

Ingestion in Mammals

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Ingestion in mammals is distinguished from that of other vertebrates by mastication, suckling, and complex food transport and swallowing. The teeth, cranial bones, and musculature of the head reflect these distinguishing features.

Introduction

Ingestion is a series of biologically complex activities (capture, incision, transport, mastication, swallowing and, in infant mammals, suckling) performed by the oral apparatus. The oral apparatus includes the dentition, the masticatory muscles, numerous bones of the cranium, the squamosal–dentary joints connecting the lower jaw to the skull, the tongue, and many other structures in the head.

Mammals are distinguished from other vertebrates in many aspects of ingestion. For example, in most other vertebrates, mastication does not occur. Also, food transport and swallowing are less complex in other vertebrates and generally involve the coordination of fewer muscles and other soft tissue structures. Furthermore, suckling is a behaviour that is unique to mammals. It is not surprising, therefore, that mammals have many bony, muscular, neural and other specializations for ingestion that distinguish them from other vertebrates. Among mammals, interspecific variation in these anatomical specializations frequently reflects the dominant component of a species' diet, so that we speak of herbivores, carnivores, insectivores, frugivores and omnivores. Structures that are adapted in mammals for use during ingestion include the dentition, the chewing muscles, the lips and the lip musculature, the cheek musculature, the cranial bones, the palate, the tongue, and the pharynx.

The dentition of mammals is heterodontic, which means that the teeth do not all look alike as they do in fish, reptiles and most other vertebrates. Instead, mammals have incisors, canines, premolars and molars in both the upper and the lower jaw. These tooth types are structurally different and each has a specialized function. The incisors are at the front of the mouth and are usually spatulate in shape. They are used to grab food items, to break small pieces of food away from larger pieces, to kill live prey and to gnaw. In some mammals, for example rodents, the central incisors are robust, ever-growing teeth specialized for gnawing and chiselling (**Figure 1a**). The canines sit behind the incisors. They are usually long, sharp and pointed, and are used to pierce food objects and for self-defence. In some mammals, for example lions and other carnivores, the upper canines are quite large and special-

ized for live prey capture and killing (**Figure 1b**). In some mammals, particularly in herbivores, the canines are absent, leaving a space, called a diastema, between the incisors at the front of the mouth and the premolars and molars at the back of the mouth (**Figure 1c**).

The premolars and molars are commonly referred to as the postcanine dentition or the cheek teeth. These teeth are sometimes used during food capture, but they are specialized to initiate the digestive process by breaking down the food so that it is the proper size and consistency for swallowing and further digestion by the gut. Premolars and molars have bumps (called cusps), ridges (called crests and lophs) and basins that function to crush, grind, tear, cut and/or pulp food items. The cusps on the lower postcanine teeth fit snugly into the basins on the upper postcanine teeth, and vice versa. This is called occlusion. The shape of the postcanine dentition varies dramatically among mammals because it strongly reflects diet. Carnivores and insectivores have postcanine teeth with tall, sharp, vertically oriented cusps and crests that are good for tearing and cutting meat. Herbivores have postcanine teeth dominated by elongate, sharp, horizontally oriented lophs and crests that are good for cutting and grinding grasses and leaves. Frugivores have postcanine teeth with low cusps and large basins that are good for crushing and pulping fruits.

The cranial bones support and serve as attachment sites for the teeth, the masticatory muscles and many oropharyngeal structures. The teeth are attached to three jaw bones: the premaxilla, the maxilla and the mandible. The premaxilla and maxilla together form the upper jaw. In many mammals, the mandible is two separate bones called dentaries which are joined anteriorly in the midline at a mobile symphysis. In some mammals, the dentaries fuse at the mandibular symphysis to form a single bone in the lower jaw. Each dentary articulates with the squamosal surface of the temporal bone on the undersurface of the skull, forming a squamosal–dentary joint (SDJ).

