

The evolution of the mammalian pharynx

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Data derived from studies of comparative anatomy, development, neuroanatomy, behaviour and the reconstruction of fossils are combined to evaluate the evolution of the oral-pharyngeal region in mammals. An important event in the evolution of the mammalian feeding apparatus was the development of a novel neuromuscular apparatus, consisting of a large series of striated muscles. The most important of these muscles are the pharyngeal elevators and constrictors, which appear to be without homologues in other amniotes. In addition to considerable peripheral neural and muscular modifications, the motor nuclei of the brain stem in mammals exhibit significant differences from other amniotes. The morphological features characteristic of mammals are reflected in behavioural differences, most significantly during swallowing and suckling. The neuromuscular changes in the mammalian oral-pharyngeal apparatus are at least as extensive as those involving the masticatory system, and have importance far beyond the separation of the airway and foodway, the foci of most previous studies. The hypothesis of neuromuscular conservatism in the evolution of the mammalian feeding mechanism is considered and it is concluded that few data exist to support this hypothesis.

KEY WORDS—Pharynx – tongue – mammal – reptile – evolution – neuromuscular.

CONTENTS

Introduction	313
Morphology of the oral-pharyngeal region	315
Palate	315
Pharynx	317
Facial musculature	321
Tongue musculature	322
Innervation of oral-pharyngeal muscles	327
Use of the oral-pharyngeal muscles during feeding	329
Intra-oral transport	329
Swallowing	331
Discussion	333
Transformation of the mammalian oral-pharyngeal region	333
Conservatism of neuromuscular control	337
Are reptiles the appropriate outgroup?	339
Functional significance	341
Conclusions	343
Acknowledgements	344
References	344

INTRODUCTION

The evolution of the mammalian masticatory apparatus is one of the best known and most studied examples of a step-by-step transformation of a complex

system. Numerous authors have used data obtained from the reconstruction of fossils, comparative anatomy and embryology to examine and interpret the changes in the form of the teeth, cranial bones and masticatory muscles (e.g. Allin, 1975, 1986; Barghusen, 1973, 1986; Bramble, 1978; Crompton, 1958, 1963, 1971, 1980, 1989; Crompton & Hylander, 1986; Crompton & Jenkins, 1968, 1973; Crompton & Parker, 1978; Davis, 1961; Osborn & Crompton, 1973; Romer, 1956; Thomason & Russell, 1986; and references therein). Additionally, hypotheses on the functional significance of the reorganization of the masticatory system in mammals have been tested by experimental studies of living animals (e.g. Crompton & Hiimae, 1970; Crompton & Hylander, 1986; Crompton, Taylor & Jagger, 1978; Crompton *et al.*, 1977; Hiimae, 1976; Oron & Crompton, 1985; Thomason & Russell, 1986).

In contrast, the evolution of structures such as the mammalian tongue, hyoid, larynx and oral-pharyngeal muscles has received little attention, perhaps largely because these structures consist primarily of soft tissues and are not preserved commonly in the fossil record. As a consequence, the magnitude of the structural and functional differences between mammals and reptiles remains unappreciated for the muscles of the oral-pharyngeal region. When the evolution of the secondary palate, larynx and epiglottis is considered, they are usually regarded primarily as adaptations that allow mastication and breathing to occur simultaneously. I argue here that such views are inadequate and the differences between mammals and non-mammalian amniotes in the morphology and function of the oral-pharyngeal region are extensive. Further, the oral-pharyngeal region is central to all mammalian oral behaviour, and an appreciation of the full extent of the modifications in this region in mammals is necessary to understand the innovations of the mammalian feeding apparatus.

In addition to substantial modifications in the bone and muscle systems of the pharyngeal region, there are major changes of the pattern of motor innervation. Cranial nerves V, VII, IX, X, XI and XII are involved in the sensory and motor control of the oral-pharyngeal region; the neuromuscular repatterning necessary to transform a non-mammalian to a mammalian condition involved considerable peripheral as well as central nervous system reorganization. This is in contrast to the masticatory system where the trigeminal nerve (V) is largely responsible for both the afferent and efferent components in all tetrapods, and neuromuscular patterning appears to be relatively conservative. A comparison of the condition in non-mammalian amniotes and mammals allows a discussion of the general issue of neuromuscular conservatism and change.

In this essay, I will trace some of the important events in the transformation of the oral-pharyngeal region in the evolution of mammals. This analysis will rely primarily on data derived from studies of the comparative and developmental anatomy of the muscular system, the comparative anatomy of the nervous system and the functional morphology of feeding. Where available, information about the structural transformation evident from fossils will be considered. The specific goals of this paper are: (1) to outline the differences in the morphology of the tongue, hyobranchial and pharyngeal muscles in mammals and non-mammalian amniotes, (2) to review the functional differences in this region between these taxa, (3) to consider the possible homologies (or lack thereof) between non-mammalian amniote and mammalian structures, and (4) to introduce hypotheses on the functional significance of the transition from the

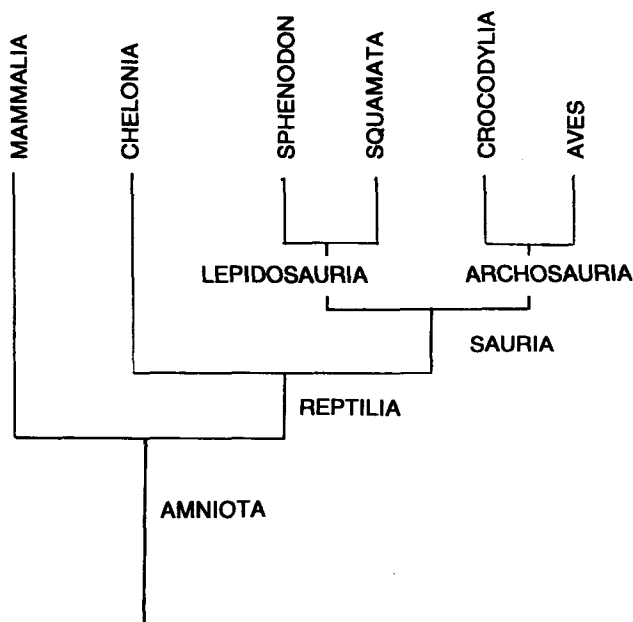


Figure 1. Phylogenetic context and systematic terms used in this paper. Phylogeny redrawn from Rowe (1988) after Gauthier, Kluge & Rowe (1988).

primitive to the mammalian condition. In each section below I will define the primitive condition as the condition found most commonly across the Reptilia (as defined in Figure 1), the extant outgroup to the Mammalia. I will then discuss the derived condition in mammals. In the discussions below, unless otherwise noted, the condition of the Reptilia refers to conditions held in common in squamate reptiles, chelonians, crocodylians and birds (i.e. 'conventional reptiles' + birds). Conditions described for mammals refer to conditions held in common in monotremes, marsupials and placental mammals (other taxonomic references as in Fig. 1; from Rowe, 1988 and Gauthier, Kluge & Rowe, 1988).

MORPHOLOGY OF THE ORAL-PHARYNGEAL REGION

Palate

The evolution of the mammalian palate has been well studied, in part because it is one of the few structures of the oral region that is preserved in the fossil record (e.g. Barghusen, 1986; Crompton, 1989; Hopson & Barghusen, 1986; Romer, 1956; Thomason & Russell, 1986; and references therein). In the pelycosaur *Dimetrodon*, primitive therapsids and the extant reptiles (with the exception of crocodylians), the roof of the mouth is comprised of the premaxillary, vomer, palatine and pterygoid bones. The internal choanae are large and lie anteriorly in the oral cavity and open directly into it (Fig. 2A).

