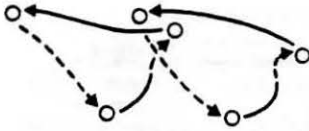


Chapter 14



Mastication, Food Transport, and Swallowing

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Food has metabolic value only when the products of its digestion enter the blood stream. For most mammals a high metabolic rate depends on regular ingestion of food items, which in most cases must be mechanically broken down in the oral cavity before they can be chemically simplified in the gut. Thus, food is taken into the mouth (ingestion), processed (mastication), and then swallowed (deglutition). Enzymes in the saliva of most mammals begin to act as the material is readied for swallowing and, depending on the rate of both gastric secretion and gastric movements, continue to act for a limited time. Although some living reptiles shred or puncture food before swallowing (Throckmorton, 1976, 1980; Smith, 1982), that process can be seen as facilitating food intake and swallowing, rather than as producing the extensive mechanical reduction of food within the oral cavity that is characteristic of mammals.

Chewing, or mastication, serves two functions: first, material is reduced to a condition suitable for swallowing; second, the resulting increase in surface area facilitates the penetration of the digestive enzymes and so expedites the rate of chemical breakdown. Foods with resistant cell walls, such as grasses, require extensive mechanical breakdown before digestive enzymes are maximally effective. It is also necessary to expose the cellulose cell walls to the digestive enzymes of bacteria.

Studies of feeding mechanisms in mammals have concentrated on the morphology, or both the morphology and function, of the jaw apparatus (including teeth, mandibular joint, and ele-

vator muscles) in relation to broad dietary habits (for example, Hiiemae and Ardran, 1968; Turnbull, 1970; Kallen and Gans, 1972; Herring and Scapino, 1974; Weijs and Dantuma, 1975; Weijs and de Jongh, 1977; Gorniak, 1977; Janis, 1979; Hylander, 1977, 1979; Fish and Mendel, 1983; Oron and Crompton, unpublished data). Further, the teeth of mammals (and other dentate vertebrates) vary widely in shape, and there are unequivocal associations between tooth form and general dietary habits. It is not, therefore, surprising that teeth and jaws have major taxonomic significance, especially in the analysis of the fossil record, and that much experimental effort has been devoted to analyzing the movements of jaws in feeding.

Mammalian mastication can be characterized (except in some highly specialized forms) as having the following features: (1) active breakdown of food is unilateral, that is, it occurs on one side of the jaw at any one time; (2) there is some element of transverse movement during food breakdown, which is minimal in carnivores and maximal in some herbivores; and (3) upper and lower molars accurately "fit" one another, although their tight occlusion is, to some extent, developed with wear. These features are found in the jaw apparatus of the earliest mammals (known from 180 million years before Pleistocene) and sharply separate them from their immediate ancestors, the mammal-like reptiles.

Limited attention (for instance, Hiiemae and Ardran, 1968; Weijs, 1975, for rats; Gordon, 1984, for walrus) has been paid to the mechanisms involved in the ingestion of food or its

transport and manipulation within the oral cavity. Swallowing has been extensively studied in humans but almost ignored in nonhumans. It is only recently that experimental studies have shown that the tongue and the hyoid apparatus, as well as the soft palate, have a pivotal role in the feeding process and, indeed, may have the primary role (at least in the ontogenetic sense). This chapter is, therefore, focused on the oral management of food rather than simply on the form of the teeth and jaws and the movements of the head and lower jaw in mastication.

Despite the differences in the morphology of the jaw apparatus in mammals, synchronous cine-fluorographic and electromyographic studies of feeding in a variety of mammals—the American opossum *Didelphis marsupialis*, a carnivore/omnivore; the tenrec *Tenrec ecaudatus*, predominantly an insectivore; the hyrax *Procavia capensis*, a herbivore; the cat *Felis catus* and dog *Canis familiaris*, both carnivores; the pig *Sus scrofa*, an omnivore; and a higher primate, *Macaca fascicularis*, have shown that the mechanisms by which solid food is transported, processed, manipulated, and swallowed are essentially the same in all. Such differences as are found, for example, in the position of bolus formation or in the transport of food to the back of the tongue in higher primates, reflect minor, albeit significant, modifications of the basic pattern.

Food Processing and Transport: Overview

Recent experimental studies have shown that liquid food is moved into and through the mouth in a three-stage process; solid food requires five (Fig. 14-1). Chewing, or the breakdown of food by the teeth to a condition suitable for further transport, is simply a stage, though an important one, in the more general process. The stages are sequential and usually involve different parts of the mouth in the processing of each unit, or aliquot, of food, although more than one stage can occur concurrently in relation to additional aliquots. Feeding depends on the synchronized and cyclical movements of the jaws, that is, the cranium on the cervical vertebral column (upper jaw) and the mandible on the cranium (lower

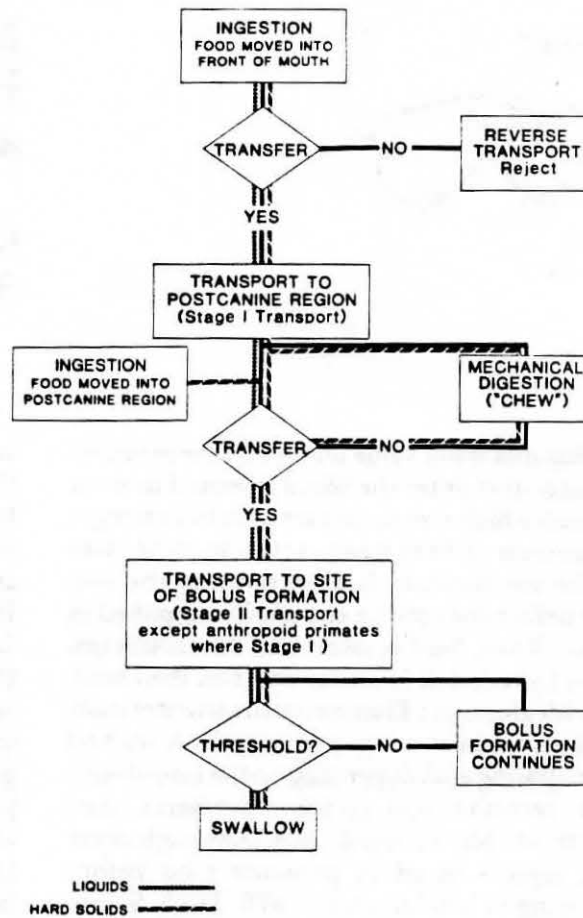


Figure 14-1 Flow chart of food processing in the mouth. Liquids and very soft foods of low viscosity are moved directly from the front of the mouth to the oropharynx for bolus formation. Solid food is ingested either through the anterior part of the mouth or, if very hard, through the postcanine region (ingestion by mastication). The number of times such food passes through the chew loop depends on its initial particle size and consistency. Stage I transport moves food posteriorly within the oral cavity; stage II transport moves food into the oropharynx (see Fig. 14-3).

jaw); the tongue base (hyoid apparatus) and the body of the tongue; as well as the soft palate (Fig. 14-2). Movements of the soft palate occur throughout the process but are highly patterned, as are those of the walls of the oropharynx in swallowing.

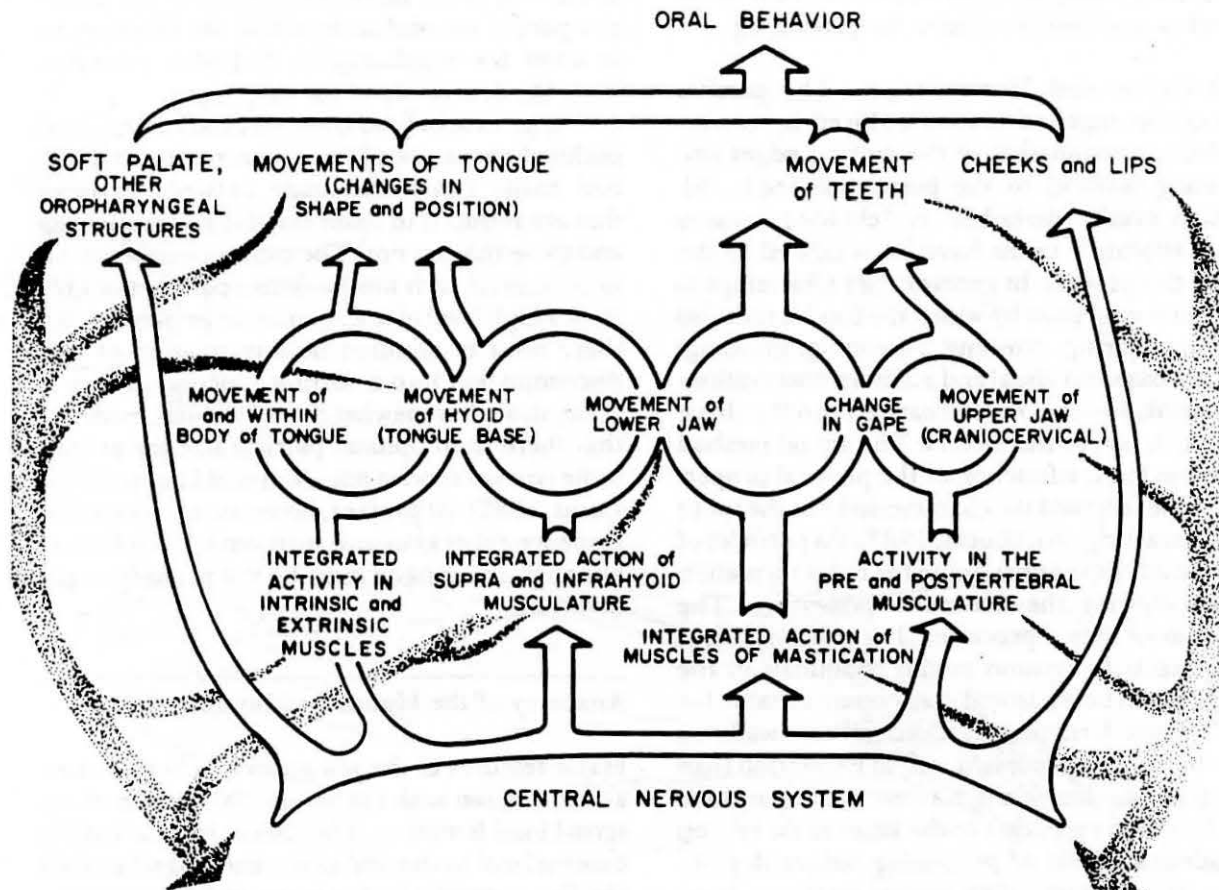


Figure 14-2 Functional relationships of the major anatomical elements in the feeding apparatus. The effector system is shown as solid arrows linking components in sequence. Dotted arrows indicate the sources of sensory input that can modulate effector activity. "Other oropharyngeal structures" include the hard palate (especially its mucosa), the epiglottis, the pharyngeal musculature, and the oropharyngeal mucosa.

Ingestion and Stage I Transport The process by which food is transferred from the external environment to the oral cavity is called ingestion. Liquids are usually lapped (a rhythmic behavior in which aliquots are collected by the tongue during jaw movements of low amplitude) or are sucked (a rhythmic reduction in intraoral pressure).

The ingestion of solids is the most variable and least well understood of the feeding processes; its pattern depends largely on the condition of the food item. Vegetation such as leaves or grasses is plucked or cut by the action of lips, tongue, and anterior teeth. Depending on size and hardness, solids may be ingested in a series of bites or gnaws,

while usually, but not always, held in one or both hands. If the material is very hard, the force needed to separate a bite may require the use of the cheek teeth. Such behavior is routinely seen in primitive mammals and in carnivores feeding on bones or attempting to pull flesh from a carcass. Small food items may simply be picked up by the anterior teeth or tongue and passed into the front of the mouth or, especially in primates, manually placed in the mouth.

Stage I transport is the movement of liquid and solid food from the anterior part of the mouth back toward the cheek teeth (premolars and molars). Some rodents and primates have well-developed cheek pouches. After rapidly ingesting

food, they transport it posteriorly, store it in the pouches, and remove it later for processing.

Mastication and Manipulation The particle size of the ingested food is reduced by the repeated approximation of the cutting edges and crushing surfaces of the postcanine teeth. Although usually described as "chewing," many other evocative terms have been coined to describe this process. In general, they all attempt to explain the method by which the food is reduced (cutting, tearing, crushing, chomping, grinding) and are based on visual and auditory observations of animals feeding or, alternatively, on the shape and occlusion of the molars. The actual method of reduction is a function of the physical properties of the food and the characteristics of the tooth surfaces acting on it (Lucas, 1982). As particles of food reach a size appropriate for bolus formation and swallowing, they are moved posteriorly. The residuum is then reprocessed. It is clear that there is substantial variation among mammals in the range of particle size and consistency suitable for swallowing. A ruminant artiodactyl can swallow a less thoroughly processed wad of vegetation than can a perissodactyl: the former will regurgitate the food and reprocess it; the latter must rely on an adequate level of processing before deglutition. In contrast, a carnivore swallows large lumps of barely processed material. During a chewing sequence food is moved either from one side of the oral cavity to the other or to a more distal position. This is referred to as manipulation.

Stage II Transport and Deglutition As mastication proceeds, reduced foods are moved posteriorly to form the bolus, first to a position below the soft palate and then farther to the vallecular regions and the pyriform recesses (defined below and in Fig. 14-3). This is termed stage II transport.

When a sufficient volume of liquid or solid has accumulated, the bolus is swallowed. Swallowing (deglutition) is a stereotypical behavior that occurs during feeding—every few cycles in lapping or intermittently during and, finally, at the end of a masticatory sequence. In either case the regular pattern of jaw movement is transitorily

suspended as the bolus is moved from the posterior part of the oral cavity across the oropharynx to enter the esophagus or, in higher primates, from the oral cavity to the esophagus.

The process of food transport and reduction as outlined above presupposes that receptors in the oral cavity can discriminate between particles that are reduced to a size suitable for swallowing and those that are not. The concept of selection is important; if such mechanisms operate, not only must a high level of discrimination be present, but there must in addition be a translation of that discrimination into a sorting function. There is good, though somewhat circumstantial, evidence that there is an optimal particle size for at least some types of food in man (Kay and Sheine, 1979; Lucas, 1982). At present, however, no acceptable evidence exists as to how such sorting is achieved, although the tongue must be the primary organ involved.