Mammals are also distinguished by the number and structural complexity of their masticatory muscles. Whereas reptiles typically have two major jaw-elevating muscles, mammals have three major muscles: the medial pterygoid muscle, the masseter muscle and the temporalis

Introductory article

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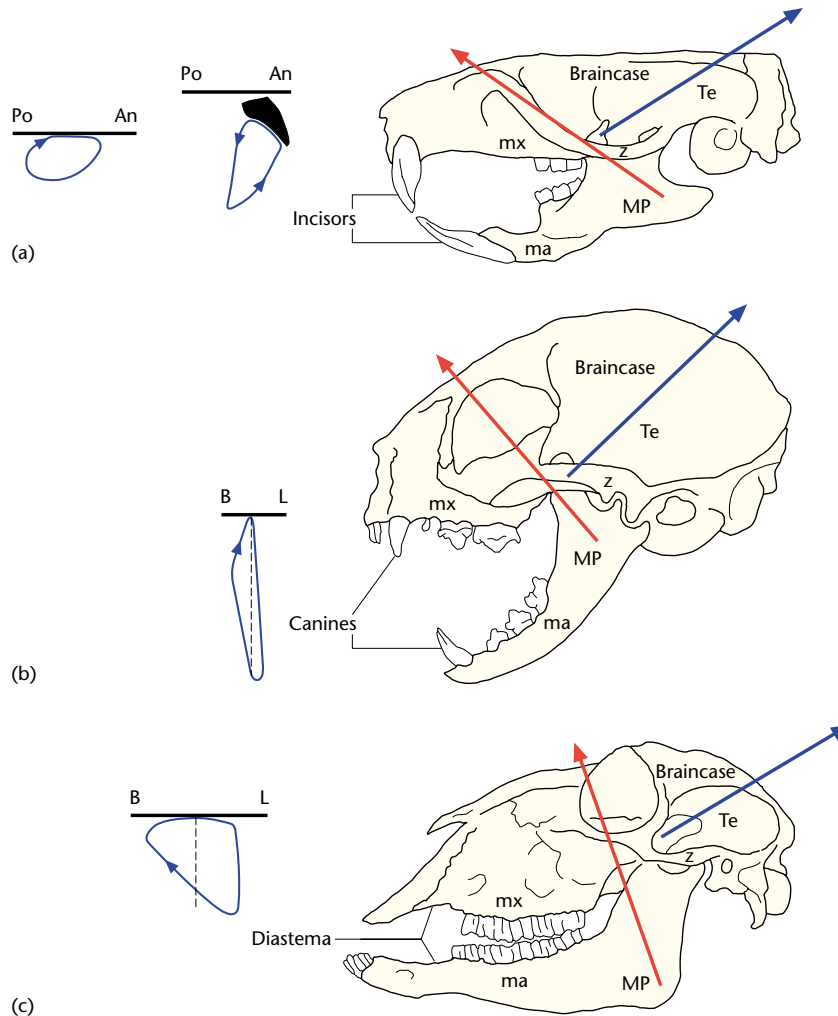


Figure 1 (a) Lateral view of the movement of the mandible during propalinal mastication in a rodent, during propalinal gnawing in a rodent, and a rodent cranium (note the large and procumbent incisors). In this and subsequent figures, the approximate directions of pull of the masseter and medial pterygoid muscles (MP) are shown by the green arrow, and the direction of pull of the temporalis muscle is shown by the blue arrow. The arrows on the movement orbits indicate the direction of mandibular movement. As the arrow approaches the horizontal line, the mandibular teeth approach the maxillary teeth and the power stroke occurs. (b) Frontal view of the movement of the mandible during mastication in a carnivore and a carnivore cranium. Note the large and sharp canines, and the vertical orientation of mandibular movement during the power stroke. (c) Frontal view of the movement of the mandible during mastication in a herbivore and a herbivore cranium. Note the large transverse component to the power stroke, and the large diastemata between the anterior and cheek teeth. Po, posterior; An, anterior; mx, maxilla; ma, mandible; MP, masseter and medial pterygoid muscles; Te, temporalis muscle; B, buccal; L, lingual; z, zygomatic arch. Adapted from Hiimeae K (2000).

muscle. These muscles are arranged to close the jaws and also to allow transverse jaw motion, which are important during mastication. The modification of these jaw muscles to allow transverse jaw motion is an important adaptation in mammals. The medial pterygoid muscle originates from the medial surface of the lateral pterygoid plate on the sphenoid bone. It inserts on to the medial surface of the ascending ramus of the mandible. The masseter muscle arises from the inferior surface of the zygomatic arch and inserts on to the lateral surface of the ascending ramus of the mandible. The temporalis muscle has a fan-shaped

origin from the side of the braincase (usually including the frontal, sphenoid, temporal, parietal and occipital bones) and inserts on to both sides of the coronoid process of the mandible, between the masseter and medial pterygoid muscles. Each of the elevator muscles is structurally complex with many tendinous sheets and intersections, and can therefore be divided into smaller structural units based on fibre orientation (and therefore direction of pull). The lateral pterygoid muscle is a jaw depressor muscle arising from the lateral surface of the lateral pterygoid plate and inserting on to the medial aspect of the mandible

just inferior to the SDJ. The digastric muscle also depresses the jaws. It arises from the underside of the skull and inserts on to the lower border of the mandible.