A bony secondary palate, consisting of medially extending flanges of the maxillary and palatine bones, appears later, gradually and in parallel in

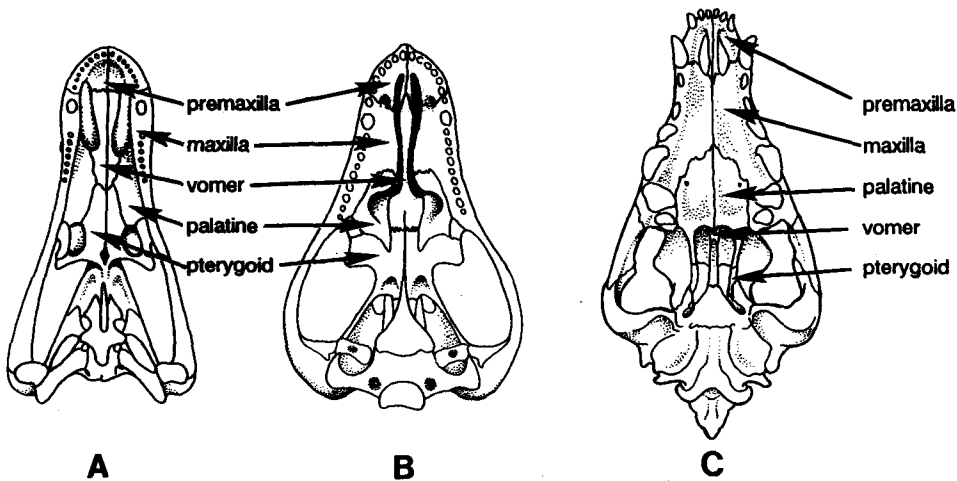


Figure 2. Condition of the palate in mammal-like reptiles and mammals, showing A, primitive condition (*Sclerosaurus*, a therocephalian); B, partial closure (*Procynosuchus*, a cynodont); and C, mammalian condition (*Canis*). Redrawn from Romer (1956).

numerous lineages (e.g. Hopson & Barghusen, 1986; Romer, 1956; Thomason & Russell, 1986). A partial hard palate (e.g. maxillary processes extending horizontally, but not meeting in the centre) is present before a complete palate with midline fusion appears (Fig. 2B). The soft palate of fossil forms is not preserved, but Barghusen (1986) reconstructs the soft anatomy of cynodonts such as *Cynognathus* and *Diademodon* and suggests that a soft palate was present.

The derived condition, found in extant mammals (Fig. 2C), consists of a complete separation of the airway and the oral cavity by hard as well as soft palates. The soft palate possesses two major muscles, the tensor veli palatini and the levator veli palatini. Barghusen (1986) summarizes the case for deriving the former muscle from the posterior pterygoid muscle of reptiles. The derivation of the levator veli palatini, as well as the palatoglossus (running from the soft palate to the posterior portion of the tongue) is less certain, but these latter muscles appear to develop from the same mass of musculature giving rise to the pharyngeal constrictors. The levator veli palatini is innervated by cranial nerve VII (Ibuki *et al.*, 1978).

Ferguson (1981: 432) has claimed that "crocodilians have undergone few major morphological alterations, so that their structure and development should reflect that of ancestral thecodonts" and that "it is possible" that crocodilians and mammal-like-reptiles have "retained a similarity in palatal structure and development". However, a secondary hard palate is unlikely to have been a primitive character in amniotes. The secondary hard palate appears within the therapsid line, and is not primitively present in the first members of this group. Further, a complete hard secondary palate is found only in the latter members of the Crocodylia (Carroll, 1988) and is absent in other members of the Reptilia (including fossil forms). Therefore, the secondary hard palates of crocodilians and mammals are most parsimoniously regarded as independent acquisitions. The crocodilian palate is not likely to provide direct information relevant to the primitive amniote condition or the evolution of the mammalian palate.

Pharynx

Primitively in tetrapods, a single continuous cavity connects the oral, nasal, tympanic and pharyngeal regions (Fig. 3). With the exception of a few derived cases (crocodilians, some lacertilians), the oral and nasal cavities are not separated by either hard or soft tissues. The larynx lies at the base of the tongue, with no close proximity to the internal choanae in most reptiles. The entrance to the trachea is directly into the oral cavity and is opened and closed by laryngeal dilators and constrictors (Fig. 4), acting on laryngeal cartilages (e.g. Oelrich, 1956; Schumacher, 1973; Zweers, 1982; Zweers, van Pelt & Beckers, 1981). There is no constriction or separation between the oral and pharyngeal cavities and no muscular pharynx. No striated musculature lies within the pharyngeal walls or runs from the cranial base to the pharyngeal walls or tongue (Edgeworth, 1935). The primary swallowing muscle of non-mammalian amniotes is the *M. constrictor colli*, which lies external to the hyoid apparatus and is innervated by the facial nerve (VII). These basic features characterize chelonians, lepidosaurian reptiles and birds. Crocodilians do possess a secondary palate and a means to constrict the pharynx, but this constrictor is a derivative of the constrictor colli muscle (Schumacher, 1973). Additionally, in crocodilians,

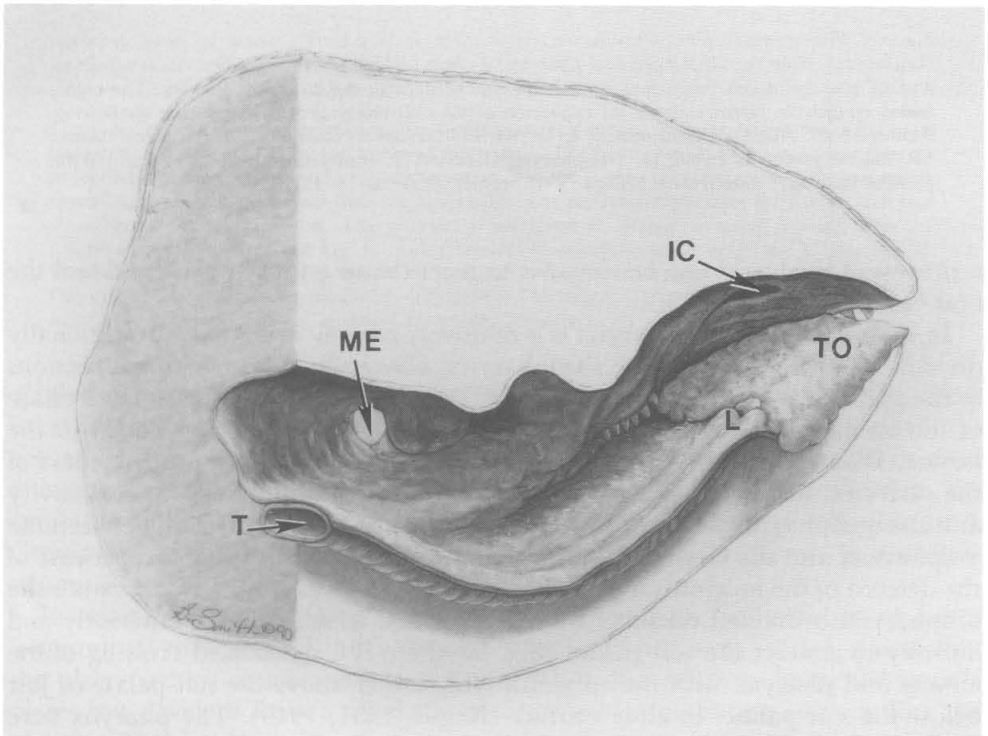


Figure 3. Cut away view of the reptilian condition of the oral-pharyngeal cavity. Note the single large open cavity that comprises the nasal, oral, pharyngeal and middle ear cavities. The tongue is relatively short and the opening for the larynx lies at the base of the tongue. No musculature connects the tongue, larynx or ventral portion of the oral and pharyngeal cavities to the palate, base of the skull or dorsal portion of the pharynx (see also Fig. 4). Abbreviations: IC, internal choanae; L, laryngeal opening; ME, middle ear cavity; T, trachea; TO, tongue. Drawing is a posterior-oblique view of a preserved specimen of a juvenile *Ctenosaura similis*.