Anatomy of the Mouth and Jaws

Major features of the jaw apparatus in mammals are correlated with the sequential pattern of internal food handling. The cheeks form a flexible external seal to the oral cavity and, together with the lips, a mobile intermittent seal (the anterior oral seal) in front of the incisors and canines. The space from the lips to the opening of the pharynx is divided into the oral cavity and the oropharynx. The hard palate is covered, to a variable extent, with transversely oriented rugae; the soft palate is highly mobile (Fig. 14-3). The oral cavity extends from the lips posteriorly to the pillars of the fauces, which flank the aperture between mouth and oropharynx and contain the palatoglossus muscles running from the external surface of the tongue into the soft palate. Anteriorly the oral cavity can be sealed off by the muscles of the lips (the orbicularis oris and associated muscles); posteriorly it can be separated from the oropharynx by a sphincter or intermediate seal formed by the contraction of the palatoglossi and a change in tongue shape.

The oropharynx has two distinct compartments in all mammals except adult *Homo sapiens*; the anterior compartment (or vallecular region)

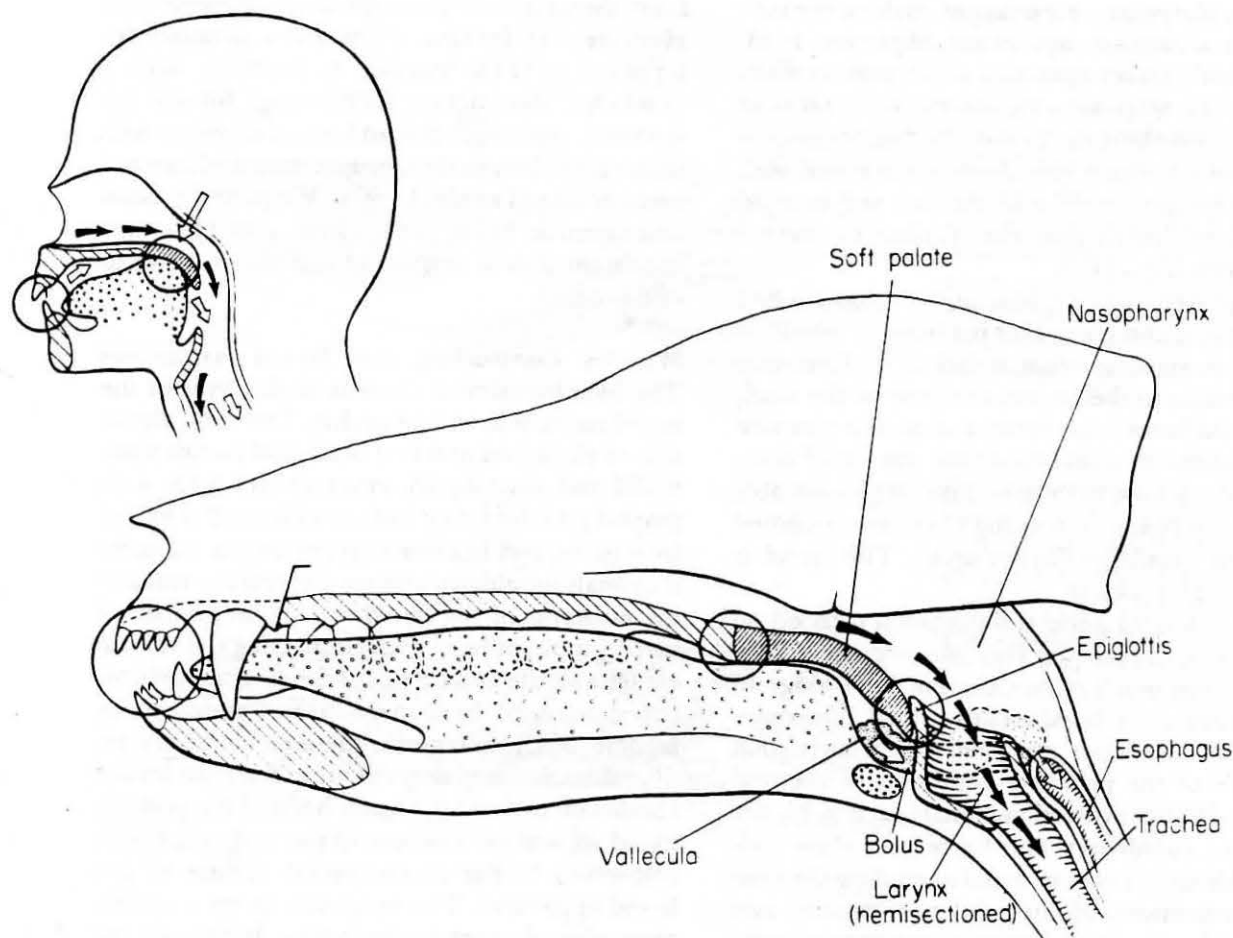


Figure 14-3 Hemisection showing the general form of the oral cavity and oropharynx in the opossum. The oral cavity extends posteriorly to the contact between the soft palate and the tongue (middle oral seal). The area between the middle and posterior oral seals is part of the oropharynx. The space between the posterior part of the tongue and the anterior surface of the epiglottis (the vallecule) communicates with a potential space, the pyriform recess, which extends laterally and posteriorly around the larynx, between it and the lateral wall of the pharynx (dotted line). In opossums a bolus accumulates in both the vallecule and the pyriform recess (shaded). The human head is shown for contrast.

extends from the pillars of the fauces in front and below the soft palate to the epiglottis posteriorly. The posterior surface of the tongue forms the floor of this compartment, which is normally closed posteriorly by the posterior oral seal formed by the overlap between the soft palate and the epiglottis (Fig. 14-3). In most mammals the anterior compartment extends distally on either side, external to the soft palate–epiglottis–larynx contact, into flaccid recesses referred to as the pyriform recesses. Food can be stored in the

anterior compartment and in its extension, the pyriform recess. In anthropoid primates the pyriform recesses are reduced to furrows lying alongside the larynx and do not serve for the transient storage of a bolus. The posterior compartment of the oropharynx extends from the plane of the soft palate–epiglottis to the posterior wall of the pharynx. Except during swallowing, this posterior part is confluent with the nasopharynx above and the laryngopharynx below. Adult *Homo sapiens* have no soft palate–epiglottal seal; the poste-

rior oral seal is between the tongue and the soft palate at the pillars of the fauces, making the oropharynx a single compartment. However, in infants a soft palate–epiglottal seal is present; milk reaches the esophagus via the pyriform recesses without disturbing the airway. During normal development humans lose the posterior oral seal, and adults rely on the intermediate seal to separate the oral cavity from the oropharynx and nasopharynx (Fig. 14-3).

Posteroventrally the base of the tongue is tied to the hyoid complex. This is a bony or osteocartilaginous structure that is linked by ligaments and muscles to the larynx, the base of the skull, the mandibular symphysis, and to the sternum and scapula. In many mammals the hyoid complex is also joined to the basicranium (presumably a primitive condition) through a system of jointed bones or cartilages (hyoid arch). The hyoid is always highly mobile.

The following general description is based on the American opossum *Didelphis virginiana*, chosen because much of our current knowledge of food transport is based on this animal. The opossum provides what is presumed to be a fairly good example of the primitive condition of the oral region. Highly evolved mammals such as higher primates, carnivores, and herbivores show considerable differences in detail (including the relative proportions of the adductor muscles and form of the digastric), but not in the general organization of the system.

Adductors In some mammals the adductors form a series of discrete muscles; in others, such as the opossum, the divisions are less clear. However, it is always possible to recognize the temporalis, masseteric, internal pterygoid, and external pterygoid muscle masses. The temporalis mass inserts on the medial and dorsal surface of the ascending ramus of the dentary (hemimandible) and arises from the dorsal region of the temporal fossa (Fig. 14-4). The masseteric mass arises from the zygomatic arch and inserts on the external and ventral surface of the mandible. The superficial fibers of this mass extend obliquely backward from the anterior region of the zygoma to the angular region of the mandible, whereas the deep fibers have a more vertical orientation and arise

from the wide region on the zygomatic arch behind the origin of the superficial masseter (see Hiemae and Jenkins, 1969, for a detailed description of these muscles in *Didelphis*, with a somewhat idiosyncratic terminology for the adductors). Although the adductors of other animals vary widely in their proportions and internal architecture (Turnbull, 1970; Weijs, 1975; Gans and Gorniak, 1978; Janis, 1979), they have very consistent sites of origin and insertion relative to one another.

Muscles Controlling the Hyoid Apparatus

The hyoid apparatus consists of elements of the hyoid and first branchial arches. The ventral portion of the hyoid and first branchial arches (basihyoid and thyrohyoid, respectively) form a C-shaped structure that both cradles and is joined by muscles and ligaments to the larynx. In some mammals (ungulates and carnivores) the remaining elements of the hyoid arch form a series of cartilaginous or bony rods connecting the ventral element to the auditory capsules (the integrocornate condition). In primates, as well as opossums, lagomorphs, and tenrecs, these elements are reduced to varying degrees (the discretocornate condition) to form the lesser horn of the primate hyoid apparatus. The base of the tongue is firmly connected to the anteroventral surface of the hyoid apparatus. The epiglottis forms a mobile anterodorsal cover to the larynx. It extends upward inside the body of the C formed by the ventral portion of the hyoid apparatus, with its anterior surface facing the tongue and the posterior surface the laryngeal inlet and oropharynx.

The principal muscles that control hyoid movement are two suprahyoid muscles, the geniohyoid (mandibular symphysis to hyoid) and the stylohyoid (basicranium to ventral surface of hyoid); and two infrahyoid muscles, the sternohyoid and omohyoid (scapula to hyoid). Minor elements of other muscles contribute to the anterior suprahyoid muscles, for example, fibers of the mylohyoid and genioglossus. Some mammals, including opossums, have lost or greatly reduced the stylohyoid muscle, and its function is taken over by an equivalent muscle that parallels a larger stylopharyngeus (Fig. 14-4). A complex set of muscle sheets originating on the basicranium

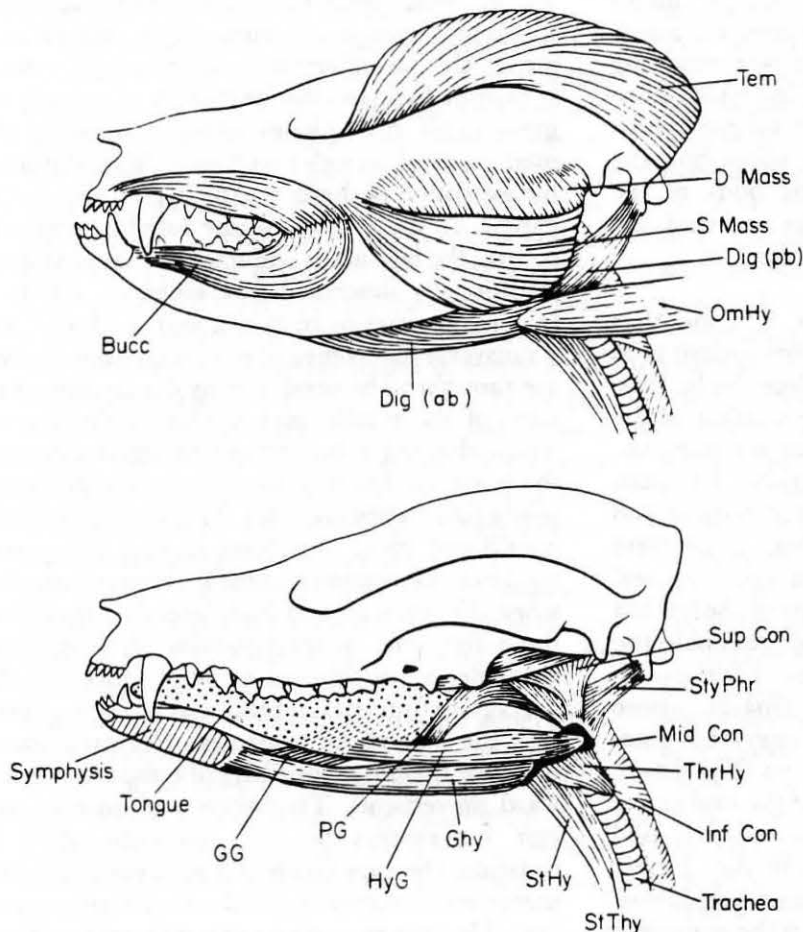


Figure 14-4 Lateral views of the head of the opossum showing structures associated with feeding. *Above:* Muscles of the jaw and hyoid. *Tem* = temporalis; *D Mass* and *S Mass* = deep and superficial masseter; *Bucc* = buccinator; *OmHy* = omohyoid; *Dig* = digastric, which has anterior (*ab*) and posterior (*pb*) bellies. Not shown are the large internal pterygoid (deep to the *Mass*), the small internal pterygoid (attaching to neck of mandibular condyle), and the mylohyoid (between the rami of the jaws). *Below:* Muscles of the tongue and pharynx. *GG* = genioglossus; *Ghy* = geniohyoid; *HyG* = hyoglossus; *PG* = palatoglossus; *StHy* = sternohyoid; *StyPhr* = stylopharyngeus; *Sup Con*, *Mid Con*, and *Inf Con* = anterior (or superior), middle, and posterior (or inferior) constrictors; *ThrHy* = thyrohyoid.

make up the dorsal pharyngeal wall—some of these insert directly on the dorsal surface of the thyrohyoid. The sternohyoids parallel the sternohyoids. In primates and opossums some fibers of both the anterior and posterior bellies of the digastric insert on the ventral surface of the hyoid apparatus. This appears to be the retention of a primitive condition that is lost in more specialized mammals. The hyoid-jaw link means that the hyoid muscles and the digastrics can affect jaw opening.

