertial transport is especially typical of many reptiles, including some lizards, crocodylians, and birds (Gans, 1969; Smith, 1986; Zweers et al., 1994; Cleuren and de Vree, 2000; Schwenk, 2000c; Tomlinson, 2000), but it is also exhibited by ancestral mammals such as opossums, tenrecs, and tree shrews (*Tupaia*), as well as carnivoran species that bolt chunks of flesh (Hiiemae and Crompton, 1985; Van Valkenburgh, 1996).

In snakes, the hyolingual apparatus is so specialized for chemosensory function that its role in feeding is entirely lost (Schwenk, 2000c). Intraoral transport is accomplished with movements of the highly kinetic skull, including unilateral movements of toothed jaw and palatal bones that alternately “grasp” a prey item on one side and then the other. Although small prey items are potentially pulled through the mouth and into the pharynx, most snakes feed on relatively large prey. In these species the kinetic skull mechanism is more accurately said to pull the snake’s head and body over a stationary food item stabilized by its own mass. Thus, the snake transport mechanism is considered to be a type of inertial feeding (Cundall and Greene, 2000). Scolecophidian snakes employ unique mechanisms of upper and lower jaw kinesis to “rake” prey into the mouth and push it into the pharynx (Kley, 2001). Axial bending of the anterior trunk supplements cranial transport once the bolus is far enough back (Moon, 2000; Kley and Brainerd, 2002).

Surface tension transport is a specialized mechanism of intraoral transport characteristic of shorebirds. Tiny prey items are suspended within a drop of water between the jaws while surface tension drives the drop along the bill as upper and lower jaws are spread apart (Rubega and Obst, 1993; Rubega, 1996, 1997).

In all cases, the outcome of transport is placement of food in the pharynx, ready to be swallowed. In many taxa, however, the food is mechanically reduced or otherwise processed before transport is completed.

### Processing

Processing refers to any mechanical reduction or preparation of the food before it is swallowed. However, many taxa, including most fish, most amphibians, many birds and snakes, do not process their food at all (other than lubrication with saliva) — they simply swallow it whole directly after ingestion and transport. And although most processing occurs within the oral cavity, some vertebrates do a significant amount of food preparation before or during the act of ingestion. Carnivoran mammals, for example, often rend pieces from their prey with the jaws, sometimes aided by the forelimbs (Ewer, 1973). Many terrestrial turtles do something similar by pinning a food item against the substrate with the forelimbs while tearing pieces off with the beak (KS, pers. obs.), as do many raptorial birds. Mammals, especially rodents and primates, hold a food item in the forelimbs and bite off small pieces for further processing within the mouth. Galápagos land iguanas often use their forelimbs to scrape the spines off the prickly pear cactus fruit they favor (H. K. Snell, pers. comm.). Crocodylians rend chunks from large prey by grasping the prey in the jaws and spinning violently on their axes (Cott, 1961; Pooley and Gans, 1976; Taylor, 1987). They also sometimes cache dispatched prey underwater to store it for later consumption and possibly to soften it before ingestion. Similarly, shrikes (passerine birds) impale prey on thorns or barbed wire, returning to feed on it later. Many sharks and other predatory fish tear or bite pieces from larger prey (Frazzetta and Prange, 1987; Motta and Wilga, 2001), as do some bony fish. Although processing of any kind is otherwise unknown in snakes, two species tear apart freshly molted crabs by pulling them through a loop of the body (Jayne et al., 2002). Granivorous birds sometimes hold hard seeds with the feet while cracking them with the beak, or husk them directly in the bill, ingesting only the inner kernel (Ziswiler and Farner, 1972; Zweers et al., 1994; Nuijens and Zweers, 1997). Parrots employ an elaborate shelling behavior involving the beak and tongue (Homerger, 1980, 1986). Kingfishers beat a captured fish against a perch, both to subdue and to soften it by breaking bones, then swallow it whole. Uniquely, many birds process food *after* it is swallowed, in specialized partitions of the esophagus and stomach (see later).