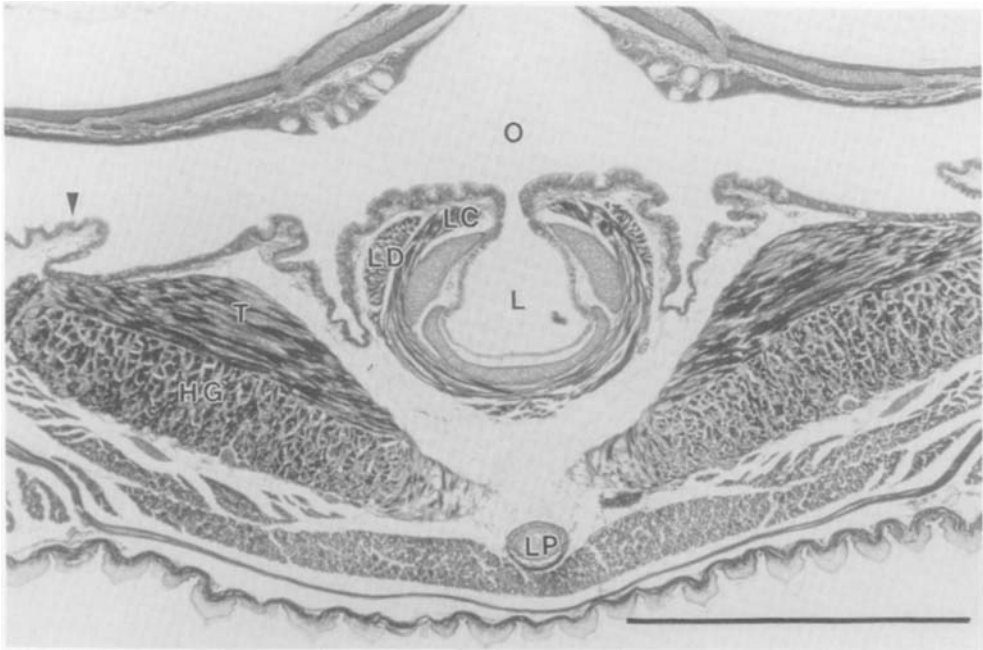


Figure 4. Photomicrograph of a transverse section through the posterior tongue in *Anolis carolinensis* (Iguanidae). Note the large open oral-pharyngeal cavity, which serves as an oral cavity, pharynx and air passage at this point, and is in direct continuity with the laryngeal opening. The highly folded epithelium (arrow) allows for expansion of the oral-pharyngeal cavity during swallowing. Abbreviations: HG, hyoglossus muscle; L, larynx; LC, laryngeal constrictor; LD, laryngeal dilator; LP, lingual process of hyoid; O, oral-pharyngeal cavity; T, transverse muscle of tongue (10 μ m paraffin histology; stained with Milligan's trichrome). Scale bar = 1.0 mm.

a process of the hyoid can be elevated to meet the secondary palate and seal the oral cavity (Busbey, 1989).

In most mammals the pharynx is a relatively narrow tube that is traditionally divided into three regions: the nasopharynx, above the palate, with connections to the middle ear cavity via the auditory tube; the oropharynx, between the base of the tongue and the larynx; and the laryngopharynx, a region dorsal to the larynx. Wood Jones (1940) argues that the nasopharynx is not properly part of the pharynx, which was originally defined as the region linking the oral cavity and the oesophagus, and the term should be dropped*. The division between the oropharynx and the laryngopharynx is most distinct in adult humans because of the descent of the epiglottis and larynx (see below). In non-human mammals the oropharynx is divided medially by the epiglottis, which projects anteriorly and dorsally to contact the soft palate (Fig. 5); there is a specialized crossing of the airway and pharynx with the epiglottis lying either above the soft palate or just below the soft palate, in close contact (Negus, 1931, 1949). The pharynx here consists of two narrow passages on either side of the epiglottis (Fig. 6). This

*In non-mammalian amniotes the middle ear cavity is in direct communication with the pharynx. If the middle ear is homologous in mammals and non-mammalian tetrapods, the nasopharynx would represent this portion of the pharynx. However, recent papers (e.g. Allin, 1975; Lombard & Bolt, 1979) question the homology of the middle ear cavity in mammals and non-mammalian amniotes. This latter position would support Wood Jones' contention.

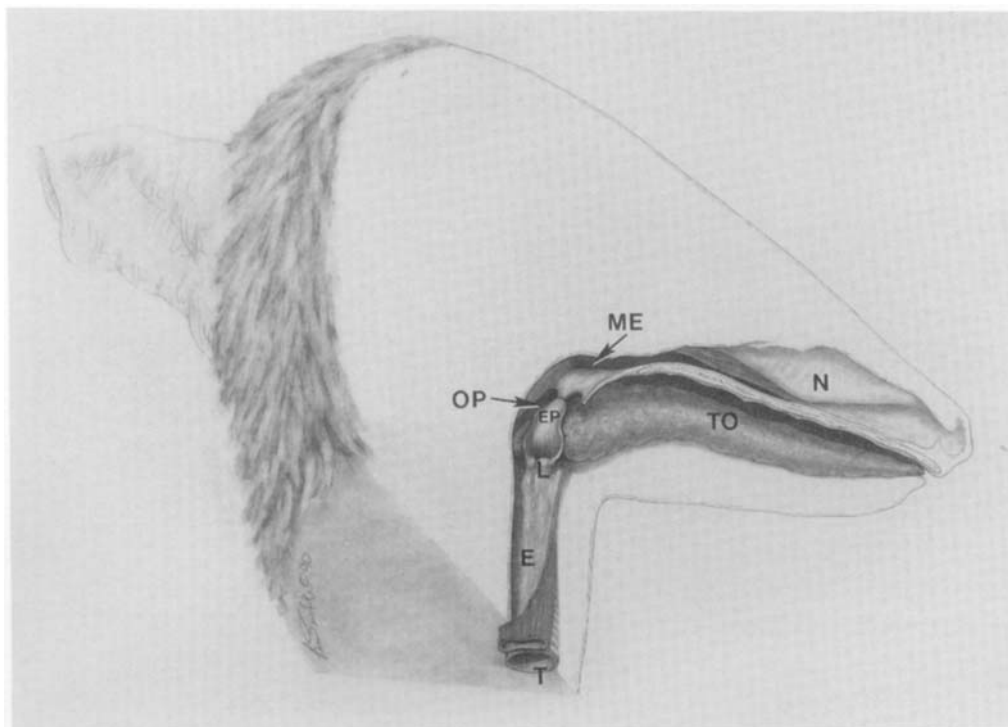


Figure 5. Cut away view of the mammalian oral-pharyngeal region. Note the separation of the nasal passage and the oral cavity by the hard and soft palates. The larynx lies at the base of the tongue, as in reptiles, but the epiglottis, which is at the entrance to the larynx, is in contact with the soft palate to maintain an airway separate from the oral cavity. The pharyngeal passages are narrow and pass on either side of the epiglottis. The pharynx is narrowed by muscles running dorsally from the tongue and oral base (see also Fig. 6). Abbreviations: E, oesophagus; EP, epiglottis; L, larynx; ME, approximate location of the opening of the auditory tube into the nasopharynx; N, nasal passage; OP, oral-pharyngeal passage (foodway); T, trachea; TO, tongue. Drawn as a posterior-oblique view from a preserved specimen of an adult *Monodelphis domestica*.

epiglottal position is thought to maintain the airway, and therefore allow breathing during suckling, mastication and swallowing. The extent to which it is actually maintained during these activities has not been demonstrated in most animals. It has been demonstrated that in some animals, such as the dog, the epiglottis/palatal contact may be broken during panting (Biewener, Soghikian & Crompton, 1985). It is likely that in most mammals the larynx is a mobile structure.