Muscles Controlling the Tongue The tongue can be regarded as a bag of highly specialized epithelium filled by muscle fibers. These fibers have conventionally been regarded as clearly separated into two groups of anatomically distinct muscles: the intrinsic muscles (vertical, trans-

verse, and longitudinal) running within the substance of the tongue; and the extrinsic muscles, which have a single bony attachment external to the body of the tongue (hyoglossus, genioglossus, styloglossus, and palatoglossus). It has been argued that the extrinsic muscles regulate tongue position in space, whereas the intrinsic muscles control tongue shape (Livingstone, 1956). Such a clear and arbitrary division of function is not valid, since all the extrinsic muscles can also change the shape of the tongue; for example, the genioglossus can depress the posterior surface and the hyoglossus can shorten the posterior region of the tongue. The division of muscles into protractors and retractors (see Lowe, 1981) is also an oversimplification. The experimental evidence suggests that both groups of muscles produce changes in tongue shape and may affect

minor changes in position, although major changes in position certainly depend on movement of the hyoid (that is, tongue base) resulting from differential contraction of the hyoid muscles, rather than on those of the tongue. However, we know virtually nothing about how the series of muscles making up the body of the tongue or the extrinsic muscles entering the tongue actually control tongue shape.

Muscles of the Cheeks and Lips The mouth is surrounded by a ring of muscle (orbicularis oris) that functions as a sphincter to close the lips and form the anterior oral seal. (The mobility of the lips, characteristic of man and higher primates, reflects the absence of a rhinarium. In many mammals the upper lip is tied to a rhinarium and is relatively immobile. Nevertheless, a complete anterior oral seal can be formed since the seal depends not on the overall mobility of the lips but on the ability of the animal to approximate the upper and lower lip margins even if the mouth extends far posteriorly. The buccinator, whose fibers pass anteroposteriorly and intermesh anteriorly with those of orbicularis oris (Fig. 14-4), forms the muscular lateral wall of the oral cavity and thus the bulk of the cheeks. It is attached posteriorly to the pterygomandibular raphe, which passes vertically from the pterygoid hamulus to attach to the inner surface of the mandibular body behind the molars. Its fibers then pass forward and lateral to the postcanines to form the cheek.

Muscles of the Soft Palate and Pharynx The pterygomandibular raphe also forms the anterior attachment of the anterior (superior) constrictor of the pharynx. This is one of three constrictors whose overlapping fibers form the muscular posterior and lateral walls of the pharynx. Internal to the raphe, the palatoglossus connects the soft palate and tongue, running in the folds of mucosa called the pillars of the fauces. The middle oral seal is formed between the soft palate, the pillars, and the tongue. The soft palate is highly mobile and changes shape during feeding. The movements of the palate are produced by four extrinsic muscles, the levator and tensor veli palatini, the palatoglossus, and the palatopharyngeus. The

last of these helps form the palatopharyngeal sphincter during swallowing, which assists in closing off the nasopharynx from the oropharynx.

Mammalian jaws can be moved to varying degrees in all three planes, anteroposteriorly and mediolaterally as well as vertically. With the possible exception of the lateral pterygoid and the digastric, all the muscles whose sole function is to control the jaws act as adductors. They have been traditionally described (see Hiiemae, 1978) as forming a series of couples about the lower jaw. Transverse (lateromedial or ectental) movements are thought to be produced by the combined actions of the medial pterygoids of the side on which chewing is occurring (the active side) and the posterior fibers of the temporalis on the opposite (the balancing side). This couple has been considered most important during the power stroke of mastication and the first part of opening when the jaw is moved from lateral to medial on the active side. Anteroposterior (or propalinal) movements are thought to be produced by the pterygoids (internal and external acting together) and the superficial masseters (forward movement) or the posterior fibers of temporalis (backward movement). Transverse and anteroposterior movements do not normally occur in isolation; they are combined with vertical movements in the normal cyclical activities of mastication. The only exception so far documented is the anteroposterior shift of the lower jaw to bring the incisors or molars into occlusion in rodents (Hiiemae and Ardran, 1968; Weijs and Dantuma, 1975, 1981), where the simultaneous occlusion of anterior and postcanine teeth is precluded by the geometry of the jaws.

More recent experimental work has demonstrated, however, that such biomechanical explanations of adductor muscle function are simplistic. Although "couples" may operate to produce jaw movement, electromyographic and movement analysis show that muscles, or parts thereof (and not always those predicted by their theoretical vector mechanics), are active on both sides of the jaw during the feeding cycle. Further, there is a marked and changing pattern of differential activity between corresponding muscles on the active and balancing sides. The explanation for these findings will require further studies with

the level of analysis used by Weijs and de Jongh (1977) in their study of the rabbit.

The mechanics of jaw opening have been classically described as based on a downward and forward pull on the condyle, coupled with a downward and backward pull on the anterior part of the mandible from the lateral pterygoid and the digastric, respectively. This mechanically simple explanation is complicated by the variability of digastric form in mammals (du Chaine, 1914; Edgeworth, 1935) and confounded by the experimental observation that not only does jaw opening occur in two separate stages in many mammals (see below and Figs. 14-5, 14-6, 14-8), but that even in those cases where it appears to be a simple movement, it results from the complex interplay of all the muscles of the hyoid apparatus (Crompton et al., 1977). Further, when the central tendon and hyoid connection of the digastric are severed, leaving both anterior and posterior bellies free, there is no observable change in the pattern or amplitude of jaw opening. It might reasonably be argued that the opossum is a less than ideal subject from which to make generalizations on digastric function; however, the digastric in that animal does have a hyoid linkage, as it does in all primates and some other mammals. This kind of experiment should be done in animals such as cats where the digastric has no hyoid connection.

Although all these muscles can be described as belonging to specific muscle groups, it is important to appreciate that no muscle contracts in isolation. The complex cyclical movements of the jaw and tongue observed in feeding depend on a highly integrated and patterned cycle of activity in all these muscles (Fig. 14-2).

Mechanisms of Intraoral Food Handling

Until recently almost nothing was known of the mechanisms by which food was transported through or manipulated in the mouth. Our knowledge of masticatory movement was limited to naked eye observation or the analysis of cinefilms of wild or laboratory animals. Although these methods provided useful information on

feeding behavior and the general pattern of jaw movements, it was difficult (even under laboratory conditions) to correlate the observations with the condition or position of the food. The only exceptions to this of which we are aware are Abd-el-Malik's observations of human tongue movement (1955) and an extraordinary film taken of intraoral food manipulation in a patient in whom the cheek and part of the left upper jaw had been surgically removed (Veterans Administration, E. L. DuBrul, personal communication).

However, in the last decade cinefluorographic and electromyographic techniques have been used to examine mandibular and oral function. Technical problems have so far limited our knowledge of tongue movements in the coronal plane to what can be seen when the mouth is open or partially open. Cinefluorographs show the movements of such radiopaque structures as bones and teeth. With careful adjustment of the radiation levels, soft tissue outlines can also be recorded. Food can be mixed with barium salt and its position then tracked. However, the most important development has been the regular use of metallic markers (Crompton and Hiimae, 1970). The insertion of small fillings in selected teeth in both upper and lower jaws permits very accurate measurement of changes in jaw position (Hylander and Crompton, 1980); a marker sutured to the dense fascia on the anterior (ventral) surface of the body of the hyoid reflects changes in the position of that bone (Crompton et al., 1977). Similarly, the insertion of small segments of surgical wire into the muscles of the tongue below its surface led to the discovery that the mechanism of food transport involves differential longitudinal contraction and expansion of various parts of the tongue (Crompton and Sponder, 1981, 1982). Analysis of high-speed cinefluorographic film is now based on digitization of significant reference points in each frame of film. The x-y coordinates of each point are entered into the computer and a variety of manipulations performed (McGarrick and Thexton, 1981).

Figure 14-5 shows typical movements over time of gape, hyoid, and tongue markers for the opossum and macaque. The profiles have been smoothed by connecting the individual com-

puter-generated points with a solid line. Lapping by the opossum is associated with high amplitudes of anterior and middle tongue markers (*ATM* and *MTM*) owing to the extensive protrusion of the tongue (see also Fig. 14-12). The spaces between the vertical lines indicate (*left to right*) the durations of first opening (*O1*), second opening (*O2*), and close (*C*) phases, which are not homologous with phases of the masticatory cycle. In eating soft food the opossum has no clear division between fast close (*FC*) and slow close (*SC*) because of the negligible resistance of the food. Long slow open (*SO*) and hyoid protraction are associated with stage I transport. In contrast to lapping, all tongue markers have nearly equal anteroposterior movement when hard food is eaten. Phases *FC*, *SC*, *SO*, and *FO* (fast open) are distinct. The *FC-SC* transition occurs as upper and lower teeth come into contact with the food.

Macaques do not lap; Figure 14-5 represents drinking from a water bottle with spout just anterior to the incisors. The amplitude of jaw movement is about the same for soft and hard food, but the profiles differ. The gape plot for soft food has no distinct phases. Movements of the markers indicate active transport. For hard food this power stroke is long and the opening phase short. Movement of food is minimal.

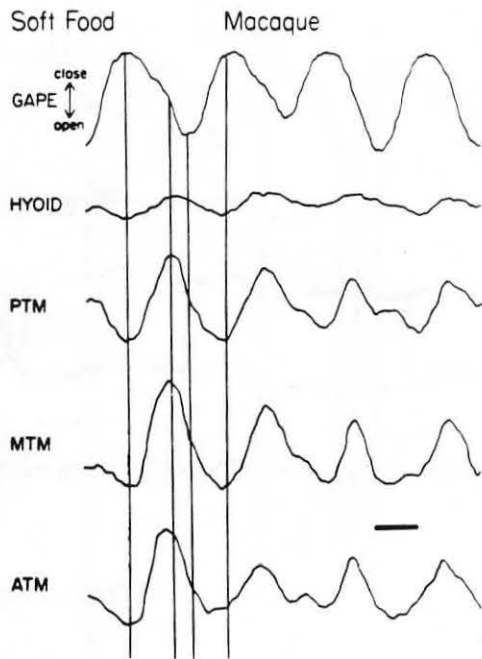
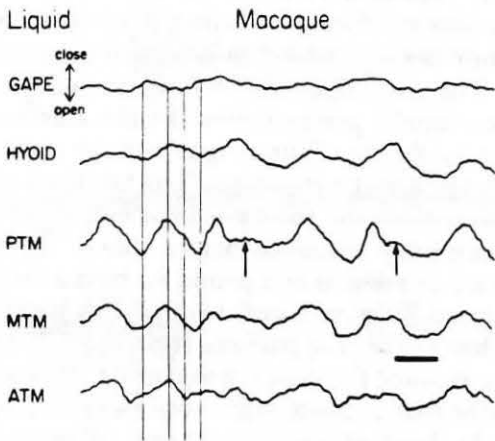
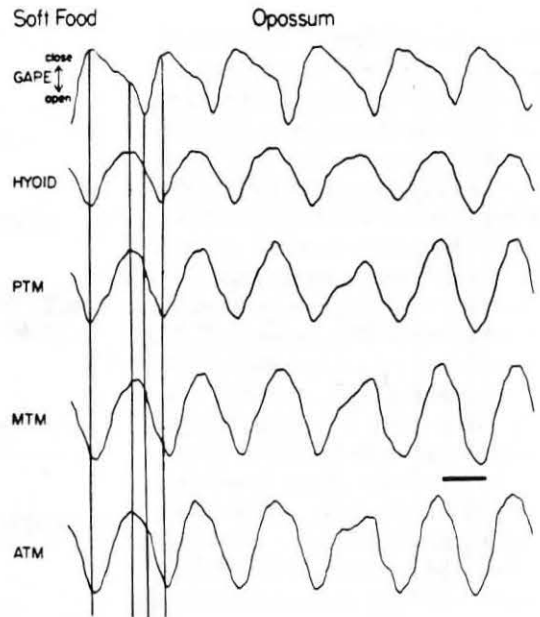
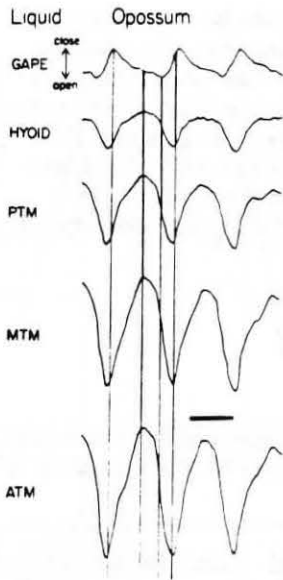
Correlation of data from cinefilms with electromyograms (Figs. 14-6, 14-7) show the pattern of muscle activity associated with each behavioral event. Hylander (1977) and Weijs and de Jongh (1977) have pioneered the use of strain measurement to examine the biomechanics of jaws and skulls. Single elements or rosette strain gauges are attached to the bony surface and strain levels accurately correlated with electromyograms and movement patterns (Fig. 14-6).

Behavior recorded experimentally shows that some of the processes to which the food is subjected in the oral cavity occur concurrently. Each depends on the synchronization of the activity of numerous muscle groups controlling the jaw, tongue, hyoid, soft palate, and pharynx. These muscles show modifications of their basic activity in response to changes in the size, shape, or consistency of the food and therefore in the relative movement of the structures they control during a

sequence of cycles involving the opening and closing of the jaws and the coordinated movements of the hyoid apparatus, the body of the tongue, and the soft palate (Fig. 14-8).

Food is transported through the mouth, broken down by the teeth, and manipulated by the tongue and cheeks. The shape of the tongue at any moment is a function of activity in its intrinsic and extrinsic (especially genioglossus and hyoglossus) muscles. The position of the tongue is largely determined by the position (relative to the palate) of its structural base—the hyoid. The tongue is linked both directly to the symphyseal region of the lower jaw by the genioglossus and indirectly to the body of the lower jaw through the anterior suprahyoid muscles. Franks, German, and Crompton (unpublished data) have shown that the activity of the muscles that regulate tongue surface, hyoid, and lower jaw movement is coordinated. The repetitive movement of the jaws, hyoid apparatus, and tongue body are, however, linked (at least in the opossum and hyrax) only at one point in each of their cycles: the time just before the jaw leaves minimum gape. This represents the end of the power stroke, occurring after the cessation of adductor activity and at the beginning of protraction of the hyoid and of markers in different parts of the tongue. It also marks the beginning of lengthening (anteroposterior expansion as seen in lateral projection) of the posterior third of the tongue. The times at which the jaw reaches maximum gape and when the markers begin to return or the posterior tongue starts to shorten (contract) are not synchronous. It is possible for the sake of convenience to refer to jaw, hyoid, and tongue cycles; if these are defined as beginning at minimum gape, it follows that the synchronous jaw, hyoid, and tongue cycles always have the same time base. The pattern of jaw, hyoid, and tongue activity changes as the food is progressively broken down and portions swallowed. Despite the variations in behavior, it is clear that there is a basic pattern in all three systems and that this pattern is found in all mammals so far studied.