In tetrapods, most processing occurs within the mouth by crushing or biting with the teeth. Sometimes this is restricted to cropping during ingestion, or killing bites and head shakes immediately upon capture, but usually prey is further chewed with the teeth. Chewing involves repeated, cyclical biting movements that crush, puncture, shear and/or grind the food item, mechanically reducing it in preparation for swallowing. In nonmammalian taxa that chew, this behavior is referred to descriptively as puncture-crushing, as typified by lizards (Schwenk, 2000c; McBrayer and Reilly, 2002). Food is pierced by sharp, pointed teeth or crushed between blunt, molariform teeth, but there is little, if any, fragmentation of the bolus

and certainly no true comminution (see below). Puncture-crushing serves to soften the food item, to lubricate it with copious saliva, and potentially to introduce salivary enzymes into the bolus, initiating chemical digestion. Durophagous species feeding on snails and large arthropods may use temporal summation of pulsatile adductor contractions to increase bite force (Gans and De Vree, 1986).

Chewing in nonmammalian taxa is often erroneously referred to as “mastication”, but this term is accurately applied only to mammals (Davis, 1961; Schwenk, 2000a). Mastication is a derived and specialized form of chewing associated with a suite of mammalian novelties, including functional specialization of teeth along the tooth row (heterodonty), precise, unilateral occlusion of upper and lower teeth, a masticatory cycle including lateral and/or anteroposterior movements of the lower jaw, a derived tongue morphology, and the evolution of a muscular pharynx associated with a unique form of swallowing (Hiiemae and Crompton, 1985; Crompton, 1989, 1995; Smith, 1992; Herring, 1993; Weijs, 1994; Thexton and Crompton, 1998; Hiiemae, 2000; Schwenk, 2000a, 2001a). The important feature of mastication, in contrast to puncture-crushing, is that it reduces ingested food to a fine slurry of tiny particles mixed with saliva, a process referred to as comminution (Fig. 1.2). Food in this semiliquid state is moved during stage 2 transport into the pharynx where it is temporarily held or swallowed immediately. Uniquely, mammals often interpose swallow cycles amidst a series of masticatory cycles (Thexton and Crompton, 1998; Hiiemae, 2000), whereas other tetrapods only swallow a bolus once chewing is completed. Some mammals have secondarily reduced or lost their ability to masticate. This is usually correlated with modification, reduction or loss of the teeth associated with specialized diets such as insectivory and piscivory (e.g. odontocete cetaceans) or secondary reversion to suspension feeding (e.g. mysticete cetaceans). Modern monotremes have lost their teeth altogether, substituting keratinized structures on the tongue and palate to rasp their food (Owen, 1868; Doran and Baggett, 1972; Griffiths, 1978).

Turtles and modern birds entirely lack teeth and rely on the keratinous rhamphotheca for whatever oral processing they do (Fig. 1.6). In turtles the apical edges of the beak are sharp and the lower jaw fits snugly within the upper forming an effective shearing mechanism. Some turtles also crush food between upper and lower plates (tritulating surfaces) at the beak’s front end (Gaffney, 1979). Birds, in general, do very little oral food processing, for reasons discussed in a subsequent section; however some birds shear food with the sharp edges of the beak. Owls and raptors, for example, often hold prey with the feet and use the beak to tear it into bits and some frugivorous parrots similarly shear off pieces of fruit (Zweers and Berkhoudt, 2001).

Most sharks do no processing with the marginal teeth other than killing bites and/or excision of pieces from larger prey (Frazzetta and Prange, 1987; Frazzetta, 1994; Motta and Wilga, 2001). Some elasmobranchs, however, crush

hard-bodied prey, such as mollusks, with plates of flattened teeth (Moss, 1977; Summers, 2000; Wilga and Motta, 2000). In these taxa the cartilaginous jaws may be strengthened by unusual "trabecular cartilage" (Summers, 2000). Relatively few bony fish use the jaws and marginal teeth for processing, probably because without cheeks and lips, reduced food particles would be lost in the water (Vandewalle et al., 1994). However, some taxa do manage to reduce food in the marginal jaws (e.g. Hernandez and Motta, 1997), but in most bony fish that process their food, it is crushed, ground or pierced by intraoral and/or intrapharyngeal teeth on the palate and hyobranchial skeleton. Indeed, in derived taxa, such as the Cichlidae and Labridae, teeth are restricted solely to tooth plates on the pharyngeal jaws which are used to process the food before it is swallowed (e.g. Liem, 1973; Sibbing, 1982, 1991; Liem and Sanderson, 1986; Vandewalle et al., 1994; Galis and Drucker, 1996; Grubich, 2000). Some aquatic taxa pump water in and out of the mouth, lacerating prey as it is raked across the marginal teeth (Bemis, 1987; Elwood and Cundall, 1994). Although salamanders virtually never process their food, one group (the desmognathine plethodontids) routinely delivers crushing bites using "head tucking" behavior in which force is transmitted to the lower jaw via a ligamentous connection to the cervical vertebrae (Schwenk and Wake, 1993).