In mammals the striated musculature of the pharynx consists of outer longitudinal muscles and inner circular muscles. Edgeworth (1935) claims that the pharyngeal musculature of mammals is not derived from branchial muscle plates but develops from a separate condensation of myoblasts surrounding the pharyngeal epithelium. He does not consider it homologous with the amphibian pharyngeal musculature. The longitudinal musculature in mammals varies slightly among taxa (e.g. Dutta & Basmajian, 1960; Dyce, 1957; Edgeworth, 1935; House, 1953; Jouffroy, Lessertisseur & Saban, 1971; Saban, 1968) but generally consists of muscles that run from the auditory tube (salpingopharyngeus), palate (palatopharyngeus), styloid process

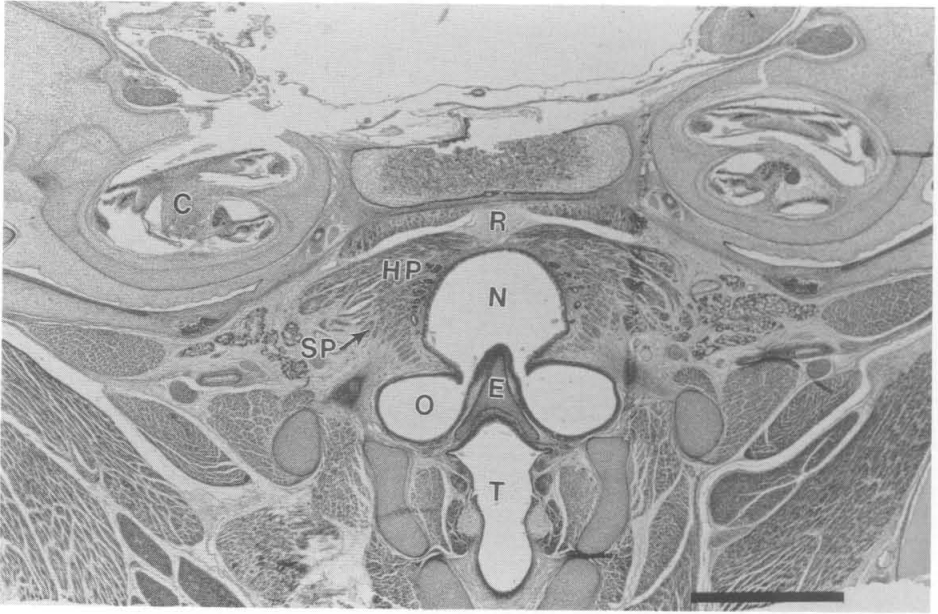


Figure 6. Photomicrograph of a transverse section through the laryngeal region in a mammal (1-day-old laboratory rat). Note the narrow oral passages on either side of the epiglottis. Key to abbreviations: C, cochlea; E, epiglottis; HP, hyopharyngeus (middle constrictor) muscle; N, air passage; O, oral-pharyngeal passage; R, dorsal midline intramuscular raphe; SP, bundle of stylopharyngeus muscle; T, trachea (10 μ m paraffin histology, stained with hematoxylin and picroponceau). Scale bar = 1.0 mm.

(stylopharyngeus), pterygoid hamulus, and tongue (glossopharyngeus) (Fig. 7). The inner circular muscles are the pharyngeal constrictors. Three constrictors are typically present, although variation exists in relative development, attachments and distinctions of individual muscle masses. The superior constrictor (pterygopharyngeus) originates from the bucco-pharyngeal fascia, the pterygomandibular raphe, the pterygoid hamulus and posterior border of the medial pterygoid plate. In various studies portions also have been reported to arise from soft tissues such as the soft palate, side of the tongue and external acoustic meatus. The superior constrictor inserts in a dorsal midline raphe, with

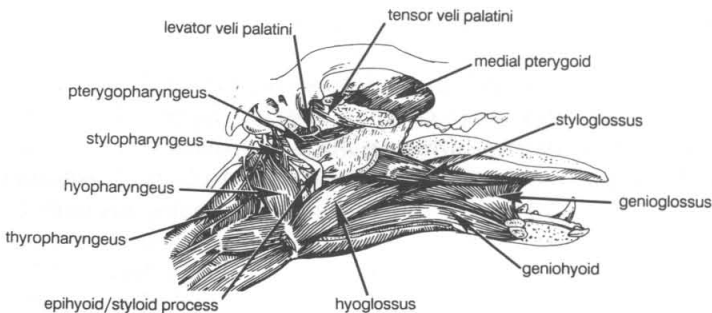


Figure 7. Pharyngeal muscles in mammals (*Canis*). Redrawn from Miller, Christensen & Evans (1964).

the anterior-most portion of the raphe inserting on the basioccipital bone. The middle constrictor (ceratopharyngeus or hyopharyngeus) originates in various taxa from the lesser and/or greater cornu of the hyoid, and the inferior constrictor (laryngopharyngeus) originates from the thyroid and cricoid cartilages (forming distinct thyropharyngeus and cricopharyngeus portions). Both the middle and inferior constrictors also insert on the dorsal midline raphe (Fig. 6).

There is notable variation in the superior constrictor of mammals. Edgeworth (1935) states that it is absent in "lower mammals", but House (1953) comments that the portion of the longitudinal musculature that arises from the pterygoid hamulus in rats, for example, is homologous to the superior constrictor and only appears longitudinal because of differences in the alignment of the cranial base. Monotremes possess the least differentiated condition of the pharyngeal muscles in mammals, represented only by the stylopharyngeus, palatopharyngeus and an undifferentiated constrictor pharyngeus (Jouffroy, Lessertisseur & Saban, 1971; Saban, 1968).

The configuration of the adult human pharynx is different from other mammals (Fig. 8) because the descent of the larynx and epiglottis below the soft palate has produced a distinct oropharynx (Bateman & Mason, 1984; Bosma, 1961, 1985). This descent occurs ontogenetically; at birth, the epiglottis is in contact with the palate (Bosma, 1985). The descent of the human larynx and epiglottis elongates the longitudinal musculature, so as to make the distinction between the muscular elements particularly clear.

To summarize, the mammalian oral pharyngeal region is characterized by hard and soft palates that separate nasal and oral cavities, a specialized arrangement for the crossing of the airway and food passage that normally consists of an epiglottis that is in contact with or lies above the soft palate and an elaborate system of striated pharyngeal and palatal muscles.

Facial musculature

Living reptiles have no muscles of facial expression, but do have musculature innervated by the facial nerve (cranial nerve VII), the Mm. constrictor colli, intermandibularis posterior and depressor mandibulae. The constrictor colli is a thin sheet of muscle, external to all other hyoid muscles, that wraps the hyopharyngeal region. It acts as the major swallowing muscle of reptiles and birds. The intermandibularis posterior is essentially an anterior extension of this muscle. The depressor mandibulae is a jaw opening muscle, originating on the fascia overlying the dorsal aspect of the neck and inserting on the retroarticular process of the mandible (Fig. 9A).