Capture

Food capture is the process of bringing a food object into the oral cavity. Most vertebrates rely on the dentition and/or the tongue for food capture. Capture in mammals differs from capture in other vertebrates because mammals have highly mobile lips that surround the mouth. Mammals use their lips and teeth to grab and hold food while the neck and/or the hand muscles contract to pull a bite of food away from a larger object. When the anterior teeth are used together with the lips, capture is usually referred to as incision. Once food is captured, the upper and lower incisors may be brought together to remove a smaller piece from the food item. Then it is transported, usually by the tongue, to the postcanine teeth for mastication.

Gnawing is a specialized form of incision seen in many rodents and a few other mammals, in which the mandibular incisors undergo forward and backward (i.e. propalinal) motion through a food object. Occlusion of the tips of the upper and lower incisors often occurs during gnawing, and the lower incisor is then raked backward against the upper incisor (**Figure 1a**). To accommodate propalinal motion, the mandible is shorter than the upper jaw in mammals that gnaw.

Oral Transport

Oral transport is the term given to the process of moving a food bolus through the oral cavity toward the oesophagus. In mammals, oral transport is a sophisticated process in which the food is both moved through the oral cavity and processed by the teeth. Transport and mastication involve the dentition, the tongue and its musculature, the hard and soft palate, and the muscles of the pharynx. Transport is divided into stages I and II. Stage I transport occurs before mastication and is described here. Stage II transport occurs after mastication is completed but before swallowing, and is described along with swallowing.

During stage I transport, the food bolus is moved from the position from which it first enters the oral cavity to the postcanine dentition. In mammals, the direction of stage I transport is usually posterior (from the anterior part of the oral cavity to the postcanine dentition). In some mammals, large food items are transported inertially when the head is moved forward over the food bolus. In most mammals, structures of the oral apparatus, particularly the tongue, take an active role in moving food posteriorly to the postcanine teeth. In active transport, the tongue holds the food bolus against the hard palate (which has well

developed ridges that aid in this) while it lengthens and moves anteriorly. By lengthening and moving anteriorly, the tongue forms a depression for the food bolus which is then carried posteriorly. The tongue then positions the food bolus between either the left or the right upper and lower postcanine teeth for unilateral mastication.

Mastication

Once a food bolus has been acquired and transported to the postcanine teeth, mastication commences. The goal of mastication is for the cusps, basins and crests on the lower and upper postcanine teeth to move forcefully against the food bolus, thereby breaking it into smaller pieces and mixing saliva into it. Saliva initiates the breakdown of certain compounds found in food and also adds fluid to the food, facilitating bolus formation and making it easier to swallow.

Unilateral mastication and transverse tooth movement during the power stroke are two of the most important innovations characterizing mammalian mastication. Mammals chew with the food bolus between the upper and lower teeth on either the left or the right side (unilateral mastication). The side of the mouth where the food is located during chewing is called the working side, and the other side is called the balancing side. Although bilateral mastication occurs in some rodents, unilateral mastication is the predominant type of mastication in mammals and distinguishes mammals from other vertebrates. A very important mechanism of food breakdown in mammals is by transverse movement of the lower teeth relative to the upper teeth (**Figure 1**). The postcanine dentition and the masticatory muscles have evolved to accomplish varying degrees of transverse tooth movement during unilateral mastication.

Mastication involves rhythmic motion of the upper and lower jaws and the tongue. It is the motion of the mandible that is usually analysed in quantitative studies of mastication. This is done by using the upper jaw as a reference plane and analysing the movement of the mandible relative to this reference plane. Movements of the mandible can be resolved into dorsal (up), ventral (down), anterior (forward), posterior (backward), buccal (lateral toward the teeth) and lingual (medial toward the tongue) directions.

The basic movements of the mandible during a chewing cycle are a power stroke, an opening stroke and a closing stroke. A food bolus usually requires numerous chewing cycles before it reaches the right size and consistency for swallowing. The teeth always make contact with the food bolus during a chewing cycle, but the upper and lower teeth do not always contact one another in each chewing cycle.