### Swallowing

During swallowing (also called pharyngeal emptying; Smith, 1992; Schwenk, 2000a), the bolus is moved from the pharynx into the esophagus where peristalsis takes over the task of its transport through the remainder of the gut. Depending on the particular mechanism of swallowing used and/or the relative length of the prey item compared to the pharynx, the transition between intraoral transport and swallowing is often blurred. An extreme example is evident in macrostomatan snakes, which typically eat relatively large or elongate prey (Cundall and Greene, 2000). One end of a prey item often extends from the mouth even as the other end enters the esophagus! Initially, unilateral, alternating movements of the kinetic skull and jaws are used to move the prey toward the esophagus. These are supplemented and then replaced by axial bending movements of the trunk as the food item moves farther into the esophagus (Moon, 2000; Kley and Brainderd, 2002), so that one feeding stage blends imperceptibly into the next. A similar situation occurs in some seabird chicks feeding on relatively long fish. In most taxa there is a somewhat gradual transition between transport and swallowing cycles rather than a sharp demarcation. In mammals, as noted, swallowing cycles are often interposed among a series of masticatory cycles so there may not be a terminal swallowing stage, *per se*.

Swallowing in fishes is poorly understood, but in many teleosts, at least, it is accomplished with manipulatory movements of the pharyngeal jaws that push the bolus into the esophagus (Lauder, 1983a, b, 1985a). How it

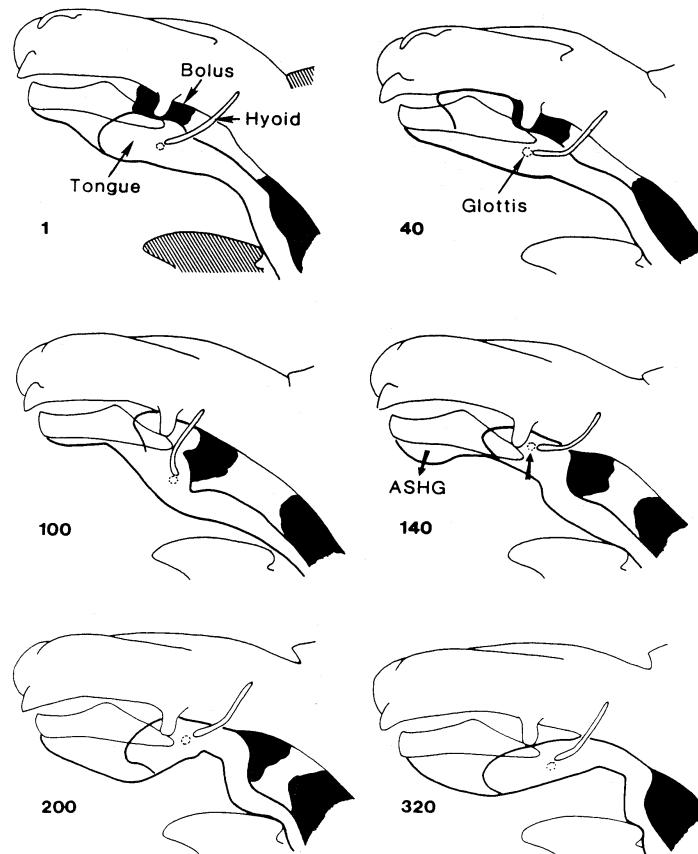
occurs in taxa lacking pharyngeal jaws is not clear (see Lauder, 1983a). Some suspension feeding fish trap small food particles in mucous strands that move into the esophagus with water flow (Sanderson et al., 1996). Recently, Sanderson et al. (2001) showed that suspension-feeding teleosts do not trap particles directly in the gill rakers as previously thought (“sieving”), but rather capture them using “crossflow filtration” in which food particles are concentrated in the oral cavity and then swept across the rakers toward the throat, thus solving “the mystery of particle transport to the oesophagus” (Sanderson et al., 2001). Teleosts have an esophageal sphincter that putatively prevents them from swallowing too much water (Stevens and Hume, 1995).