The facial muscles of mammals are, like the pharyngeal muscles, unique to this class. However, in contrast to the pharyngeal muscles, which have no obvious homologue in reptiles, the facial muscles in mammals are thought by most authors to be derived from the constrictor colli (e.g. Huber, 1930; Romer, 1970; Jouffroy, Lessertisseur & Saban, 1971). Edgeworth (1935) claims that the two groups of muscles are not homologous and states that the facial musculature of mammals is a neomorphic complex that develops from a new muscle primordia, the subcutaneous colli (see also Székel & Matesz, 1989). The relative development of facial musculature in mammals varies, but generally consists of

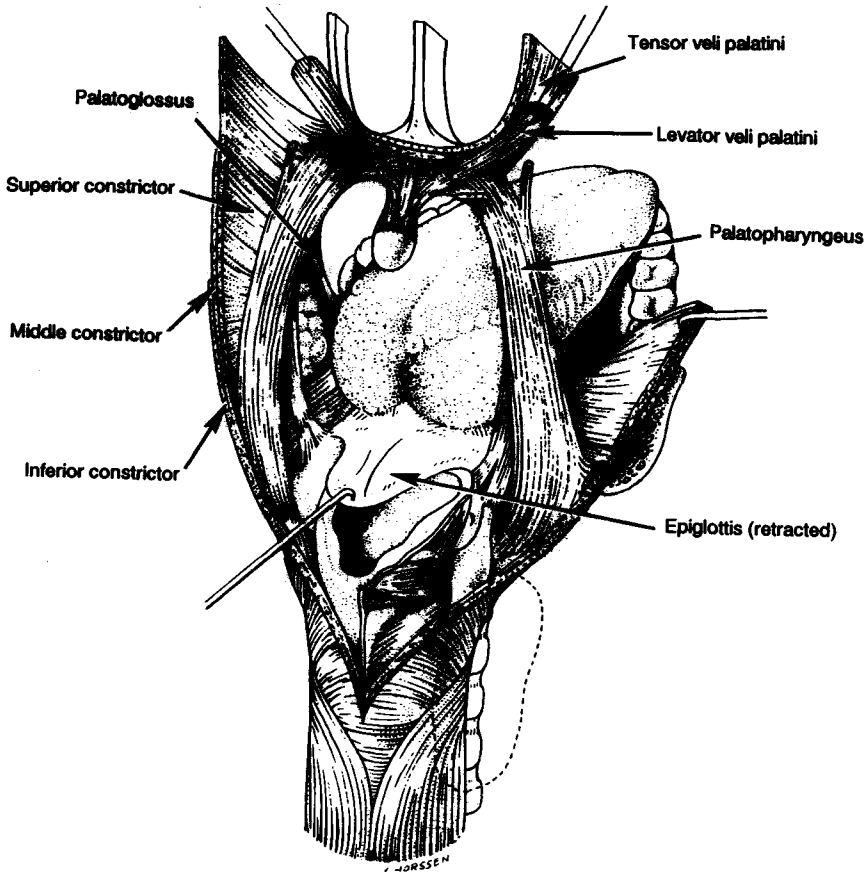


Figure 8. A posterior-oblique view of human pharyngeal muscles. Note the descent of the epiglottis to form a large oropharynx between the epiglottis and the soft palate. This condition is quite different from the primitive condition in mammals depicted in Fig. 5. The superior constrictor of humans is homologous with the pterygopharyngeus; the middle constrictor with the hyopharyngeus; the inferior constrictor with the thyropharyngeus of Fig. 7. Figure by A. A. van Horsen, reproduced courtesy of Dr W. A. Weijs.

two layers: a superficial layer, the sphincter colli, which gives rise to the platysma, and a deep layer, the sphincter colli profundus, which gives rise to most facial muscles including the buccinator (or cheek muscle) and musculature forming and attaching to the mobile lips, nose, eyelids and ears of mammals (Fig. 9B). In therian mammals the posterior belly of the digastric is innervated by VII and is a jaw opening muscle, but is unlikely to be homologous with the jaw opening muscle of reptiles. Monotremes differ from marsupials and placentals in that the superficial sphincter colli is well developed, extending even into the forelimbs, but the musculature derived from the sphincter colli profundus (i.e. facial musculature) is not well developed (Huber, 1930).

Tongue musculature

Within amniotes there is far more diversity in the intrinsic morphology of the tongue than is generally recognized (e.g. Livingston, 1956). In most

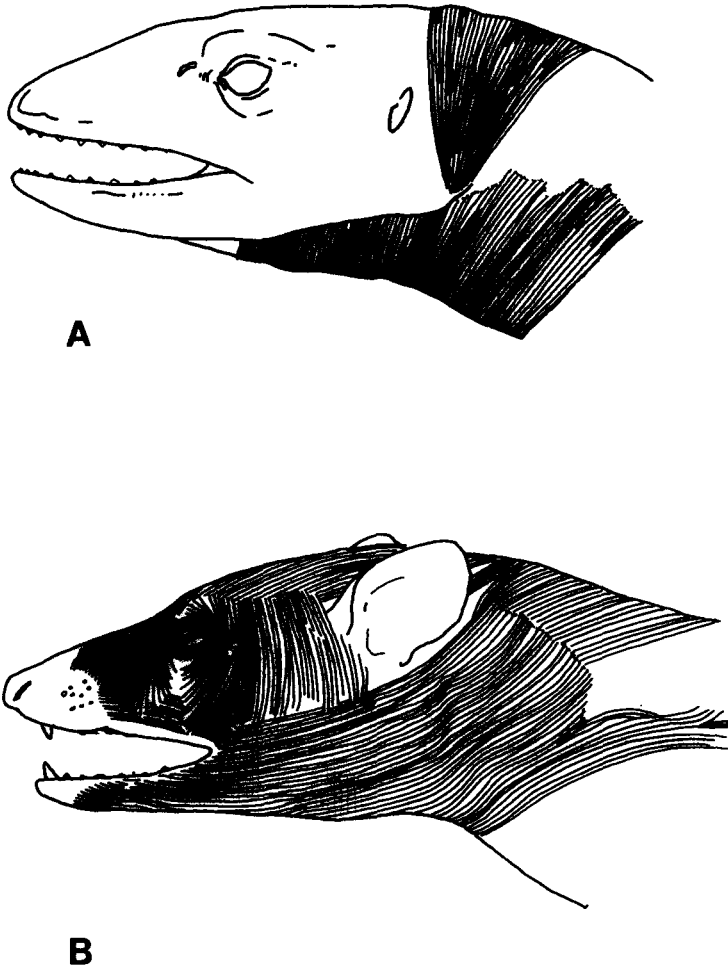


Figure 9. Muscles innervated by the facial nerve (VII) in A, a lizard, *Varanus*, and B, a mammal, *Didelphis* (B redrawn from Huber, 1930).

lepidosaurian reptiles the intrinsic musculature of the tongue is well developed and the tongue is capable of movements that are independent of those of the hyoid. In crocodylians, the tongue is little more than an amuscular flap on the floor of the mouth (Schumacher, 1973). In birds the tongue is mobile but is largely a muscular-epithelial coating around the mobile hyoid apparatus (except for parrots which show a derived condition within birds—Homberger, 1986). The hyoid musculature in birds is quite elaborate and subdivided, because movements between elements of the hyoid apparatus are responsible for lingual movements (e.g. Homberger, 1986; Homberger & Meyers, 1989; Zweers, 1982). Chelonians have a mobile tongue with a fleshy surface, but a neomorphic skeletal element, the hypoglossum, lies in the centre of the tongue and provides the major support for the tongue. In chelonians there are minimal intrinsic tongue muscles (Schumacher, 1973). Because significant variation in the composition of the tongue exists within amniotes (and even more when the