The power stroke begins when tooth–food–tooth contact is made. During the power stroke, muscle forces are applied to the food bolus and a reaction force is applied

to the jaws and the SDJs. The reaction force applied to the jaws is called the bite force and is a measure of how much of the muscle force was used to break down the food bolus. The reaction force applied to the SDJs is called the joint reaction force.

The power stroke in mammals includes dorsal, anterior and transverse motion of the working-side lower teeth through the food bolus and frequently against the upper teeth. As noted above, mammals emphasize transverse motion in comparison with other vertebrates. Early in the power stroke in many mammals, a small buccal shift of the working-side lower teeth probably occurs. Throughout the remainder of the power stroke, the lower teeth on the working side move lingually. The dentaries may also undergo significant rotation about their long axes during the power stroke in animals with unfused mandibular symphyses. This rotation may aid in breaking food down, particularly during tooth–tooth contact chewing cycles.

As tooth–food–tooth or tooth–tooth contact is lost, the opening stroke begins. At this time, the working side of the mandible moves rapidly ventrally. The direction of transverse movement during the opening stroke is variable from cycle to cycle within an individual animal. The closing stroke begins when the mandible begins to move dorsally toward the upper jaw. During closing, the working side of the mandible also moves buccally.

The pattern of contraction of the chewing muscles has been studied in numerous species using electromyography (EMG). This technique allows the duration and the amplitude of the electrical activity associated with muscular contraction to be recorded. EMG studies have revealed a basic ‘triplet’ pattern of elevator muscle activity during mastication. Interspecific variation in the pattern depends, in large part, on the amount of transverse movement during mastication. As the jaws begin to close, muscles with a strong vertical pull, such as anterior temporalis, begin to contract. Next, as the power stroke begins, triplet I begins to contract. Triplet I consists of the balancing-side medial pterygoid and superficial masseter muscles and the working-side temporalis. Activity in triplet I early in the power stroke is thought to cause a lateral shift in the working-side lower postcanine teeth. Triplet II consists of the working-side medial pterygoid and masseter muscles and the balancing-side temporalis muscle. Activity in triplet II begins after activity in triplet I and peaks later in the power stroke. This is thought to cause lingual movement of the working-side postcanine teeth. Finer divisions of force- and movement-related functions are present in the adductor muscles, leading to significant functional heterogeneity within each muscle within a species, and also to interspecific variation in the recruitment patterns of these muscles.

There are significant interspecific differences in the path of the teeth during the power stroke that are due in part to the shape of the teeth and also to the activity patterns and structural characteristics of the masticatory muscles

(**Figure 1**). Carnivores and insectivores have sharp, transversely narrow and vertically steep cusps on the postcanine teeth. As a result, they emphasize vertical motion during the power stroke and tend to have small transverse tooth movements. The narrow offset in peak activity in triplet I and triplet II seen in cats and dogs reflects these vertical movements. Herbivores usually have transversely wide teeth with transversely oriented lophs and upper and lower teeth, and are also frequently anisodontic and/or anisognathic. Anisodonty means that the lower teeth are narrower than the upper teeth. Anisognathy means that the mandible is narrower than the upper jaw so that the mandibular teeth are lingual to the maxillary teeth. The wide offset in peak activity in triplet I and triplet II seen in goats, rabbits and, to some extent, in pigs and primates reflects these transverse movements.

The morphology of the bones that support the oral apparatus reflects, to greater or lesser degree depending on the bone, the mechanical effects of ingestive activity. These effects are usually inferred from biomechanical theory, but have also been studied in live animals using strain gauges to measure the strain, and to infer the stress, in the bones of the oral apparatus. Strain gauge data have shown, for example, that a joint reaction force is present during mastication – a phenomenon that had been controversial for a number of years.

Swallowing

A swallow in mammals is among the most complex neuromotor reflexes known. The act of swallowing involves over 25 muscles, innervated by five different cranial nerves, and can be invoked by a single central nervous system stimulation. It is among the first motor reflexes to appear during embryonic development. Swallowing is first seen in human embryos at about 10–12 weeks of gestation, and by birth a fetus is swallowing almost half the amniotic fluid each day. This neuromotor reflex is unique to mammals and is not seen in any other vertebrate. Before reviewing the act of swallowing, more properly called deglutition, we first briefly consider the unique anatomy of the mammalian pharynx (**Figure 2**).