Three stages (ingestion, stage I transport, and stage II transport) have been identified in the intraoral transport of liquids, and five stages (in-



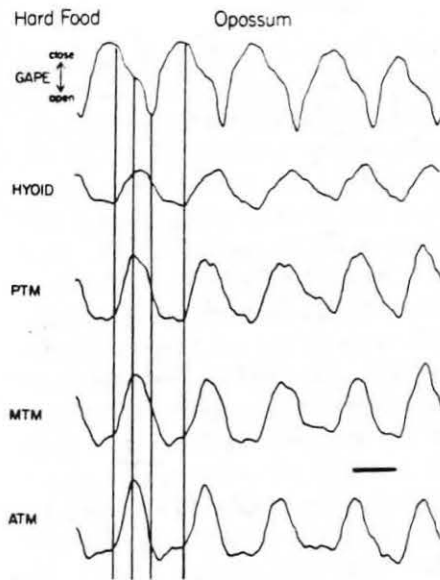
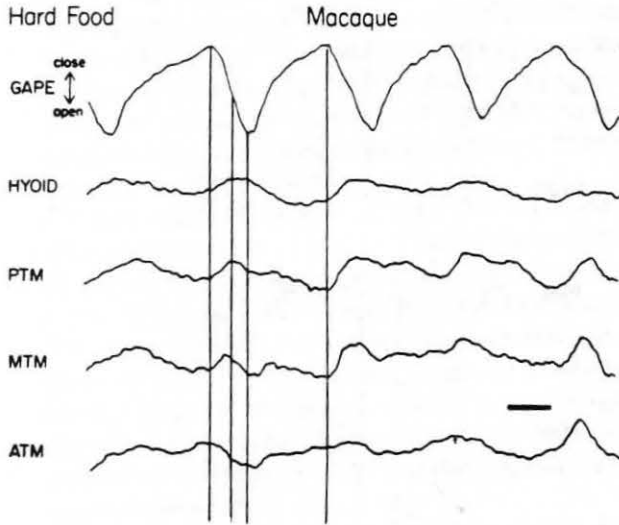


Figure 14-5 Movements of the jaw, hyoid, and tongue in the opossum and macaque when feeding on liquids and soft and hard solid foods. The heavy line shows 250 msec elapsed time. Vertical reference lines show minimum and maximum gape and *PTM* reversal (compare with Fig. 14-8). *ATM*, *MTM*, and *PTM* = anterior, middle, and posterior tongue markers. Arrows (macaque for liquid) show times of swallowing.



gestion, stage I transport, mastication and manipulation, stage II transport) in the handling of solids (Fig. 14-1).

Ingestion of Solid Food Solid food is either picked up and collected by the tongue and anterior teeth, often with the assistance of the lips (as in grazing herbivores), or is forcibly separated from the matrix using the anterior (but in some cases the postcanine) teeth (as in opossums, rodents, primates). Pickup or collection cycles have frequently been recorded in laboratory experiments. The jaw is opened, the food often licked and then rapidly grasped either by the anterior teeth or by the tip of the tongue and the upper anterior teeth as the jaw closes. The head is then withdrawn from the food source, elevated, and the masticatory sequence begins. Many mammals, such as rodents and primates, hold a food object (a nut, fruit, or a leafy twig) in their hands. They then cut or tear portions from it using the incisors as much for grasping as cutting; the portion of the food in the mouth is torn away from its matrix by head or hand movement. When rats gnaw on hard, brittle bariumized biscuit (Hiimeae and Ardran, 1968), pieces are chipped away by a series of repetitive cyclical chiseling movements in which the lower incisors move upward into the food (closing and power strokes) and then downward (opening stroke). With each repetition small fragments of material accumulate in the diastema immediately behind the incisors. Whatever method is used to take material into the front of the mouth, it is then transported to the postcanines for processing.

In many tetrapods, including mammals (the

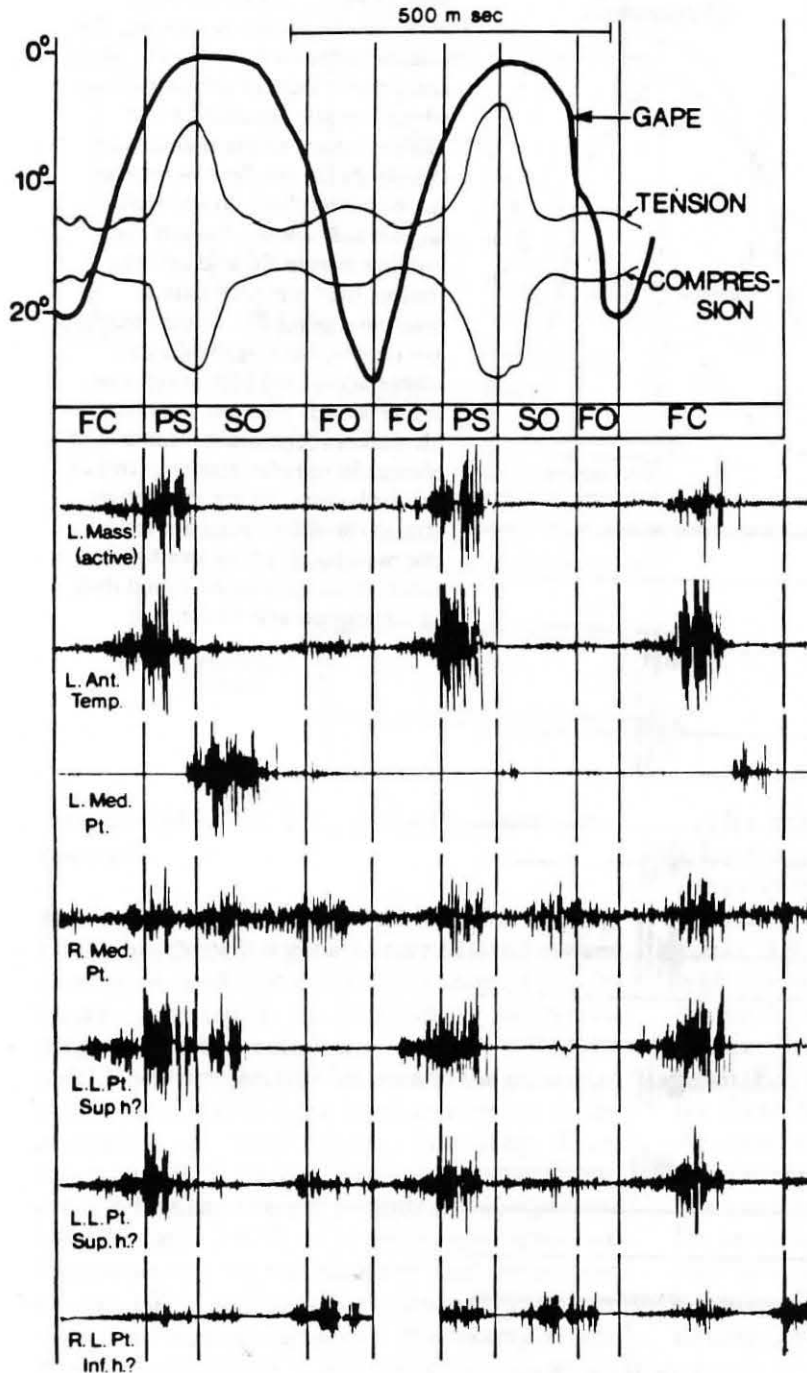


Figure 14-6 The relationships among jaw movement (*heavy line*), analyzed from 16-mm X-ray cinefilm; strain (*fine lines*), measured from gauges attached to the bone of the lower jaw; and electromyograms for two successive chewing cycles in a macaque. Electromyography from the left masseter and left anterior temporalis show peaks early in the power stroke. Strain in the jaw peaks at near minimum gape and tails off rapidly. Activity in the medial pterygoid during slow open is associated with lateral translation of the lower jaw. The sites of the electrodes in the lateral pterygoid were not determined by post mortem dissection. *FC* = fast close, *PS* = power stroke, *SO* = slow open, *FO* = fast open.

opossum, the tenrec, and small carnivores), food is ingested by inertial feeding (Chapter 13). Food is gripped by the incisors and the head is rapidly withdrawn and brought to a sudden stop; at the same time the jaws are rapidly opened to release

the food, which then moves under its own inertia into the oral cavity. Detailed records and analyses of the path of jaw, tongue, and hyoid movements during the ingestion of solid food have not been published for any mammal, although they are

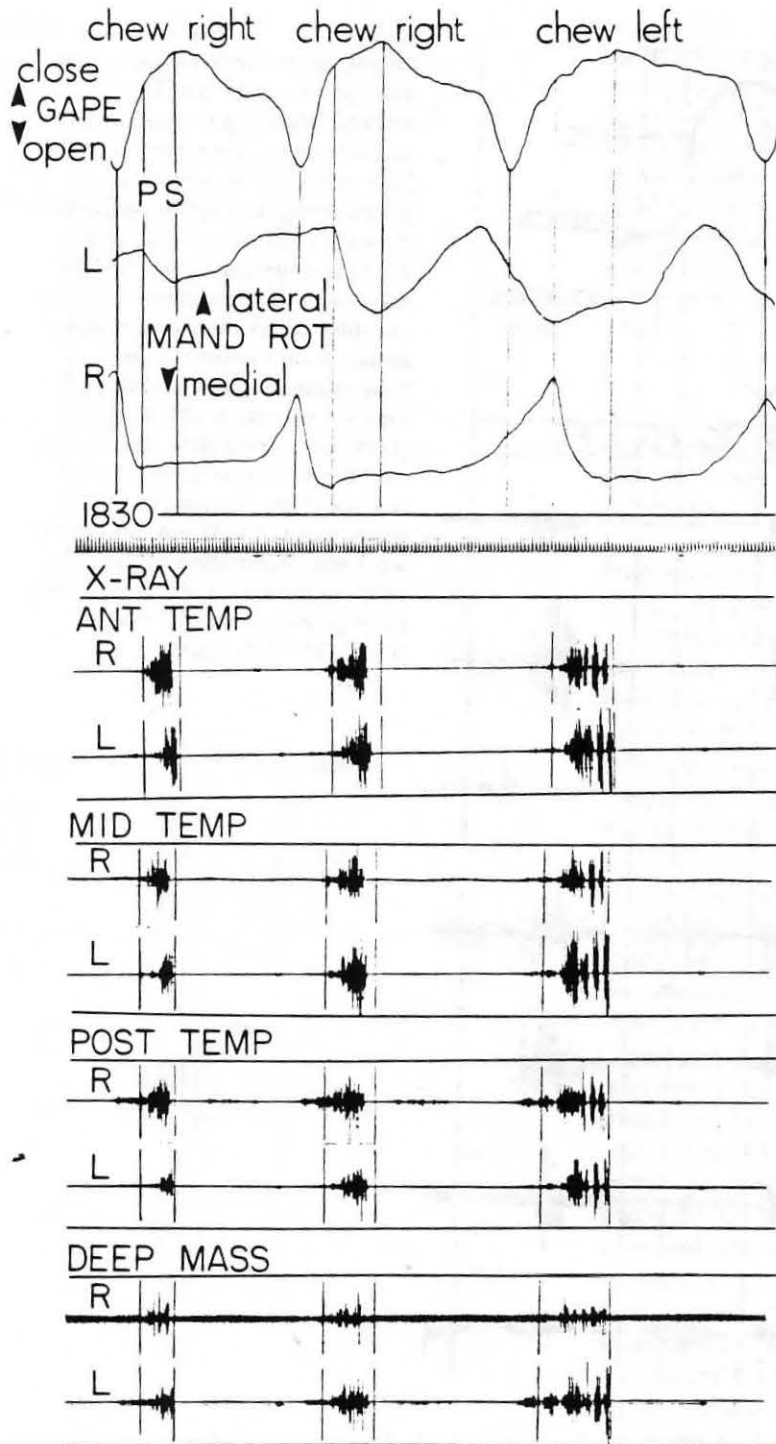


Figure 14-7 Three chewing cycles in the opossum showing the relative rotation between the active and passive sides of the mandible, which is made possible by the mobile nature of the mandibular symphysis. In the first two cycles the hemimandible on the right (active) side rotates toward the midline during *FC* and returns toward the "straight" lateral position during *PS*. These rotations are reversed in the third cycle where active and balancing sides are reversed. The left hemimandible makes reciprocal motions. The change in the electromyograms of the adductors during *PS* demonstrates the differential activity of the muscles of active and balancing sides. (Based on unpublished data of Crompton and Crabtree.)

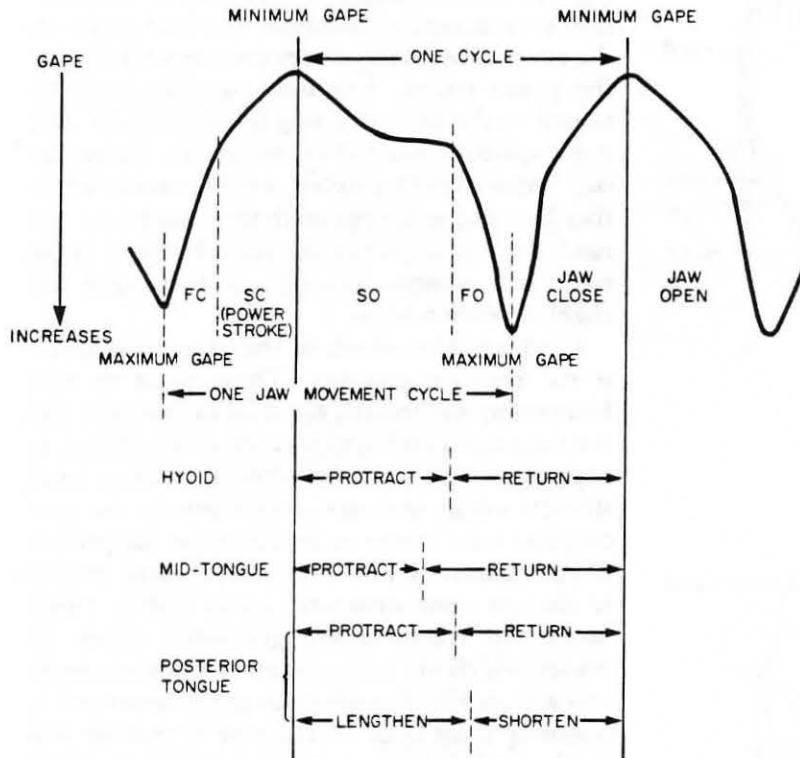


Figure 14-8 The relationship of tongue and hyoid movement to the cycle of jaw movement. Data from hyrax and opossum show that hyoid and tongue movements correlate predictably with jaw movement only at minimum gape when the hyoid and posterior two thirds of the tongue begin to protract and the posterior third to expand. SC = slow close; other symbols identified in Fig. 14-6.

now available for cat, opossum, tenrec, and macaque.