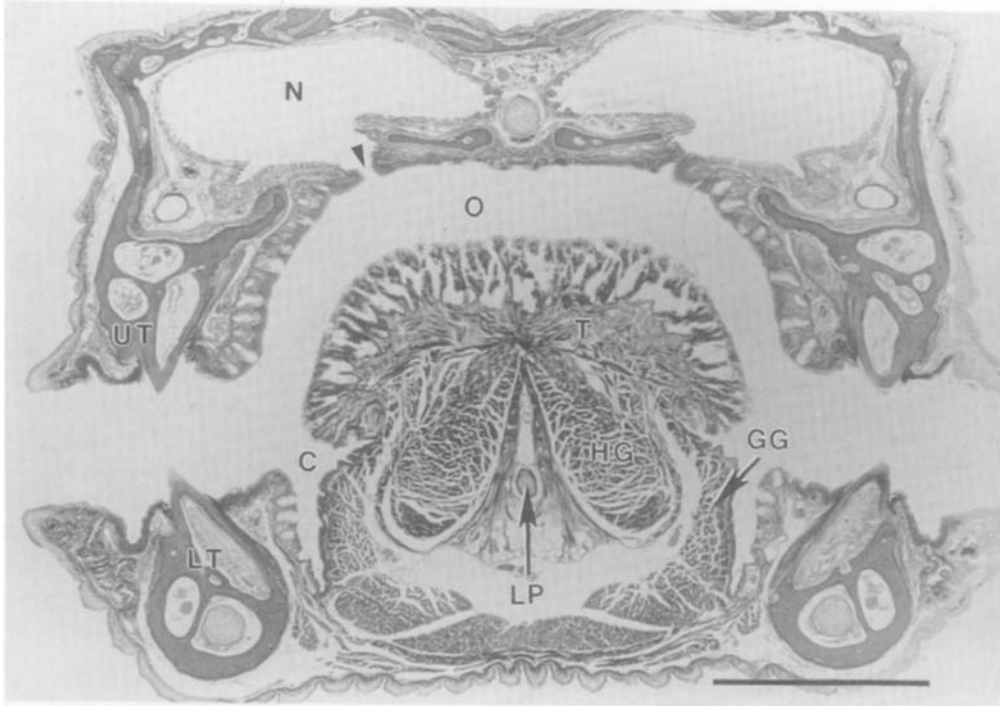


Figure 10. Photomicrograph of a transverse section through the head of *Anolis carolinensis*. The section shows the intrinsic musculature of the tongue and the relation of the head of the tongue and the oral and nasal cavities in a reptile. Note the lateral passage of the genioglossus muscle into the tongue, the central position of the hyoglossus muscle and the absence of cheek muscles or muscles dorsal or lateral to the tongue. The arrow points out the internal choane. Abbreviations GG, genioglossus muscle; HG, hyoglossus muscle; LP, lingual process of hyoid; LT, lower tooth; N, nasal muscle; O, oral cavity; UT, upper tooth (10 μ m paraffin section stained with Milligan's trichome). Scale bar = 1.0 mm.

outgroup, the Lissamphibia, are considered; e.g. Emerson, 1976; Gans & Gorniak, 1982a, b; Lombard & Wake, 1976, 1977; Ozeti & Wake, 1969; Regal, 1966; Regal & Gans, 1976; Trueb & Gans, 1983), it is difficult to define a primitive condition. In most groups there is significant structural support provided by the hyoid apparatus. This condition may be primitive.

The morphology of the tongue is better studied in lizards than in other reptilian groups. In lizards the bulk of the intrinsic tongue musculature is formed by the paired, longitudinally oriented bundles of the hyoglossus muscle. These two bundles are central in the tongue, separated from each other only by a single sheet of intrinsic musculature. The genioglossus muscle inserts peripherally and contributes to the lateral intrinsic musculature. All extrinsic tongue muscles pass into the tongue ventrally. There are four major groups of intrinsic tongue muscles in lizards: the verticalis, the dorsal and ventral transverse and the dorsal longitudinal muscle, although variability in specific form exists (Oelrich, 1956; Schwenk, 1984, 1988; Sewertzoff, 1929; Smith, 1984, 1986, 1988; and references therein). In the majority of squamates the verticalis, dorsal transverse and ventral transverse combine to form a circular muscle that surrounds the hyoglossus (Fig. 10). In the most primitive groups such as *Sphenodon* (Schwenk, 1986), and agamid and iguanid lizards (Smith, 1984, 1988) the tongue receives

substantial structural support from the lingual process of the hyoid, although many tongue movements are independent of hyoid movement. Tongues that are totally independent of internal hyoid structural support are derived within lepidosaurs.

The tongue in mammals is one of the most complex muscular units in vertebrates, consisting of an elaborate three-dimensional array of mutually perpendicular muscle bundles with no internal hardened skeletal support (Kier & Smith, 1985; Smith & Kier, 1989). Although structural details vary, the condition described below is a general pattern, found, for example, in didelphid marsupials, rodents, carnivores and primates. The extrinsic tongue muscles in mammals are the genioglossus, hyoglossus and styloglossus, which originate from the mandibular symphysis, the greater cornua and body of the hyoid bone and the styloid process respectively and the palatoglossus, running from the palate to the tongue base (e.g. Abd-el-Malek, 1938; Bateman & Mason, 1984; Doran, 1975; Doran & Baggett, 1971; Halpern, 1977; Hellstrand, 1980; Saito & Ikenoya, 1988; Smith, 1989). Monotremes lack a styloglossus muscle (Jouffroy *et al.*, 1971). In mammals, in contrast to most lizards, fibres of the *M. genioglossus* pass into the tongue medial to all other extrinsic muscles (Fig. 11A; Doran, 1975; Doran & Baggett, 1971, 1972). The *Mm. hyoglossus* and *styloglossus* enter the tongue lateral to the fibres of the *M. genioglossus*. Fibres of these two muscles contribute to the longitudinal intrinsic musculature (e.g. Benoit, Lemire & Saban, 1985). It is noteworthy that the relation of the genioglossus and hyoglossus muscles is reversed in mammals and reptiles: in reptiles the hyoglossus is central and the genioglossus is lateral, whereas in mammals the genioglossus is central and the hyoglossus lateral. One of the most significant anatomical differences between the tongue of mammals and that of other amniotes is the existence of elevators of the tongue base. Most mammals possess both styloglossus and palatoglossus muscles running from the cranial base and palate respectively (Fig. 11B). These muscles form a sling that elevates the tongue base and also separates the oral and pharyngeal cavities. Unlike reptiles, where the tongue is connected only to the mandible and hyoid (Figs 4, 10), in mammals the muscles of the posterior tongue are part of a continuous ring of muscles that links the intrinsic tongue muscles and the palatal and pharyngeal muscles (Fig. 11B). This is in contrast to all non-mammalian tetrapods.