Most tetrapods use cyclical movements of the tongue and hyobranchial skeleton, as well as compression of the pharynx with the superficial constrictor musculature, to push or squeeze food into the esophagus. In lizards and terrestrial turtles, for example, the posterior end of the tongue is used to tamp food into the throat (“pharyngeal packing”) and this is followed or in some cases, replaced with pharyngeal compression (Fig. 1.7; Smith, 1984, 1986; Bels et al., 1994; Schwenk, 2000c). In amphibians, swallowing is accomplished primarily with pharyngeal compression, often accompanied by retraction of the eyeballs, which may help to force the bolus into the esophagus (Duellman and Trueb, 1986; Deban and Wake, 2000). In taxa with reduced tongues, such as crocodylians and birds, pharyngeal compression is supplemented with inertial movements of the head, as well as gravity (Cleuren and De Vree, 2000; Tomlinson, 2000; Zweers and Berkhoudt, 2001). Some birds also use sinuous contractions of the floor of the pharynx (“peristalsis”) to move food into the esophagus (Zweers, 1985; Zweers and Berkhoudt, 2001).

Mammals employ a uniquely derived form of swallowing called deglutition (Thexton and Crompton, 1998; Hiiemae, 2000). Like the term “mastication”, deglutition is often incorrectly applied to nonmammalian taxa. Mammalian deglutition is associated with a derived tongue morphology and especially the presence of a soft palate and pharyngeal musculature (Smith, 1992; Hiiemae, 2000). Mammals can form a sphincter-like seal at the base of the tongue (at the fauces), functionally subdividing the buccal and pharyngeal space (Hiiemae, 2000). Masticated food is passed through this seal during stage 2 transport to accumulate in the oropharynx. When a bolus is sufficiently large, an explosive contraction of the tongue base and soft palate, in conjunction with peristaltic waves of contraction in the pharyngeal musculature, propel food into the esophagus.

### **CONSEQUENCES OF FEEDING—TAXONOMIC HIGHLIGHTS**

Vertebrate feeding systems were surveyed above according to the mechanical task associated with each feeding stage. The review revealed a great deal



*Fig. 1.7.* Swallowing in a terrestrial turtle based on individual frames from cineradiographic film. Numbers indicate frame number. Note shape changes in the tongue as it moves in front of the bolus and forms a seal with the palate. It then pushes the bolus posteriorly, into the esophagus, where peristalsis takes over. Tongue movement is accompanied by hyobranchial movement. ASHG: anterior suprahyoid muscles. From Bramble and Wake (1985), reprinted by permission of the publisher and President and Fellows of Harvard College.

of diversity in the manner that vertebrates procure, process, transport, and swallow food. Despite this diversity, all systems share the common outcome of moving the bolus into the esophagus for further digestion and nutrient assimilation. Therefore, the mechanical and chemical condition of the bolus at the point of swallowing, as determined by the front-end feeding mechanism, has obvious significance for physiological functioning in the remainder of the gut and it is this inescapable connection we turn to here.

### Fishes

Obviously, fishes are phylogenetically and taxonomically disparate, but within any clade the nature of the food swallowed devolves to one of five

types: particulate food collected by suspension feeding; tiny food items taken individually; relatively larger, whole, unprocessed food items; minimally processed food consisting of large pieces or chunks excised by the marginal teeth; and food that is processed, sometimes significantly, by the marginal or pharyngeal jaws.