Mastication Although it has long been recognized that there is a general correlation between tooth form and type of diet in mammals (for instance, carnassials in carnivores, lophodont molars in herbivores), it is only recently that the mechanical properties of foods and the pattern of their comminution have been considered in the evaluation of tooth form. Following Rensburger's (1973) study of occlusion and wear patterns in fossil and recent rodents and comparable work by Janis (1979) on hyraxes, more attention has focused on the mechanics of food breakdown (Lucas, 1979, 1980) and the relationship between wear and enamel structure (for example, von Koenigswald, 1982). A new and important area is the form of microwear on the tooth surface and its value as an indicator of both direction of movement and of diet (for example, Walker, Höeck, and Renez, 1978; Ryan, 1979; Covert and Kay, 1981; Grine, 1981; Kay and Covert, 1983; Gordon, 1984).

The molars of metatheria and eutheria are derived from the basic tribosphenic form found in the early mammals of the Cretaceous, family Aegialodontidae (Crompton and Kielan-Jaworowska, 1978). These teeth are characterized by high pointed cusps, long shearing edges (blades) on the slopes of the cusps, and a limited "mortar and pestle" system in the protocone and talonid basin (Fig. 14-9). The efficiency of this design for the breakdown of a wide variety of foods has been documented in the American opossum, which can rapidly reduce materials as hard as chicken bone and as fibrous as skin to a condition suitable for swallowing. With the expansion of mammals into new habitats in the Paleocene and Eocene, modifications of this basic design developed, producing the long, high-profile blades of the carnassials of carnivores, the parallel arrays of low-profile blades found on the ridges of the molars of rodents and herbivores, and the enhanced mortar and pestle system of the Anthrozoidea (Fig. 14-10).

For food to be broken down, it must first be positioned between the occlusal surfaces of the

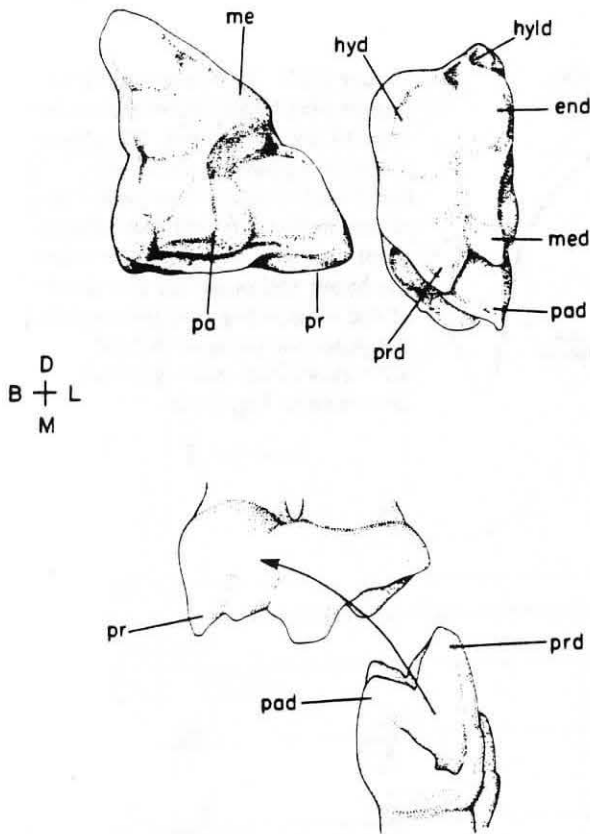


Figure 14-9 Above: Occlusal views of upper and lower molars of the American opossum showing the basic tribosphenic pattern with its combination of ridges (blades), cusps (pestles), and basins (mortars). Below: Mesial (lower molar) and distal (upper molar) profiles of the molars of the opossum to show the main matching shearing surfaces. Since the lower molar occludes between the upper molar of its own number and the molar distal to it, the upper molar in the figure has been rotated to show the distal surface, that is, the surface across which the large blade on the lower molar cuts during the power stroke. *end* = entoconid; *hyd* = hypoconid; *hyld* = hypoconulid; *me* = metacone; *med* = metaconid; *pa* = paracone; *pad* = paraconid; *pr* = protocone; *prd* = protoconid.

teeth on the working side (in most mammals mastication is unilateral). In a few animals, including man and rodents, the transverse distance between the upper and lower molar rows is similar (isognathous); bilateral mastication can occur in rodents (Hiemae and Ardran, 1968) and some

coincidental trituration may occur on the balancing side in man. Regardless of whether mastication is unilateral or bilateral, the food to be reduced must be retained between the teeth during the power stroke. The food particles are positioned by the tongue acting in conjunction with the buccinator muscles of the cheeks. Retention (see Osborn and Lumsden, 1978) is achieved either by features on the teeth (the notch in a carnassial, for example) or, for large lumps of material, by the continued action of the tongue and cheek or even a hand.

Food is broken down by the generation of internal fracture patterns. These patterns may form so rapidly and the effect be so dramatic that the material is cleanly separated in one stroke, as happens when a blade cuts through fruit or a nut shatters under pressure. Alternatively, the process may take longer or be slower, as happens in fibrous materials, which require repeated strokes to disrupt their structure. Lucas (1982, 1983) notes that fractures are generated either by blades, which are very narrow in one dimension and are usually, but not exclusively, arranged in opposing pairs (Fig. 14-10B); or by mortar and pestle combinations, where the "pestle" is a blunt convex surface and the "mortar" a reciprocal and, usually, larger concave surface (Fig. 14-10A). Both elements can be found in serial arrays or in combinations. A third pattern is a serial array of low-profile blades that act as a milling machine (Fig. 14-10C).

Foods that are hard and brittle (nuts) or turgid (fruit pulp) are most effectively crushed by a mortar and pestle system (Fig. 14-10A). Secondary fractures are propagated through brittle material. Turgid food requires that the cell walls fail, but no further comminution is needed; a mortar and pestle can crush many cells with a single stroke, blades only a few. A tight-fitting pestle increases retention but creates problems in clearing the fractured particles from the working surfaces. A mortar and pestle that do not fit tightly permit both vertical and transverse movement, first compressing the material and then rolling it (compression crush and rolling crush, respectively, Osborn and Lumsden, 1978). A spider monkey *Ateles* has molars functioning as mortars and pestles to break up fruit pulp. The ridges

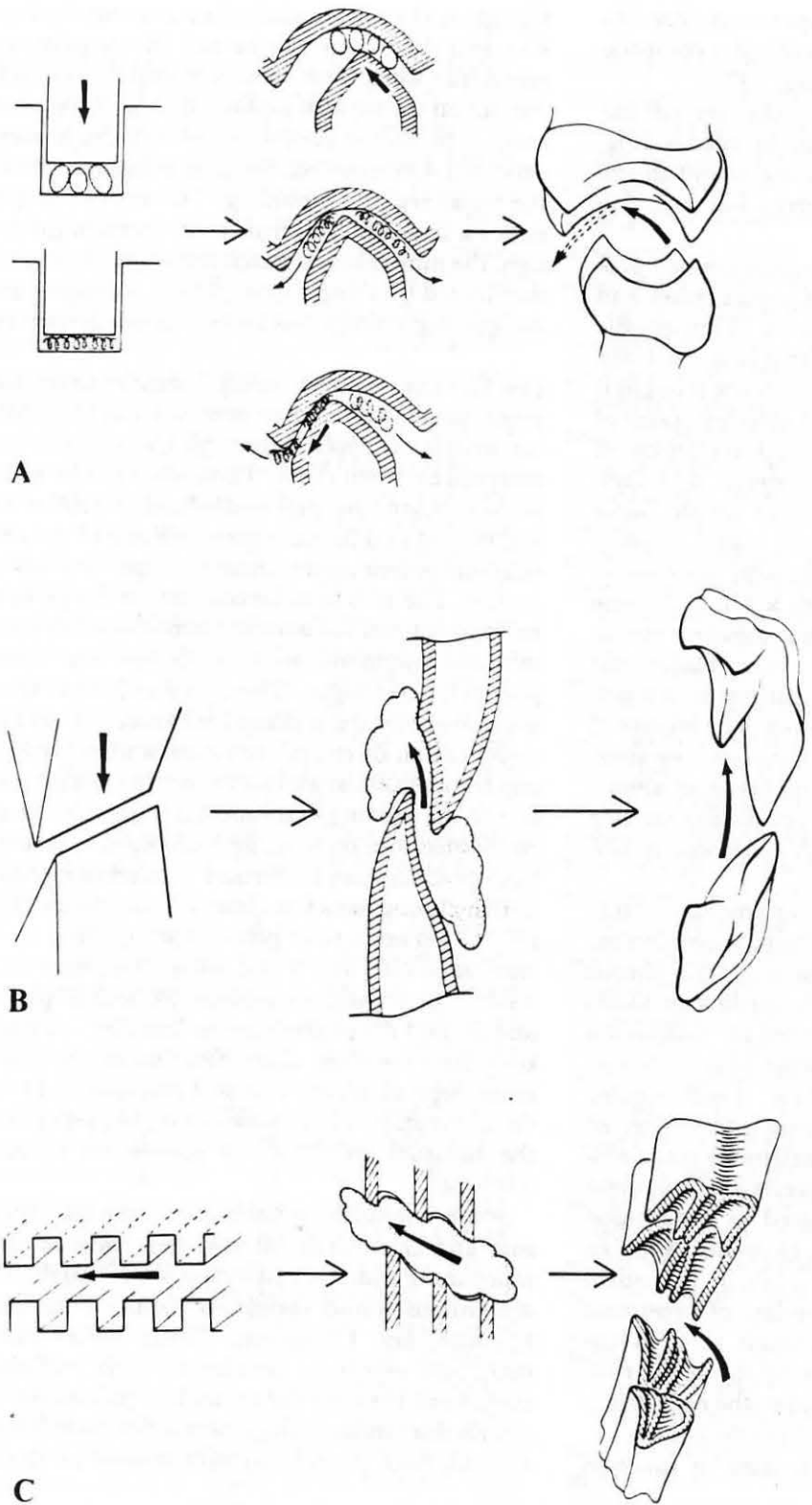


Figure 14-10 Mechanical principles of tooth design in relation to the nature of the food: hard, brittle, or turgid (A); soft, tough (B); or tough, fibrous (C).

forming the margin of the occlusal surface also act to cut through and compartmentalize the fruit, thereby serving as the walls of a compression chamber (Kay and Hiiemae, 1976).

Foods such as muscle and skin that are soft but tough are most efficiently cut by blades (Fig. 14-10B). The simplest blades are found in the carnassials of various carnivores but are also found on the edges of cusps.

Tough, fibrous foods such as grass are best processed by the combination of compression and tearing provided by a serial array of low-profile blades acting as a milling machine (Fig. 14-10C). A system of enamel ridges and dentine troughs is formed and maintained by the different rates of wear of these materials. Such teeth are typical of ungulates, subungulates, and rodents. Although a newly erupted tooth may have simple blade structure along the slopes of its cusps, in many mammals the enamel cover is rapidly worn away, leaving two enamel edges with a softer dentine surface between. This is the most efficient condition for a parallel array of low-relief blades that are used to reduce grasses by cutting on a transverse rather than a vertical stroke. The molars of some rodents erupt with small enamel-free areas just under the cusp tips. The tips break off almost as soon as the teeth are used, producing the two enamel edges associated with horizontally oriented blades.

Many food items contain combinations of materials, each with different fracture properties. For example, many fruits have tough, fibrous skins and soft, fleshy pulps. According to Lucas (1983), insects can be considered as "fluid-filled sealed tubes," the limiting factor in their reduction being the nature of the tube. A soft-skinned larva readily bursts in a mortar and pestle; an adult with its chitinous exoskeleton is more efficiently opened by a blade. Materials such as these can be most effectively reduced by a dentition with a combination of both elements. Such an arrangement can be found both in individual teeth, for example, in the molars of prosimian primates and primitive mammals such as the opossum or, alternatively, along the tooth row, such as the combination of blades (the carnassials) and mortars and pestles (the molars) in dogs.

A third variant is the separation of function

between anterior and cheek teeth, as in rodents that gnaw the fibrous shell of a nut using the incisors and then chew the kernel. Many primates peel a fruit using their incisors to grip the skin and the action of the arm and hand to pull the fruit away. The skin is then dropped and the process repeated. Once peeled, the flesh is transported to the molar region for pulping. The more homogeneous a dentition in terms of its mechanical design, the more likely it is that the animal has a diet dominated by a single type of food: examples are the grazing artiodactyls and the felid carnivores.

Jaw Closing Food breakage occurs during the power stroke as the force generated by the elevator muscles is applied through the teeth to the material between them. The power stroke is defined as beginning with tooth-food-tooth contact and ending at minimum gape, the end of the vertical movement approximating upper and lower molars. The jaws must be opened for the teeth to be repositioned for another stroke and for comminuted fragments to be collected and transported by the tongue. The upper and lower teeth are moved toward and away from each other by a combination of cranial elevation and depression and by mandibular elevation and depression relative to the moving cranium. Each gape cycle can be divided into opening and closing movements, both of which may be further divided into phases so that closing has a fast close (*FC*) and a slow close (*SC*) or power stroke phase, and opening has a slow open (*SO*) and a fast open (*FO*) phase (Fig. 14-8). The transitions between *FC* and *SC* phases and *SO* and *FO* phases may be indistinct in gape-time plots since the characteristics of jaw movement depend on the size and consistency of the food, the stage in the masticatory sequence, and the habitual amplitude of movement in each mammal.