The intrinsic tongue muscles in mammals are divided into three main groups, the longitudinal, vertical and transverse muscles (Fig. 11A). The longitudinal muscle possesses superior and inferior portions, which in turn split into a number of bundles that are arrayed around the periphery of the tongue. The transverse muscle originates from a midline vertical connective tissue septum and runs laterally to insert into a connective tissue matrix beneath the epithelium of the tongue. The verticalis muscle, where it is not a continuation of the *M. genioglossus*, originates and inserts into this connective tissue matrix. The verticalis and transversus muscles are arranged as alternating sheets, orthogonal to the long axis of the tongue, which maximizes the potential diversity of movement (Smith & Kier, 1989). Some mammals such as anteaters, echidnas and pangolins (Griffiths, 1968, 1978; Doran, 1973, Doran & Allbrook, 1973) possess secondarily derived, lizard-like configurations of tongue musculature with central longitudinal musculature surrounded by circular muscles.

It is important to point out an essential difference in the way that tongue

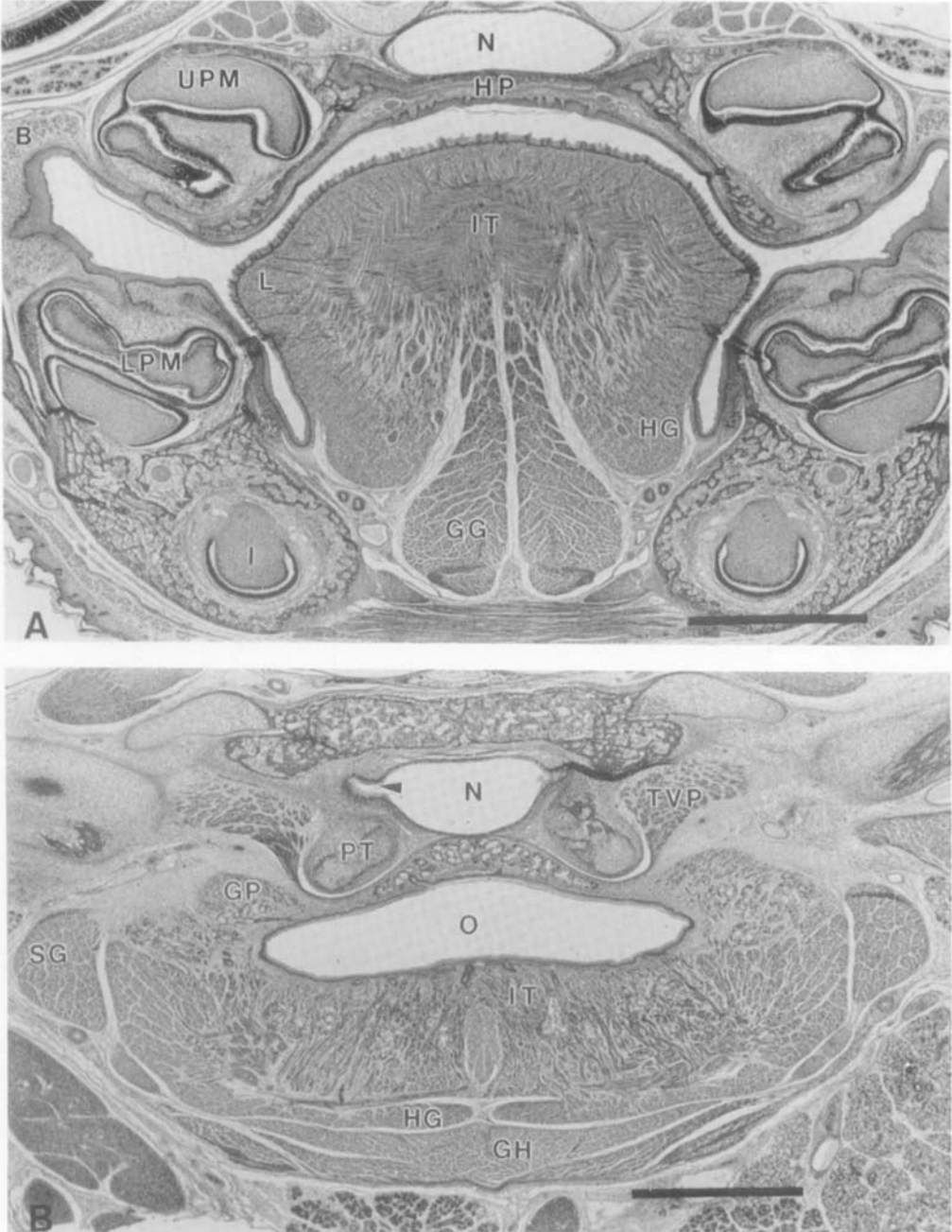


Figure 11. Photomicrographs of transverse sections of the tongue and pharyngeal region in a 1-day-old rat. A, Anterior section through the tongue. Note the complete separation of the nasal and oral cavities, the buccinator muscle forming the cheek and closing the oral cavity laterally and the passage of the genioglossus muscles internal to the hyoglossus muscles. IT labels an area of alternating vertical and horizontal intrinsic tongue muscles. B, Posterior section at the back of the tongue, just behind the hard palate. Note the ring of muscles dorsal or lateral to the tongue and the complete separation of the oral and nasal passages. The arrow represents the beginning of the auditory tube (Eustachian tube). Abbreviations: B, buccinator muscle; GG, genioglossus muscle; GH, geniohyoid muscle; GP, palatoglossus/glossopharyngeal muscles (after House, 1953); HG, hyoglossus muscle; HP, hard palate; I, incisor root; IT, intrinsic tongue muscle; L, longitudinal

TABLE 1. Major muscle groups innervated by each motor nerve in the Reptilia and Mammalia. For more information and references see text

Motor nerves	Reptilia	Mammalia
V	Muscles of mastication; intermandibularis anterior; constrictor dorsalis	Muscles of mastication; tensor tympani; tensor veli palatini; mylohyoideus; anterior digastric
VII	Constrictor colli; intermandibularis posterior; depressor mandibulae	Facial muscles; stylohyoideus; posterior digastric; stapedius; levator veli palatini
IX	Branchiohyoideus; laryngeal dilators and constrictors (reptiles)	Stylopharyngeus; superior constrictor(?)
X	?Laryngeal dilators and constrictors (birds)	Pharyngeal constrictors; pharyngeal elevators; laryngeal muscles; palatoglossus
XII	Genioglossus; hyoglossus; intrinsic tongue; anterior hyobranchial; geniohyoideus	Genioglossus; hyoglossus; intrinsic tongue; styloglossus; geniohyoideus
Cervical	Omohyoideus; sternohyoideus	Omohyoideus; sternohyoideus

movements are produced in mammals and animals such as birds, for example. In most birds, tongue movements are hyoid movements. There are minimal or no intrinsic tongue muscles; most changes in shape as well as all movements in space are produced by movements of the elaborate hyoid skeleton. This is largely true even for parrots, which possess a derived and elaborate lingual apparatus (Homerger, 1986). Similar relations appear to hold in chelonians because of the reduced intrinsic tongue musculature and elaborate hyoid support (Schumacher, 1973). In mammals, although tongue movements are supported by the hyoid and movements of the hyoid produce movements of the tongue base, the tongue is for the most part independently mobile. Many movements in space, and all changes in shape, are independent of hyoid movements in mammals.