Once food has passed through the oral cavity it is moved into the back of the mouth into a region called the pharynx, behind the oral cavity. It connects the nasal and oral cavity, and connects the oral cavity and the oesophagus, the tube that carries food into the stomach. While all vertebrates have a pharynx, this region is highly specialized in mammals. Many of these specializations are likely to be adaptations for swallowing and suckling.

Most birds and reptiles (with the exception of some such as crocodiles that are adapted for living in water) have an oral cavity that is open to the nasal cavity. The pharynx is compressed by a set of muscles largely external to the bones

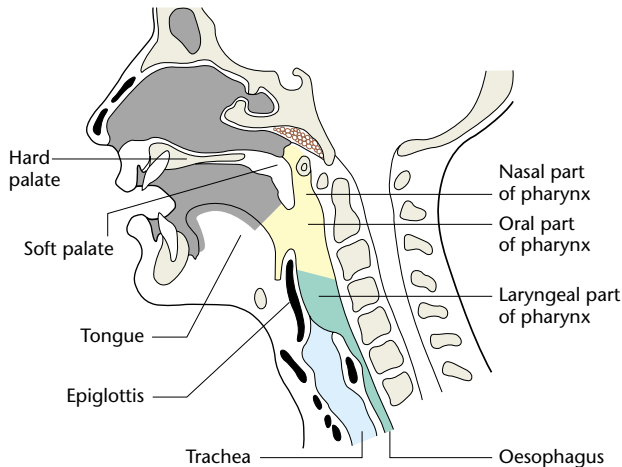


Figure 2 Lateral view of a mid-sagittal section through the oral cavity and pharynx of a human showing the different parts of the pharynx (nasal part, oral part and laryngeal part).

of the throat, the hyoid and branchial apparatus. In mammals there are several new sets of structures in the pharynx. First, in mammals, secondary hard and soft palates separate the mouth and the nasal cavity. This secondary palate first appears in the fossil ancestors of mammals about 250 million years ago. In addition to separating the mouth and nose, the hard palate probably serves several other functions. It may be important in strengthening the skull and transmitting mechanical forces during chewing. It may also be important in helping to hold food during transport and is also important during suckling (see below). The posterior third or so of the palate is a muscular flap which tightens during swallowing to keep food from moving back into the nasal passage. In most nonhuman mammals the epiglottis, which protects the opening for the airway, can contact the soft palate so that there is an uninterrupted course for the air to pass from the nasal cavity to the larynx, trachea, bronchi and lungs.

A second set of structures that distinguish mammals from nonmammalian tetrapods is the muscular walls of the pharynx. In mammals, two sets of muscles lie just external to the pharynx, internal to all the bones of the hyoid apparatus (although some attach to these bones). The first set of muscles is a series of longitudinal muscles which suspend the pharynx from the base of the skull and act to pull the pharynx up during swallowing. Although there is variability in different mammals, in general there are longitudinal muscles that run from the base of the skull and the back of the palate. In addition, a series of circular muscles, called the constrictors, serve to squeeze the pharynx. Typically, there are three constrictors: a superior, middle and inferior. Finally, mammals have a large, mobile, muscular tongue. Although a mobile muscular tongue is found in other tetrapods, the tongue appears to be more mobile in mammals than in most other vertebrates. In addition, unlike any other vertebrate, a number of muscles run from the palate and skull base to the back of the tongue so that the tongue can be pulled upwards.

The act of swallowing, which in adult humans takes between 500 and 750 ms, consists of a number of distinct stages (**Figure 3**). After food is properly masticated, it is passed to the back of the oral cavity and sits near the back of the tongue. In the first stages of swallowing, the tongue bulges up beneath and in front of the bolus of food and the muscles of the soft palate contract to tense and elevate the back of the palate, to seal the oral cavity from the nasal cavity. The second stage of swallowing consists of the simultaneous pushing of the bolus of food back and down by the tongue and the elevation of the pharynx around the bolus by the longitudinal pharyngeal muscles. This action is much like pushing a foot into a sock: the tongue pushes the food down, and the elevators act to pull the pharynx around the bolus. At the same time, the epiglottis is deflected backwards and a reflex contraction of the muscles of the larynx close the larynx to prevent food from passing into the airway. Although there has been significant discussion about whether or not an animal can swallow