Some mammals, notably the American opossum and carnivores, always open their mouths much more widely when eating solid food than its dimensions would appear to require (Thexton, Hiiemae, and Crompton, 1980). Other mammals, and especially herbivores, have indistinct transitions between the *FC* and *SC* phases and no clearly discernible change of rate between *SO* and *FO*. All four phases can nonetheless be distin-

guished on other criteria (see below). The transitions between jaw closing and opening are, however, clearly defined in behavioral records. The point at which closure ceases and opening begins (minimum gape) represents the end of food processing in that cycle and the initiation of food transport. As such it is the point in the jaw movement cycle that is highly correlated with transition points in both the hyoid cycle and the tongue surface movement cycle (Fig. 14-8). Although the power stroke ends at minimum gape, this may not coincide with full occlusion or maximum intercusation of the teeth. The opossum and the tenrec, which have high-profiled postcanines and mobile symphyses, rotate the two halves of the lower jaw along their long axes as the mandible moves through the chewing cycle (Hiiemae and Crompton, 1971; Crompton, Oron, and Crabtree, unpublished data). In the opossum the hemimandible on the balancing side both rotates (during the power stroke) and moves laterally, whereas during the remainder of the cycle it moves medially (Fig. 14-7). In contrast, the most dorsal edge of the hemimandible on the active side rotates sharply during *FC*, stays rotated through the power stroke, and rotates sharply laterally during *FO* (T. Crabtree, personal communication).

With the exception of those few mammals (some rodents) that have lower cheek teeth and jaws wider than those of the upper jaw, chewing can take place only on one side (the active or working side) at any one time. In all mammals so far examined (some rodents excepted), the direction of lower jaw movement in the power stroke is upward (toward the upper molars) and medial (toward the midline), with a variable anterior component. During puncture crushing of large, hard objects such as bone, the power stroke ceases when the teeth are still separated; medial movement of the lower jaw on the power stroke is then only minimal (Oron and Crompton, unpublished data). So consistent a pattern among mammals with very different tooth morphologies is readily explained, given the common origin of their teeth and the basic design of the mammalian jaw apparatus. As later molar forms evolved, concomitant changes occurred in the amplitude and angulation of the power stroke. For example, the

anterior component is eliminated and the medial component is very small in felids, as a scissorlike action does not require major medial movement of the carnassials; in contrast, the medial component is exaggerated in most herbivores, allowing a long lateral-to-medial traverse for the serially arranged low blades. The anterior component is elongated in many rodents, given the geometry of the dentition (Hiiemae and Ardran, 1968). The morphology of the jaw joint reflects either the predominant direction of the movement required for food breakdown (for example, the anteroposteriorly oriented condyle and glenoid fossa in rodents), or the mechanics of the system (for example, the excessive rotation of the mandible in tenrecs). The pre- and postglenoid processes of the fossa in carnivores both restrict movement and prevent dislocation.

To position the teeth for the power stroke, the lower jaw has to be moved upward and laterally from its point of widest opening. The first stages of this movement (to tooth-food-tooth or tft contact) occur without resistance, often very rapidly (*FC* phase), and are associated with low levels of activity in the adductor muscles. As soon as tft contact occurs, the rate of jaw closure slows. The rate change between *FC* and *SC* (the power stroke) and the rate at which the teeth are approximated during that stroke depend in large part on both the size and consistency of the food (Thexton, Hiiemae, and Crompton, 1980; Fig. 14-5). Activity in the elevator muscles rapidly increases on tft contact, reaching peak levels during *SC*, but ceases before or close to the point of minimum gape (Figs. 14-6, 14-7). The rapid rise in the force exerted on the food is reflected by the pattern of strain on the mandible. This peaks at or before minimum gape (Hylander and Crompton, 1980; Hylander, 1984). In animals such as the rabbit where the measurable minimum gape may not correspond exactly to maximal occlusion given the orientation and form of the tooth surfaces, the strain also peaks before completion of the power stroke (Weijs and de Jongh, 1977).

Since the action of high blades, low blades, or mortars and pestles depends on the powered approximation of their components, the power stroke is completed, strictly speaking, when the teeth reach their maximum contact (minimal sep-

aration or maximum intercuspatation in occlusion) for that cycle and when the gape is therefore least. It follows that minimum gape does not always occur with the teeth in full occlusion. It also follows that minimum gape may appear to last for some time if the teeth are moving but in occlusion. Records for complete masticatory sequences (ingestion-deglutition) in cats and opossums eating hard foods show that the teeth may fail to break the food in the earliest cycles so the minimum gape is large. With successive power strokes, some firm foods are progressively reduced and the teeth move closer together with each cycle until they finally reach full occlusion at the end of the power stroke. This is true, for example, of the hyrax eating most vegetable foods, of the opossum eating apples, and of the tenrec eating cooked flesh. When irregularly shaped hard substances such as bone are chewed, a sequence of cycles with progressively reduced gapes is not observed; instead, gapes are highly variable as the object is manipulated in the mouth and engaged by the teeth in different positions. It is only when a certain consistency is reached that progressive cycles with reduced gapes are observed.

Early cycles in a masticatory sequence have been distinguished as puncture crushing and the later ones as chewing (Hiemae, 1976). This broad categorization, although it masks the progressive change that occurs as food is reduced, does reflect both a difference in the mechanics of food breakdown and the control of the lower jaw movement. In puncture crushing the high points of the tooth crowns engage the food to break and crush it without the shearing blades being brought into play, resulting in wear predominantly on the cusp tips. In some animals food is crushed between a pestle (protocone) on the upper molars and a mortar (talonid basin) on the lower molars. Puncture crushing is less important in herbivores where small quantities of vegetation are broken down immediately at the beginning of a masticatory sequence by the low shearing blades on the molars. The opossum can generate on the order of 17 kg/mm^2 on its postcanines in a static bite; chewing forces of 5–15 kg are reported for human molars, with the potential to reach more than 100 kg in Inuit males (Jenkins, 1978). The

predominant direction of movement in the power stroke is vertical. As soon as the particle size of the food is sufficiently small for the teeth to come into intercuspal range, the precise positioning associated with a complex occlusion can be achieved. Once this occurs, subsequent movement is largely controlled by the form of the teeth (cuspal guidance). The physical dimensions of many foods, such as blades of grass, are such that the teeth can come into very close apposition at the beginning of the first power stroke. Similarly, low-resistance material, such as fruit pulp, can be fractured in a single stroke, the teeth moving through a puncture-crushing stage and into occlusion. The precision and regularity of movement during the power stroke of chewing produces a distinctive pattern of wear facets on the surfaces of the teeth, which can be used to track relative tooth movement in a given animal. This pattern of wear has also proved valuable in tracing the phylogeny of tooth form, since the fundamental occlusal relations of the primary features of the crown in primitive mammals are maintained throughout evolution (Crompton, 1971; Crompton and Jenkins, 1979).

The movement of upper and lower teeth into the food can produce two types of wear facets. In those animals that crush food the tips of cusps are often rapidly worn away, producing cavitations or basins floored by dentine and ringed by enamel (Kay and Hiemae, 1974). Similar cavitation of the cusps occurs when they are used as pestles. However, wear facets are also produced on the slopes of cusps where the ridges on those slopes are used for shearing. Almost all facets result from the wear on the teeth occurring during the power stroke. Originally called buccal phase facets by Mills (1967), Kay and Hiemae (1973) used the term *phase I facets* to denote facets formed in primates as the teeth moved into centric occlusion. The few facets formed after the teeth reach centric occlusion, that is, as the jaws begin to open but while the upper and lower teeth are still in transitory contact, were called *phase II facets*. The relationship between phase I and phase II as descriptions of facet origin and the actual movements of the jaws producing them has caused some confusion. The experimental evidence shows that electromyographic activity of

adductors ceases before centric occlusion is reached, although given the decay in tension (50–75 msec in macaque) characteristic of striated muscle, there is still some residual, albeit rapidly declining, force acting on the lower jaw (Fig. 14-6) during the period extending into the first part of opening. The beginning of the jaw opening in mammals is always associated with varying degrees of forward movement of the mandible (greatest in those forms in which the condyle lies high above the lower molar row). It is often also associated with a continuation of transverse movement (Janis, 1979). The residual elevator force coupled with the force from the muscles generating the medial and anterior movement could hold the teeth in contact until the cusps clear each other. According to Kay and Hiiemae (1974), phase II facets are formed during this process.

Figures 14-6 and 14-7 show a remarkable, if not unexpected, consistency in the general pattern of electromyographic activity during masticatory cycles. The adductors (temporalis, masseter, medial pterygoid) are primarily active during the *FC* and *SC* phases. There are, however, important differences in the timing and amplitude of activity between corresponding muscles on the active and balancing sides. It is these subtle differences that control jaw movements in the transverse and anteroposterior directions (Weijs and Dantuma, 1975, 1981). Some muscles, such as the medial pterygoids (contracting differentially) produce transverse (medial) movement and are therefore active when jaw movement is occurring in conjunction with mandibular depression or elevation. The force applied to soft food is largely derived from the adductors on the working side. As food hardness increases, the balancing-side muscles are progressively recruited until the two sides show almost identical levels of activity (Hylander, 1979). Hylander (1975) has shown that not only are the jaw joints of mammals loaded during the power stroke of mastication but that the greater load is on the joint of the balancing side.

Jaw Opening The jaws open slowly at first and then accelerate toward maximum gape. Where there is a distinct change of rate, two opening

phases (*SO* and *FO*) can be identified (Figs. 14-5, 14-7, 14-8). A two-phase opening movement is routinely seen in the opossum, tenrec, and cat, which have high-amplitude jaw movement. Such a clear phase shift is rare in macaque, hyrax, and other herbivores, which have low-amplitude cycles. Experimental work has shown that during the opening and the following closing movements of the jaws, a complex cycle of activity is occurring in both the tongue body and the hyoid, associated with food manipulation and transport. These findings demonstrate that jaw opening is not a simple behavior dependent on the activity of the digastric, which has been classically described as the depressor of the mandible, nor on the digastric and the lateral pterygoid muscles.

The specific anatomical relations of the jaw muscles differ widely among mammals. In opossums and primates the digastric is connected to the hyoid through its intermediate tendon. In the cat, tenrec, insectivores, and most herbivores the digastric has no hyoid connection. Although it is not always possible to recognize an *SO* and *FO* phase transition in gape-time plots, two distinct phases can nevertheless be recognized from tongue and hyoid movement. At minimum gape the hyoid is at its most depressed and retracted position (Figs. 14-5, 14-8). As the jaw begins to open, the hyoid moves upward and forward. This movement is associated with a powerful contraction of the anterior suprahyoid muscles, especially the geniohyoid, and is often associated with low-level activity in the elevator muscles, which can be interpreted as regulating the rate of jaw opening to allow the hyoid to achieve its full upward and forward movement (see below). In those cases where a distinct change of rate between an *SO* and an *FO* phase is seen (opossum, cat), the hyoid reaches its maximum forward and, usually, upward position either just before or coincident with the transition from *SO* to *FO* when eating soft foods. When eating hard foods there is a pause at about this point, but the reversal to hyoid retraction may occur nearer maximum gape. Even when no such clear transition can be seen in a gape-time plot, hyoid movement reverses abruptly during opening so that at some point the hyoid starts traveling downward and backward (Figs. 14-5, 14-8). Although the digas-

tric may show some electromyographic activity during the first part of jaw opening, its main burst occurs during the second phase (Fig. 14-9). In animals having the digastric connected to the hyoid, its activity contributes both to jaw opening and to hyoid retraction; in the absence of such a connection it acts as a primary jaw opener during later opening (*FO*). At this time its activity is aided by the combined action of the infrahyoid and geniohyoid muscles, which both depress the jaw and retract the hyoid.

In most of the mammals so far studied (see Thexton, Hiiemae, and Crompton, 1980) the amplitude of hyoid movement during jaw opening can vary widely, depending on the condition of the food (Fig. 14-5). Opening is not a simple vertical mandibular movement: the lower jaw is also moving transversely and anteroposteriorly.

Food Transport and Manipulation

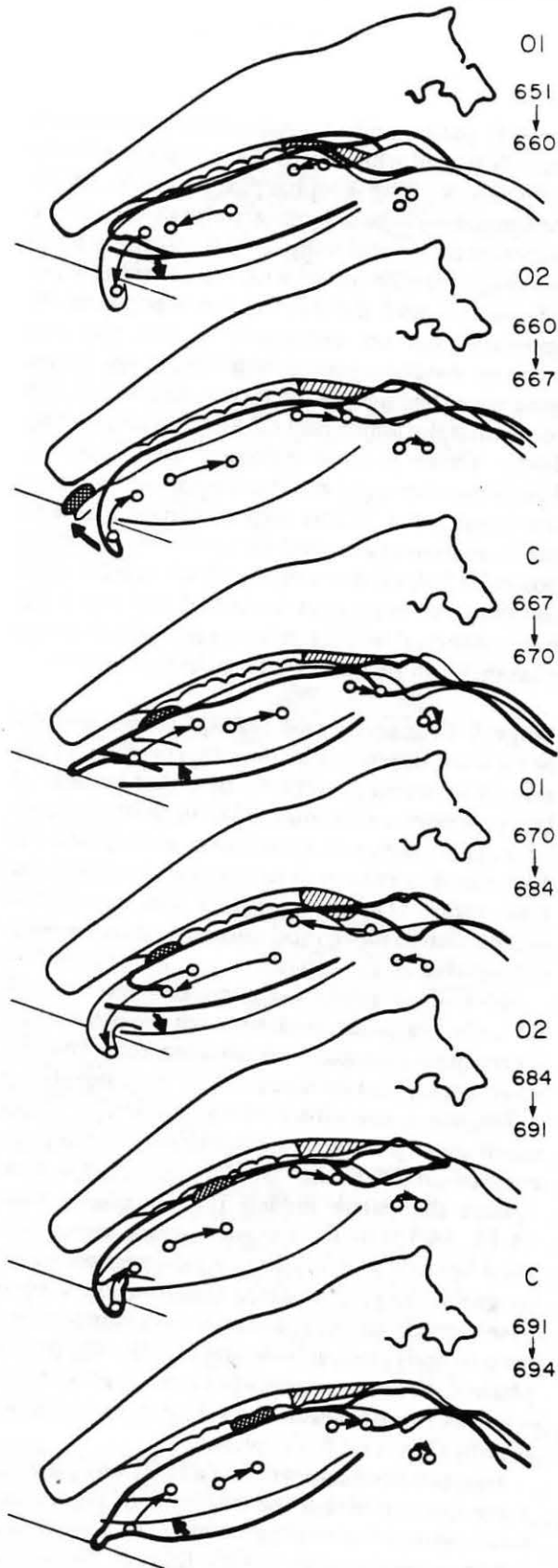
To reach the stomach food has to be actively moved through the mouth, propelled across the oropharynx (deglutition), and pushed down the esophagus (peristalsis). The work involved in moving food depends primarily on its consistency. Liquids flow and some materials such as ice cream can flow and offer little resistance, but solid materials have to be manipulated. In all cases transport movements involve the tongue and hard palate (stage I transport) and the tongue and soft palate (stage II transport).