Whether they trap suspended food from the water column or substrate, or ingest it one bit at a time, microphagous fishes swallow food that does not require further reduction and is ready for passage into the gut and assimilation. Whole food particles, however small, may nonetheless pose a different digestive challenge compared to food that has been milled, and therefore ruptured, by the pharyngeal jaw apparatus. Pharyngognathy opens the door to significant food processing potentially rivaling that of mammals (e.g. Sibbing, 1991), but the nature of the processed food is rarely studied. Stomach content analyses of labrids by Wainwright (1987, 1988) showed that snail and crab shells were crushed and fragmented by the pharyngeal jaws, with most of the shell fragments winnowed out before swallowing. Parrotfish process algae (and the coral with which it is associated) into a fine paste (Bellwood and Choat, 1990; Bellwood, 1996, Choat et al., 2002) and presumably this is why they do not require a stomach (Horn, 1989). There seems to be a strong correlation between the degree of pharyngeal processing and gut form, at least in herbivorous species (Horn, 1989, 1992). Some seed-eating species may use pulsatile contractions of the pharyngeal jaw musculature to increase crushing forces by means of temporal summation (Irish, 1983). Pharyngognathy may be particularly important to herbivorous and durophagous species, as might be expected, but this is an untested assumption.

Contrastingly, in fishes that swallow entire prey or large pieces thereof, the gut must complete digestion chemically. Such species possess an extensible stomach for storage and face the potentially daunting digestive problem of the food item's high volume-to-surface area ratio. These issues are less problematic for carnivorous species because flesh is more easily digested. Herbivorous fishes are either inefficient in digestion, highly selective in diet, restricted to microphagy, or employ significant pharyngeal processing.

### **Amphibians**

Amphibians are nearly universal in their lack of prey processing and thus, with few exceptions, swallow whole, unreduced prey items. Notable exceptions are aquatic salamanders that shred prey items against the teeth as they are sucked in and out the mouth (Elwood and Cundall, 1994), desmognathine salamanders that routinely crush prey between the jaws (Schwenk and Wake, 1993), and caecilians that shear off pieces of prey with specialized dentition and/or axial rotation of the body while withdrawing into a burrow (Bemis et al., 1983; O'Reilly, 2000). Virtually no adult amphibians are herbivorous,

although two frog species are reported to consume more than incidental quantities of fruit or leaves (da Silva et al., 1989; Das, 1995).

Despite the lack of herbivory, amphibian diets are diverse, particularly in prey size, which ranges from mites to vertebrates. Disparity in prey size and type, coupled to constraints on gut length imposed by the anuran body plan, make frogs an ideal group in which to examine diet-gut relationships. The only known folivorous frog, for example, was found to have an unusually long gut that may contain fermentative microorganisms (Das, 1995). A number of frog groups share a suite of characters related to microphagy, including cutaneous sequestering of dietary alkaloids (Vences et al., 1997/98). Microphagy increases the surface-area-to-volume ratio of the food particles swallowed (circumventing the problem of no chewing), but the arthropod prey eaten (mostly ants) tend to be noxious and/or low in nutritive value. A termite specialist, for example, was found to have a relatively longer gut than other species, putatively because termites are relatively hard to digest (Das, 1995).

### **Nonavian Reptiles**

Most reptiles do little or no processing and swallow food largely intact, either whole or in large pieces. Crocodylians exemplify this mode of feeding: small prey are simply tossed into the back of the mouth and swallowed (sometimes after a crushing or killing bite). Larger prey are dismembered or torn apart and the pieces bolted. Both feeding modes are enhanced by an exceptionally powerful bite (Ericson et al., 2003). The stomach is divided into a cranial glandular part and a caudal muscular part (the pylorus) that appears as a separate chamber when the stomach is empty (Richardson et al., 2002). The pylorus is often referred to as a "gizzard". Its homology to the bird gizzard is assumed and not certain. In any case, crocodylians, like birds, often swallow grit or small stones called gastroliths that are held within the gizzard and presumed to aid in the mechanical reduction of food. However, the evidence for this in crocodylians is weak, gastroliths may also function as ballast (Taylor, 1993). Mechanical processing in the muscular gizzard, possibly aided by gastroliths, may help to mitigate the problem of digesting large, mostly intact pieces of food. Crocodylians are also reputed to have exceptionally acidic gastric secretions that promote rapid digestion (Richardson et al., 2002).