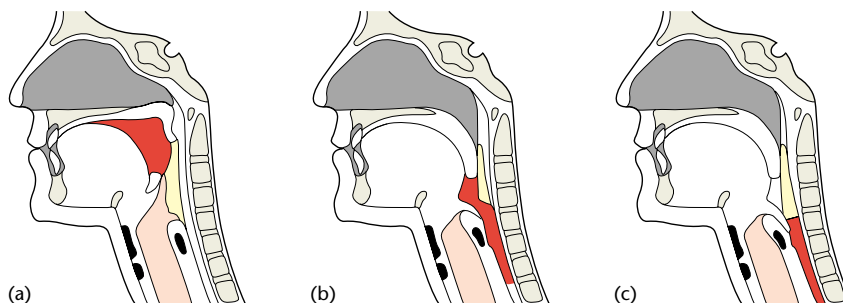


Figure 3 Swallowing. (a) The soft palate has contracted to cover the entrance to the nasal part of the pharynx and the tongue is pushing the food bolus (red) toward the oral part of the pharynx. (b) The tongue reaches its maximal posterior and superior position as the food bolus passes through the oral part of the pharynx and into the laryngeal part of the pharynx. The epiglottis is folded over the opening to the larynx and trachea, and the pharyngeal elevator muscles are contracting. (c) The food bolus is in the laryngeal part of the pharynx, which has elevated and is now constricted as a result of contraction of the pharyngeal constrictor muscles.

and breathe simultaneously, it is likely that breathing is always interrupted during the 500 ms or so of the reflexive swallow. The final stage of the swallow consists of the serial contraction of the superior, middle and inferior constrictors, which move the food backwards to the oesophageal opening. Once in the oesophagus, the smooth muscles of the oesophageal wall continue to propel the food until it reaches the stomach.

There are several specific components of the swallow in mammals that are unique. First, swallowing in mammals results from contraction of a set of muscles, including the pharyngeal elevators and constrictors that are not seen in any other vertebrate. In most vertebrates swallowing is accomplished by the contraction of muscles external to the bones of the throat; in mammals these are new muscles, internal to these bones. Second, in mammals the swallow is a highly coordinated, rapid reflex action, whereas in other vertebrates it is generally slower, and more gradual. Third, most muscles involved in swallowing are innervated by cranial nerve X, the vagus nerve. In most vertebrates, the vagus nerve innervates only the openers and closers of the larynx. Finally, in mammals, swallowing is highly integrated with the oral transport cycles, so that in most mammals a swallow occurs at regular intervals during food processing and transport.

Finally, it is of interest to note the unique pharynx in adult humans. In most mammals there is little space between the soft palate and the epiglottis, so that the epiglottis and opening to the larynx either lies above the back of the soft palate or is in direct contact for the most part. This condition characterizes human infants as well. It is thought that in animals in which the epiglottis lies above the soft palate, breathing mostly occurs through the nose (i.e. an animal either does not or cannot breathe through the mouth). In these animals, during swallowing, food is generally passed on either side of the epiglottis and laryngeal opening, so that the airway is generally protected at all times. In adult humans, however, the larynx lies far below the soft palate. This space, called the oral pharynx, probably arose in part out of the change in human posture, and in part as one of the adaptations toward greater articulation in speech. The anatomical configuration of the adult human does present particular problems in the separation of the air and food pathways, as food must be deflected over the very large laryngeal opening. During a normal swallow, the muscles of the larynx contract reflexively, thereby closing the airway, but it is not uncommon for humans to aspirate food particles into the laryngeal opening, particularly when simultaneously chewing and speaking or laughing.

Suckling

Many of the same muscles involved in the mammalian swallow are also important during suckling, and in fact it has been argued that the unique arrangement seen in mammals is in part an adaptation for infant suckling. Until recently, little was known about suckling, although in the past several years new information has appeared on normal suckling in several mammals including pigs, primates and opossums. In all species, suckling appears to operate by a dorsal–ventral pumping of the tongue. Infants appear to form a seal between the anterior parts of the tongue and the palate, so that an airtight chamber is formed. The posterior region of the tongue is then depressed, creating negative pressure, which pulls milk from the teat. In all infants studied to date there is a preferred rhythm of suckling, and in general swallowing of the milk occurs at regular periods (e.g. once every two to three tongue cycles). In addition to the modifications of the palate, tongue and pharynx discussed above, a number of other features found in mammals appear to be prerequisite for suckling behaviour. Most important among these are muscular cheeks and lips, found only in mammals.

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