Manipulation Dogs, cats, and opossums lap liquids; pigs and *Homo sapiens* (with a straw) suck fluids. When liquids are ingested and transported through the mouth, that is, are lapped rather than sucked, the tongue acts as a conveyor belt, moving successive small quantities of liquid (aliquots) from the external source to the oropharynx for bolus formation. In sucking an aliquot is both sucked and swallowed in one cycle. In lapping such a ratio is rare; each animal normally establishes a rhythm (2:1, 3:1, or even 6:1) between lap (collecting stroke/ingestion) cycles and "swallow" cycles. As explained in the section on deglutition, swallowing occurs as an interpolated behavior in the *SO* or *O1* phase of otherwise typi-

cal lap cycles. There is, therefore, no such thing as a specific swallowing cycle. The rhythm used in lapping varies not only among animals but also with the viscosity of the material lapped (Hiiemae and Abbas, 1981); once established it is very stable for that animal and food type (Hiiemae, Thexton, and Crompton, 1978; Crompton and Weijts-Boot, unpublished data).

To describe this "conveyor belt" activity (Fig. 14-11), more than one cycle has to be considered: two lap cycles and a third cycle in which both lapping and a swallow occur. In each case the jaw movement cycle of lapping has three clearly identifiable components: an initial opening movement (*O1*, Figs. 14-11, 14-12) in which the jaws are opened from minimum gape (taken as the start of the cycle) to a low-amplitude gape; a second open phase (*O2*) in which the gape is either maintained or increased, although often with some oscillation, while the now protruded tongue moves through the liquid; and last, a closing (*C*) phase in which the jaw is rapidly elevated as the tongue is retracted. Although the following description is based on lapping in the opossum, the movements of the jaw, hyoid, and tongue in the cat and dog are essentially the same. The macaque movement profiles for liquid shown in Figure 14-5 are a little different, at least for jaw movement, since the animal was taking fluid from a drop bottle. Because the tongue is barely protruded, this is an example of pure stage I transport of liquid.

At the beginning of a lap cycle (at or just before minimum gape), the hyoid begins to move upward and forward (Fig. 14-8), carrying the tongue base forward relative to the palate (Fig. 14-12, *O1*). At the same time, the posterior three quarters of the body of the tongue lengthens (expands), further assisting protraction, although the tip of the tongue contracts. Nevertheless, the resultant movement is sufficient to push the tip downward and backward into the liquid by the end of *O1*. The reversal of hyoid movement marks the junction between the *O1* and *O2* phases. As the hyoid begins to move backward, the posterior and middle thirds of the tongue begin to retract (Fig. 14-11, *O2*). At the same time, the tip of the tongue expands and moves forward through the liquid collecting an aliquot



of fluid on its surface. As the tongue tip comes into alignment with the body of the tongue, the tip is sharply withdrawn into the mouth with the aliquot on its surface. As the jaws close, the posterior three quarters of the tongue continues to contract (intrinsic movement) and retract. The anterior one quarter of the tongue remains a constant length during closure, cradling the aliquot.

During the second cycle, two separate but closely related movements of liquid occur: a new aliquot is ingested and the first one is moved distally through the oral cavity (Fig. 14-11). As the jaws begin to open (O1), the surface of the tongue elevates, trapping the first aliquot between it and the palatal rugae. The tongue surface moves forward below the aliquot. Proximal movement of the aliquot is hindered by the shape of the rugae, which have steep anterior and gentle posterior slopes. As the tongue retracts in O2, its surface loses its tight apposition to the palate; the first aliquot is released and moved posteriorly by the backwardly traveling tongue surface. This distal movement of food across the palate is facilitated by the shape of the rugae. As the second aliquot is ingested in the C phase of the second cycle, the first aliquot is carried farther posteriorly to a position immediately in front of the hard-soft palate junction.

As a result of this conveyor belt system, repeated aliquots are added to the oropharynx to form a bolus; when it reaches an optimal size it is swallowed (Hiiemae, Thexton, and Crompton, 1978). This occurs in the middle of O1 of a cycle in which lapping is still taking place. Figure 14-12 shows the orbits of movement during the same cycles illustrated in Figures 14-11, 14-13, 14-14, and 14-15. Note that during O1 the markers move on a higher plane than during O2 and C.

Figure 14-11 Two lapping (liquid transport) cycles in the opossum. In the first cycle, the first aliquot is transported as a second is ingested (*shading*). The fine arrows show the path of movement of the tongue and hyoid markers during each phase. The low amplitude of jaw movement in lapping is shown by the thicker arrows. The fluid level (*fine line*) is shown at an angle to simplify the figure. O1 = first open, O2 = second open, C = close.

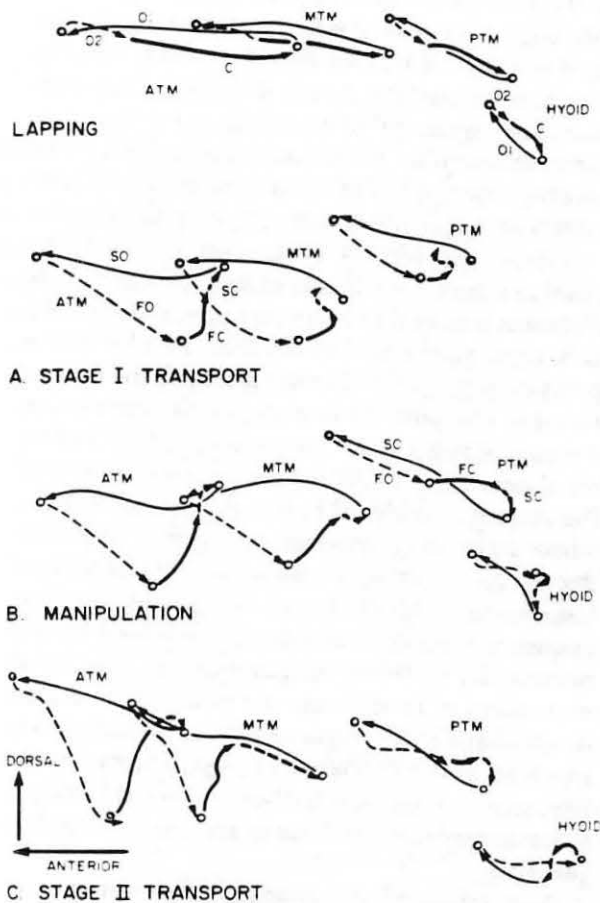


Figure 14-12 The paths of movement (orbits) of the anterior (*ATM*), middle (*MTM*), and posterior (*PTM*) tongue markers and the hyoid marker, all plotted relative to the palate during the cycles used to illustrate lapping and transport behaviors (Figs. 14-11, 14-13, 14-14). The effect of jaw movement on orbital profile is shown by the difference in orbital shape for the *ATM* and *MTM* between lapping, with very low-amplitude jaw movement, and manipulation or stage II transport, where the jaw is opened to a large maximum gape.

In *O1* of the third cycle the first two aliquots are trapped in their relative positions, and the tip of the tongue is protruded to pick up a third aliquot. During *O2* and *C* the tongue is withdrawn from its contact with the soft palate and drawn backward, carrying the first aliquot into the oropharynx. At the same time the second and third aliquots are also transported within the oral cavity. During *O1* of the fourth cycle the posterior tongue contacts

the soft palate and maintains this contact as it slides forward, which traps the first aliquot in the oropharynx. The oropharynx is bordered by the tongue-soft palate contact, the surface of the posterior part of the tongue, the anterior wall of the epiglottis (the top of which is covered by the soft palate), and dorsally by the soft palate. In opossums, but not necessarily in cats, the oropharynx extends into a large pyriform recess lying on either side of the larynx, and it is in this recess that the major part of the bolus is held (Fig. 14-3). There is some evidence (see Thexton, 1981) that the rapid distal transport of liquids to the oropharynx in cats might be attributable to the formation of a central furrow or trough in the posterior half of the tongue, which rapidly empties from the front part backward and which has been observed in decerebrate cats, where its appearance can be initiated by palatal pressure.

Stage I Transport and Manipulation (Solids)

Solid food deposited in the anterior part of the mouth is moved posteriorly by either or both of two processes: a continuation of inertial transport or stage I transport. Carnivores such as the cat and primitive mammals such as the tenrec and the tree shrew (*Tupaia*) regularly use an inertial mechanism to move food into or close to the post-canine area of the mouth.

More often, solid food is moved from the incisal to the premolar/molar area of the mouth by a mechanism essentially identical to that used for stage I transport of liquids. The only significant difference is the effect on tongue shape of the much wider jaw opening associated with the presence of an *FO* phase. Briefly, the food is held against the palate during the *SO* phase (Figs. 14-12, 14-13) as the tongue surface moves forward below it and, cradled in a depression on the tongue surface, it is carried distally as the tongue base retracts and the posterior two thirds of the tongue body contracts during *FO*. During the *FC* phase the food is transported even farther backward as the depression cradling it itself travels distally (Fig. 14-13, *FC* phase).

In summary it appears that all mammals use the same mechanism for the transport of liquids and solids within the oral cavity (that is, toward but not through the pillars of the fauces). The essen-

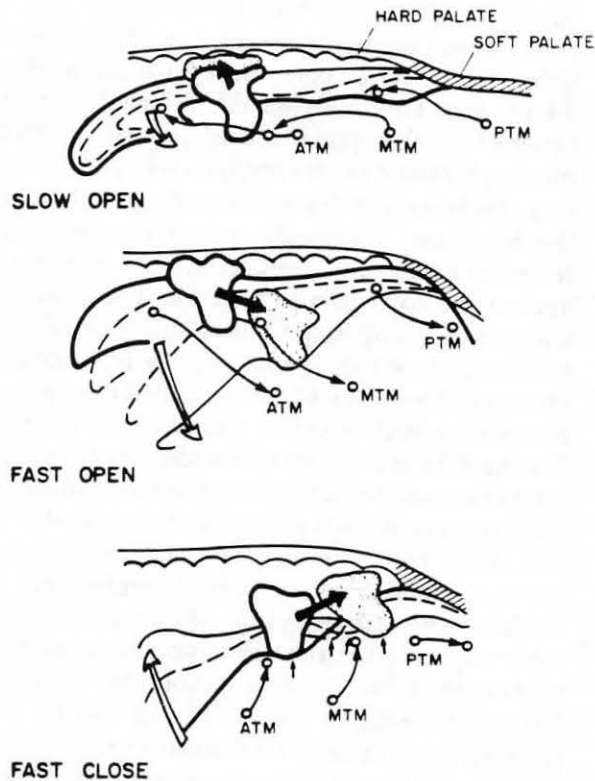


Figure 14-13 Stage I transport of solids. Large hollow arrows show direction and amplitude of jaw movement; solid black arrows show movement of food through each phase. Heavy solid line shows position and shape of the tongue and food at the beginning, and the thin solid line, their position at the end of each phase. Intermediate positions are shown by dashed lines. The position of the anterior (ATM), middle (MTM), posterior (PTM) tongue and the hyoid (HM) markers is shown at the beginning and end of each phase by hollow circles; their overall movement during each phase by the fine black arrows. The small black arrows in the Fast Close figure show the progressive distal movement of the base of the trough on the tongue surface where the food is held. The net distal travel of the trough being greater than that of the tongue body, the intrinsic musculature of the tongue not only forms a "wave" but propagates it distally.

tial elements of this process are: (1) the forward expansion of the body of the tongue beneath the food as the hyoid travels forward in the *SO* (or *O1*) phase; (2) the retraction of the hyoid and the body of the tongue during the following *FO* and *FC*

phases, which carries food on the tongue surface distally; and (3) the distal movement of a trough (or wave) on the tongue surface, cradling an aliquot of food, at a greater rate than that of the return movement of the tongue base and body during the closing phase (*FC/SC*), which, in effect, carries food distally.

As solid food is broken down by the postcanines it has to be moved within the posterior part of the oral cavity: adequately triturated material has to be collected, segregated, and moved posteriorly to form a bolus while the inadequately triturated residual lumps have to be repositioned between the teeth for further reduction. Little is known of the methods used by the tongue to segregate and reposition food particles. However, the mechanisms used to move residual material anteroposteriorly within the oral cavity are known. Figure 14-12 shows the movements of the jaws, tongue, and hyoid during a masticatory cycle in which food is being manipulated. (Manipulation is defined as the movement of food within the oral cavity, as opposed to transport which has a definite directional component). As the jaws begin to open in the *SO* phase, the tongue does not, as in stage I transport, force the food against the palate where it can be held as the tongue moves forward; instead, the tongue drops slightly away from the palate and a wall forms behind the food, which is then carried forward by the anterior movement of the tongue base and internal expansion of the posterior two thirds of the tongue, both features typical of the *O1* phase (Fig. 14-14). With the wide opening of the jaws and the retraction of the tongue seen in the *FO* and *FC* phases, the lump of food is carried backward and returned to a position in the posterior postcanine region, where it is usually positioned between the postcanine teeth. As the teeth engage the food during *SC*, the tongue continues to move and removes triturated material away from the point of bite.