Turtles do little or no intraoral processing, but do crop bite-sized pieces of food with their sharp beaks. Small, cropping bites may be particularly important in herbivorous species (Bjorndal and Bolten, 1992). Carnivorous and durophagous species generate more powerful bites than species with other diets (Herrel et al., 2002) but even extreme dietary specialization is possible without attendant specialization of the feeding system and gut (e.g. Meylan, 1988). Suction feeding aquatic species potentially swallow relatively large, whole prey.

Snakes, except for the two crab-eating species mentioned above, virtually always swallow whole prey with no intraoral processing. However, the venom that crotalid snakes (rattlesnakes and their relatives) inject into their prey contains proteolytic digestive enzymes that initiate digestion from inside-out (Thomas and Pough, 1979; Cundall and Greene, 2000). Relative prey size is exceptionally large in this group, sometimes exceeding the snake's own mass, and the prey's relatively small surface area could challenge the gut's ability to digest it extrinsically before it putrefies. This problem is exacerbated by the fact that the gut takes time to be upregulated after a period of quiescence (e.g. Secor and Diamond, 1998; Starck and Beese, 2001). Some snakes are able to crush bird eggs within the gut, retaining the liquid contents while regurgitating the indigestible shell (Gans, 1952).

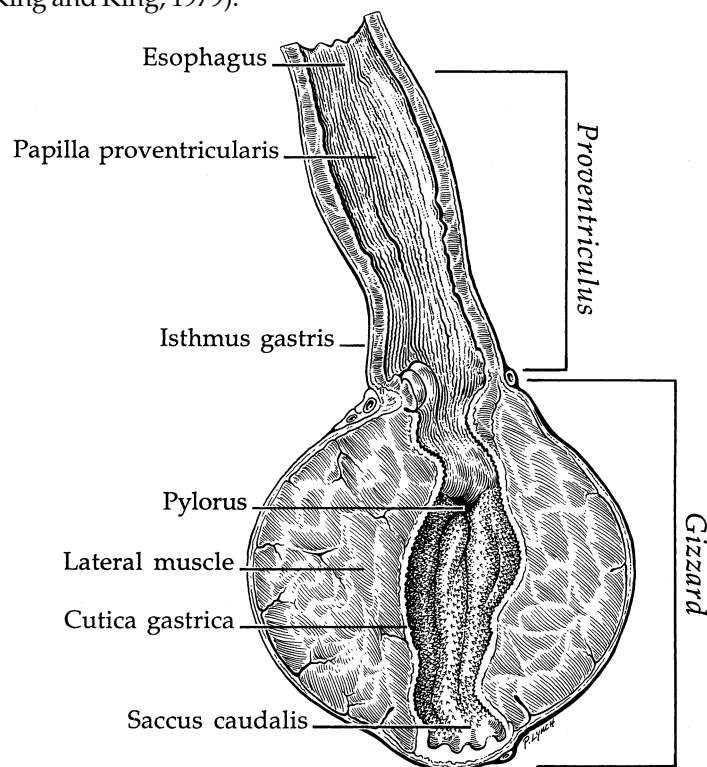
Although many lizards swallow small prey whole, lepidosaurs are exceptional among reptiles in the extent of their intraoral processing. Tuatara and many lizards initially crop larger food items into mouth-sized pieces. This is particularly true for herbivores whose teeth are often specialized for this purpose (Schwenk, 2000c). Sometimes inertial shaking is used to dismember prey. Most food is then chewed between marginal tooth rows, sometimes aided by palatal teeth. Chewing typically crushes, pierces, and softens the food item, but rarely results in significant trituration, even in herbivores. However, it is very likely that chewing introduces salivary enzymes and presumably the soft, well-lubricated bolus is more easily swallowed and digested.

### **Birds**

Although many birds reduce prey to some extent before ingestion, loss of teeth precludes significant intraoral processing. Consequently, birds often swallow whole, large, hard, or refractory food particles such as seeds without the benefit of front-end processing. Instead, they have adopted a novel strategy for processing that relies on specialization of the anterior gut. The esophagus is extremely extensible in species that swallow large prey and in many taxa it includes an expanded region where food can be temporarily stored. When evident as a distinct diverticulum, this structure is called a crop (Ziswiler and Farner, 1972; McLelland, 1979). The principal function of the crop is to store excess food and to regulate its rate of delivery to the stomach. In pigeons the crop produces and stores a liquid slurry of shed cells that is regurgitated to feed chicks. In many other species, the crop stores food and water for later regurgitation feeding of chicks. Although no significant chemical digestion occurs here, grain and other hard foods are moistened and softened. The single exception is the folivorous hoatzin in which the muscular crop serves as the site of fermentative digestion (Grajal, 1995).