Stage II Transport Stage II transport is defined as the distal movement of food through the pillars of the fauces (or the junction of hard and soft palates) to the oropharynx for bolus formation. In most mammals, but not anthropoid primates and man, a bolus is accumulated in the oropharynx (Fig. 14-3). Some mammals, including the

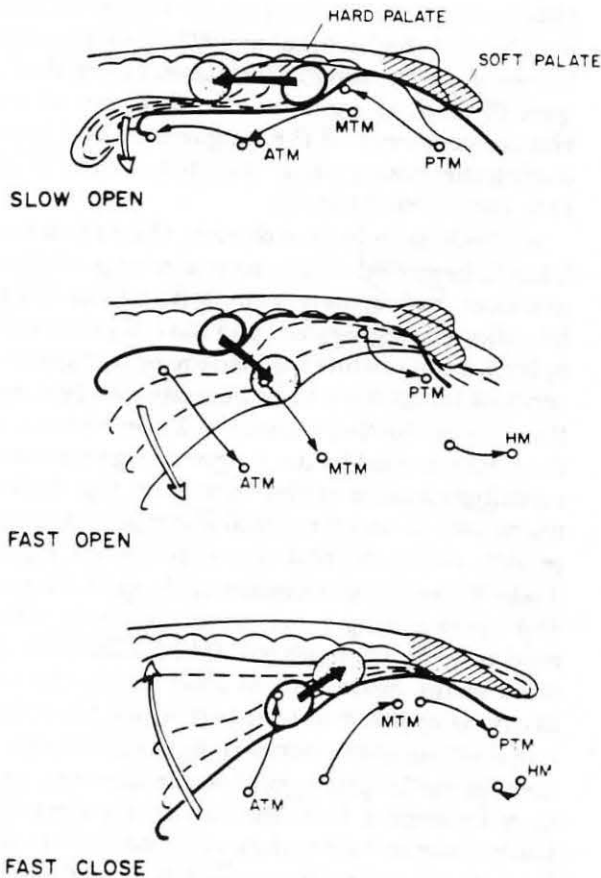


Figure 14-14 The manipulation of food during the *SO*, *FO*, and *FC* phases of a masticatory cycle (symbols are as in Fig. 14-13). The soft palate changes shape, in large part to maintain its contact with the tongue and thus the tongue-palate seal, as the tongue profile changes during the cycle.

opossum, have a large pyriform recess which, as an extension of the oropharynx, is the principal site for bolus formation. In swallowing, the bolus is moved from the oropharynx over the larynx to the esophagus. In all nonprimates studied (opossum, cat, dog, hyrax, tenrec, pig, and goat), stage II transport and swallowing are separate events.

The mechanism of stage II transport has been adequately documented only in opossums, so the actual mechanism may be slightly different in hyraxes, cats, and dogs, where it has also been recorded cinefluorographically. As mastication proceeds, food reduced to a consistency suitable for swallowing is separated by the tongue from

the remainder of the food in the mouth and is collected in a hollow on the dorsum of the tongue below the posterior part of the hard palate (Fig. 14-13, *SO*). Food already in the oropharynx is retained in that position and prevented from moving forward by the tongue-soft palate contact. As the tongue moves forward and upward in the *SO* phase, it expands around the food collected on its dorsum, compressing and trapping it against the hard palate. With the beginning of wide jaw opening in the following *FO* phase, the middle part of the tongue rises in front of the triturated food, which is then cradled in a depression with a high anterior wall (Fig. 14-15, *FO*). During *FO* the anterior and middle thirds of the tongue are carried away from the hard palate. At the same time the soft palate flattens out so that by the *FO-FC* transition an open channel between the mouth and oropharynx has been formed. As the jaws close in the *FC* phase, the tongue not only moves upward but the depression on its surface moves upward and backward (note the position of the middle tongue marker in Fig. 14-15, *FC*) pushing the triturated food under the soft palate and toward the oropharynx to form the bolus. Fig. 14-12 illustrates a marked difference in the orbits of movement of the anterior and middle tongue markers between manipulation and stage II transport in the opossum. In the case of flesh or broken bone associated with flesh, numerous (up to six) stage II cycles are sometimes required to move food through the pillars of the fauces.

Stage II transport occurs in nonanthropoid mammals because the bolus is formed within the oropharynx but anterior to the soft palate-epiglottal seal (Fig. 14-3). Adult *Homo sapiens* has no such seal, so the bolus is formed on the dorsum of the tongue in relation to the hard palate-soft palate junction and the pillars of the fauces. In swallowing the bolus traverses the oropharynx. This part of the swallow is strictly comparable to stage II transport in nonanthropoids, but it does not occur in a separate cycle from that in which swallowing occurs.

There is, however, an interesting variation of second stage transport in macaques (Franks, Hylander, and Crompton, 1981). In these forms a soft palate-epiglottal seal is maintained except during swallowing. Food to be swallowed collects

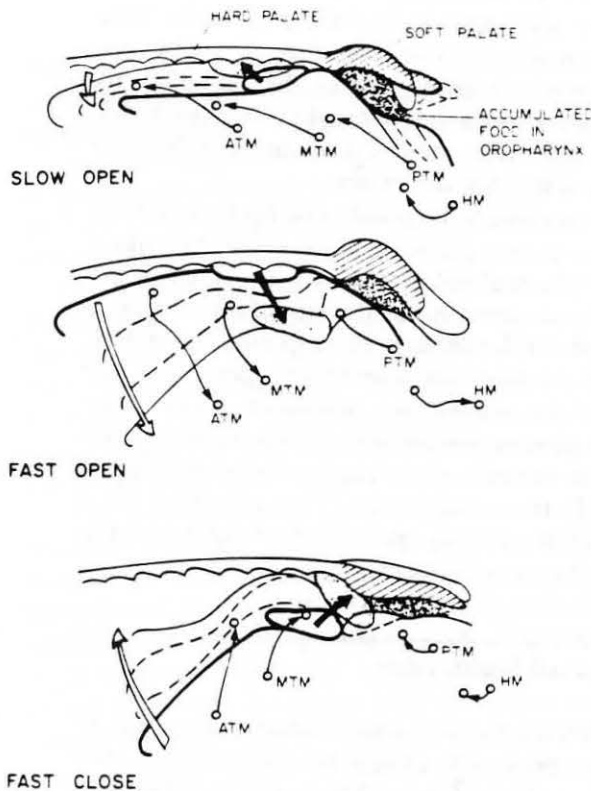


Figure 14-15 Stage II transport in which solid food is moved backward below the soft palate by a mechanism best described as "squeeze-wedge." During the *FO* phase, the contact between the palate and tongue surface (middle oral seal, Figure 14-3) travels distally, pushing food toward the valleculae. At the end of the *FO* and at the beginning of the *FC* phase, the backward and upward movement of the tongue (see *FC* phase) pushes food from the oral cavity into the oropharynx. Symbols identified in Fig. 14-13.

on the dorsum of the tongue immediately in front of the hard-soft palate junction. In the cycle preceding the swallow, a small quantity of the bolus is moved backward to lie between the back of the tongue and the soft palate (that is, in the oropharynx). However, the transport of food to this position does not take place during the *FO* and *FC* phases, as it does in nonprimates, but during the *SO* phase. As the tongue moves forward and upward during the *SO* phase, it contacts the hard palate immediately in front of that part of the bolus to be transported. As it continues to move

forward, this contact point is moved progressively backward by a sequential elevation of the back of the tongue. This posterior movement of the contact point takes place despite the fact that the tongue as a whole continues to move forward. During the swallow cycle, the main bolus on the dorsum of the tongue and the small one between the tongue and the soft palate both traverse the oropharynx in the middle of the *SO* phase of jaw movement.

Deglutition Swallowing has been extensively studied in man (Miller, 1982) because isolated swallows can be elicited on command. In mammals feeding normally, swallows occur as an integral and integrated part of the masticatory sequence. A swallow can be defined as the process by which a bolus is moved across the oropharynx to enter the esophagus. This is achieved by means of a distinct series of neuromuscular events that, once initiated, appear to be little influenced by sensory feedback (Miller, 1982). However, in all the animals so far studied, including macaques, this mechanism appears as an "insert" or interpolation in the *SO* phase of an otherwise standard masticatory cycle. As the *SO* phase begins, the characteristic movements of the hyoid and tongue also begin. When a swallow is to occur, the *SO* phase is suspended: hyoid protraction as well as tongue expansion and protraction stop. The movements of the swallow are initiated and completed, after which the *SO* phase resumes. Although it is within human experience to swallow during mastication (that is, with food in the oral cavity), a situation entirely comparable to that found in other mammals, there is no evidence presently available to show the relationship between the swallow and masticatory movements nor between the swallow and food transport.

In a typical *SO* phase in the opossum, the forward and upward movement of the tongue is produced by the contraction of both bellies of the digastric, the genioglossus, geniohyoid, and mylohyoid of both sides, with relaxation of the sternohyoid and genioglossus (Crompton and Sponder, 1982; Crompton and Weijts-Boot, unpublished data). All swallows that fall within a masticatory sequence are preceded by the hyoid and tongue protraction phases of *SO*; that is, the

posterior portion of the tongue and hyoid start to move forward and the geniohyoid, genioglossus, and digastrics contract. At rest the soft palate lies snugly against the epiglottis and forms a lateral wall that separates the pyriform recess from the nasopharynx (Fig. 14-3). When the soft palate is elevated in swallowing, the valleculae, pyriform recess, and the space above the larynx become confluent. In a swallow the digastric, genioglossus, geniohyoid, and the mylohyoid continue their activity, and in so doing form a tensed floor for the oral cavity and tongue base. Against this tensed floor the posterior portion of the tongue contracts and is forced backward against the food. At the same time a wave of contraction starts with the superior constrictors and passes ventrally. The combined contractions force the food through the relaxed esophageal sphincter into the esophagus. The posterior movement of the tongue appears to be caused in part by powerful activity of the hyoglossal musculature. During the swallow solid food passes over the epiglottis, which shifts backward to cover the opening of the larynx. After the swallow the tongue again moves forward to complete the remainder of the *SO* protraction phases; the remaining phases of the masticatory cycle and its successor follow in regular order. The sequential contraction of the middle and posterior constrictors after the initial contraction of the anterior constrictor forces the food down the esophagus during the completion of the *SO* and *FO* phases of jaw movement.

In macaques the swallowing mechanism seems to be identical to that described for nonprimates in that the soft palate is raised to meet the posterior pharyngeal wall, thus separating the nasal cavity from the pharynx; the posterior surface of the tongue is forced upward and backward; and, in conjunction with the superior (anterior) constrictor, forces the food through the pharynx (H. A. Franks, personal communication). Since adult man has lost the soft palate-epiglottal contact, it is not possible to store food in the pharynx prior to a swallow as this would interrupt or prevent regular breathing. During mastication, the fauces, the dorsum of the tongue, and the soft palate in the human adult form the seal that separates the oral cavity from the oropharynx. The nasopharynx and oropharynx form a continuous

space so that breathing and food manipulation can take place simultaneously (Fig. 14-3). This arrangement is distinct from that of nonhumans and human neonates, where the nasopharynx and oropharynx are separated during the masticatory sequence, but where the soft palate-epiglottal seal is also present.

It is customary to divide the human swallow into two distinct phases: an oral and a pharyngeal phase. The oral phase is the period in which the food is positioned on the dorsum of the tongue in front of the fauces and corresponds to the first part of the *SO* phase immediately preceding the swallow in nonprimate mammals. During the human pharyngeal phase the bolus is transported from the dorsum of the tongue to the esophagus through the oropharynx. The retention of a preswallowed bolus between the tongue and the soft palate seen in macaques is lost.

Control of Mastication

There is a large and continuously expanding literature on aspects of oral neurophysiology (Anderson and Matthews, 1976; Sessle and Hannam, 1976; Doty, 1976; Lowe, 1981; Goldberg and Chandler, 1981; Luschei and Goldberg, 1982). Much attention centers on how the rhythmic activity is initiated and maintained. Recently, a view originally propounded in 1923 by Bremer has gained new acceptance. He argued that a *centre de correlation* (often translated as an "oscillator" or "rhythm generator") is present in the hind brain. Such a center must function by integrating sensory input from the trigeminal, facial (taste), glossopharyngeal, and vagal nerves and by activating the motor components of the same nerves as well as parts of the cervical plexus. The extent to which such a center is preprogrammed to produce a standard output, which is then modulated by peripheral sensory input, is not yet clear. The very uniform firing patterns for the jaw muscles during masticatory cycles is suggestive of a basic program, but the changes in jaw, hyoid, and tongue movement profiles within a single masticatory sequence reflect the impact of sensory input on the output of such a rhythm generator. Equally, the very stereotyped activity of swallow-

ing and its interpolation into an otherwise conventional tongue-jaw cycle is highly suggestive of programming. It is expected that experiments using behavioral monitors (such as synchronous electromyography and movement recording) can be used to investigate this as yet poorly understood area.

The similarity of the basic feeding mechanisms in the extant mammals so far studied has led to the suggestion (Hiiemae, Thexton, and Crompton, 1978; Bramble, 1980) that the neural control system may be very conservative and so phylogenetically old. Further, the characteristics of the hyoid and tongue surface cycles and the pattern of their linkage to the jaw movement cycle suggests that the cyclical movements of the tongue may be the primary element in this complex system. It is clear that further studies should address several basic questions. First, is there a truly mammalian pattern? Although the answer seems to be yes, a careful analysis of jaw and tongue movement data from mammals with the more extreme forms of dietary specialization, such as anteaters and walruses, would offer a direct test. Second, if the tongue in its role as the active component of the food transport system is primary, then it should be possible to show the

dominance of a tongue cycle not only in mammalian ontogeny but also in mammalian phylogeny. Although the vertebrates available for experimentation, such as lizards, are not those currently accepted as linearly related to mammals (Throckmorton, 1978; Smith, 1982) or fish (Lauder, 1979, 1982), experimental studies designed to address the question whether the tongue and pharyngeal structures show cyclical behavior like that of mammals could contribute valuable information even if unable to confirm the pattern of evolution of this system. Third, if, as has been suggested here, the jaw apparatus functions by virtue of three separate but correlated cycles of activity—in the jaws, the hyoid apparatus, and the body of the tongue—whose characteristics can be closely defined, then it becomes possible to design experiments to test the nature of a central pattern generator. The possibility of linkage with the system controlling respiration should also be explored. Specifically, is there a common pattern to pattern generators (such generators are reported to regulate locomotion and respiration), or is there in fact an actual linkage between the cyclical behaviors of respiration and feeding, given that phylogenetically, the latter has evolved from the former?