The stomach comprises two principal chambers, a cranial proventriculus and a caudal gizzard or ventriculus (Fig. 1.8, Ziswiler and Farner, 1972; McLelland, 1979). The proventriculus is glandular and the site of most

chemical secretion and digestion while the gizzard is extremely muscular in most species and responsible for mechanical processing. The gizzard is especially well developed in taxa whose food requires mechanical reduction, i.e. omnivores, insectivores, herbivores, and granivores (in some carnivores it is reduced or virtually absent). In these species, the gizzard is lined with a thick, hard cuticle forming dorsal and ventral "grinding plates" covered with ridges. Food is ground or crushed between the plates, with reduction facilitated by grit intentionally swallowed. The amount of grit in the gizzard has been correlated with diet and found to be more prevalent in granivorous birds, while grit size correlates with body size (Gionfriddo and Best, 1996). The crushing action of the gizzard in some species is considerable, i.e. whole, hard-shelled nuts are fragmented by turkeys within hours and there are even reports of metal objects being folded and ground into fragments (Welty, 1975). The gizzard apparatus is often referred to as a "gastric mill" and has been compared to the mammalian masticatory apparatus (e.g. King and King, 1979).



*Fig. 1.8.* The stomach of a granivorous bird (rock dove), showing its division into a cranial proventriculus and a caudal gizzard. The gizzard is highly muscular and lined with a thick, abrasive cuticle which, in conjunction with swallowed grit, mechanically processes food, reducing it to small particles. From N. S. Proctor and P. J. Lynch (1993), reproduced with permission of Yale University Press.

## **Mammals**

Evolution of mastication is a key theme in the history of mammals. It is at the heart of a sweeping reorganization of the skull, palate, dentition, tongue, pharynx, jaw muscles, and ear, and is intimately associated with the evolution of endothermy. It uniquely distinguishes mammals from all other vertebrates. The masticatory apparatus evolved incrementally within the synapsid stem lineage and was present essentially in the modern form once a fully functional dentary-squamosal jaw joint replaced the increasingly weak, ancestral quadrate-articular joint (Crompton, 1989, 1995).

The critical feature of the masticatory system is its ability to reduce food quickly to a mash of tiny particles mixed with copious enzyme-containing saliva (Fig. 1.2). Compared to other vertebrates, the bolus is virtually “predigested” when swallowed. This has obvious relevance for passage rates in the gut. Although there are many secondary departures from the fundamental pattern of mastication, these usually occur in taxa that consume flesh or other types of food relatively more easily digested. Conversely, the masticatory mills of herbivores and taxa that consume other types of refractory foods are elaborate.

## **General Patterns**

One noteworthy pattern that emerges from the preceding consideration of the bolus condition is that in ectothermic vertebrates, food is processed relatively little, if at all, whereas in birds and mammals, food entering the intestine is usually extensively triturated. This distinction probably relates to the greater energetic demands of endotherms and their need to increase gut passage rates. Increased passage rates, as well as greatly increased gut surface area, are necessary in endotherms because they are no more efficient in extracting energy from their food than are ectotherms (Karasov, 1987; Karasov and Diamond, 1985, 1988). By essentially “predigesting” their food, birds and mammals decrease the time necessary to hold it in the gut for chemical breakdown. In contrast, ectotherms can afford the low gut passage rates required for adequate digestion by virtue of their modest energetic demands. Mammals employ a complex oral masticatory system to process their food, whereas birds rely on a “gastric mill”. In birds, the anterior gut effectively functions as part of the front-end feeding system. The evolutionary transfer of food processing from the oral apparatus to the gizzard, along with the loss of teeth, shifted the mass of the prey-reduction apparatus toward the center of gravity, an obvious advantage for a volant animal. These general patterns potentially have had important consequences for patterns of evolution in front-end phenotypes, a topic we explore elsewhere (Schwenk and Rubega, *in litt.*).

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