Innervation of oral-pharyngeal muscles

Table 1 lists the cranial motor nerves and the muscles they innervate in reptiles and mammals. For the most part, the muscle masses innervated by the trigeminal (V), facial (VII) and hypoglossal (XII) nerves are considered homologous in reptiles and mammals, although there are differing opinions on the homology of specific muscles. This homology is determined in large part by innervation (thus making the above statement a tautology), but also on the basis of positional and developmental criteria (e.g. Barghusen, 1986; Edgeworth, 1935; Huber, 1930; Jouffroy *et al.*, 1971; Noden, 1984; Romer, 1970; Saban, 1968; Schumacher, 1973). The glossopharyngeal nerve (IX) innervates just a few muscles in both groups. In most reptiles it provides motor innervation to the larynx (Oelrich, 1956; Schumacher, 1973; Watkinson, 1906; Willard, 1915). Reptiles and mammals are significantly different in the efferent targets of the vagus nerve (X). In reptiles little or no striated musculature is innervated by the vagus nerve (X); in birds only the muscles of the larynx are thought to receive

tongue muscle; LPM, lower premolar; N, nasal passage; O, oral-pharyngeal passage; PT, pterygoid bone; SG, styloglossus muscle; TVP, tensor veli palatini muscle; UPM, upper premolar. Both photographs are 10 μ m paraffin sections, stained with hematoxylin and picroponceau. Scale bars = 1.0 mm.

motor innervation from X (Abdulla & King, 1979; Bubién-Waluszewska, 1968, 1981; McLelland, 1989; Pearson, 1972). Auen & Langbartel (1977) report that the larynx in snakes is innervated by X; however, IX, X and XII extensively anastomose intracranially in snakes (e.g. Young, 1987) and the precise components are difficult to discern. Mammals, in contrast, possess a large and complex series of muscles innervated by the vagus nerve, including the constrictors and elevators of the pharynx, the palatal muscles and the laryngeal muscles (Bateman & Mason, 1984; Bosma, 1961; Doty, 1968; Saban, 1968). The absence of significant musculature innervated by X in the Reptilia makes it difficult to evaluate the homology of the pharyngeal musculature.

The relative development of muscles and the distribution of peripheral nerves are reflected in the relative size, differentiation and arrangement of the cranial nerve motor nuclei in the brainstem. In reptiles there is little cytological differentiation within the motor centres of either the vagus or glossopharyngeal nerves. For the most part the motor nuclei of the brainstem in reptiles and birds consists of a single column of cells (e.g. Cruce & Nieuwenhuys, 1974; Sarnat & Netsky, 1981; ten Donkelaar & Nieuwenhuys, 1979). The nucleus of the glossopharyngeal nerve is generally not distinguishable from that of the facial nerve (Addens, 1933; Cruce & Nieuwenhuys, 1974; Kappers, Huber & Crosby, 1936; Schwab, 1979; ten Donkelaar & Nieuwenhuys, 1979). In all reptiles a dorsal nucleus for the vagus nerve is present, presumably providing for autonomic innervation to the gut, as in other tetrapods (e.g. Getz & Sirnes, 1949; Lewis, Scott & Navaratnam, 1970; Mitchell & Warwick, 1955; Schwab, 1979). In many reptiles it is the only motor nucleus of the vagus nerve. The nucleus ambiguus has been described in some reptiles and birds (Black, 1922; Cruce & Nieuwenhuys, 1974; Kennedy, 1981; Pearson, 1972; ten Donkelaar & Nieuwenhuys, 1979). However, the location of the nucleus ambiguus in non-mammalian tetrapods is different from mammals and the precise targets and components (e.g. autonomic or somatic motor) are not necessarily the same (e.g. Barbas-Henry & Lohman, 1984). The hypoglossal nucleus in reptiles is well developed and distinct but is spatially continuous with the motor nerves of the spinal cord (Barnard, 1940; Kappers, Huber & Crosby, 1936; ten Donkelaar & Nieuwenhuys, 1979). In birds, the nucleus of the hypoglossal nerve is quite elaborate, but this elaboration relates to the derived condition of the syringeal mechanism*.

Four derived features of the cranial motor nuclei characterize all mammals, including monotremes (Addens, 1933; Kappers, Huber & Crosby, 1936; Sarnat & Netsky, 1981). First the hypoglossal (XII) nucleus is contained within the brainstem and is independent of the grey matter of the spinal cord. Second, the cell bodies of the motor root of the glossopharyngeal nerve (IX) are no longer associated with the nucleus of the facial nerve (VII) but are associated with the vagus nerve (X) to form a ventral motor nucleus, the nucleus ambiguus. The remaining motor nucleus of the facial nerve (VII) is large. Third, the nucleus ambiguus is relatively distinct in mammals and contains, primarily, cell bodies of motor nerves to striated muscles of the pharynx and larynx, in addition to

*Birds are characterized by a number of modifications of the laryngeal and particularly syringeal neuromuscular system. These are autapomorphies and are unrelated to either the primitive or the mammalian condition.

autonomic innervation to the heart and the carotid sinus (e.g. Beevor & Horsley, 1988; Coil & Norgren, 1979; de Groat, Nadelhaft, Morgan & Schauble, 1979; Lawn, 1966a, b; Sugimoto *et al.*, 1979). As is implied by the name, the nucleus ambiguus is less discrete than many other motor nuclei. Neurons of this nucleus are generally scattered throughout the reticular formation (Kalia & Mesulam, 1980). The nucleus ambiguus of mammals is normally divided into two compartments. The rostral region, which is often called the compact formation (Lawn, 1966a, b; Kobler, 1982) or the retrofacial nucleus (Gacek, 1975), provides motor innervation to the pharynx via the superior laryngeal nerve. The caudal or diffuse division is the source of nerves that carry efferents in the recurrent laryngeal nerve to the larynx (Kobler, 1983). Fourth and finally, in mammals all the motor nuclei are distinct and separate, unlike in the primitive condition, where there is a more or less continuous motor column (Barbas-Henry & Lohman, 1984; Sarnat & Netsky, 1981; Ulinski, 1986). In mammals the brainstem has been reorganized, with an elaboration, separation and reassociation of the motor nuclei. Of greatest significance is the association of the glossopharyngeal (IX) and vagus (X) nerves and the development of the nucleus ambiguus, the motor supply to the striated muscles of the mammalian palate, larynx and pharynx.

USE OF THE ORAL-PHARYNGEAL MUSCLES DURING FEEDING

A number of authors have noted basic similarities in feeding behaviour between mammals and reptiles. Most studies of feeding in amniotes focus on the action of jaw muscles, with few providing details on activities of the oral-pharyngeal apparatus. The feeding behaviour of lepidosaurian reptiles has been best studied among the reptiles (e.g. Gans, de Vree & Carrier, 1985; Gorniak, Rosenberg & Gans, 1982; Schwenk & Throckmorton, 1989; Smith, 1984; Throckmorton, 1976, 1980), but some data on chelonians exist (Bramble, 1980; Bramble & Wake, 1985). Both the Lepidosauria and Chelonia contain taxa that use the tongue in intra-oral transport and are most often compared with mammals. Feeding in birds is generally quite distinct (e.g. Zeigler, Levitt & Levine, 1980; Zweers, 1982), as is that of crocodiles (Busbey, 1989). The feeding behaviour of reptiles and mammals are summarized below, with focus on oral-pharyngeal structures during two major phases: intra-oral transport and swallowing.

Intra-oral transport

A four-phase jaw opening and closing cycle has been observed in some reptiles, especially chelonians and lizards, as well as many mammals (e.g. Bramble & Wake, 1985; Crompton *et al.*, 1977; Hiiemae, 1976, 1978; Hiiemae & Crompton, 1985; Hiiemae, Thexton & Crompton, 1978; Oron & Crompton, 1985; Schwenk & Throckmorton, 1989; Smith, 1984; Throckmorton, 1980). Higher primates show a similar, but modified, pattern (Hylander & Crompton, 1986). The four phases are slow opening, fast opening, fast closing and slow closing (Figs 12, 13). A stationary phase after fast closing is often present in reptiles (Gorniak *et al.*, 1982; Smith, 1984, 1986; Throckmorton, 1980). In addition, many mammals and reptiles exhibit a similar coordination between the phases of the jaw cycle

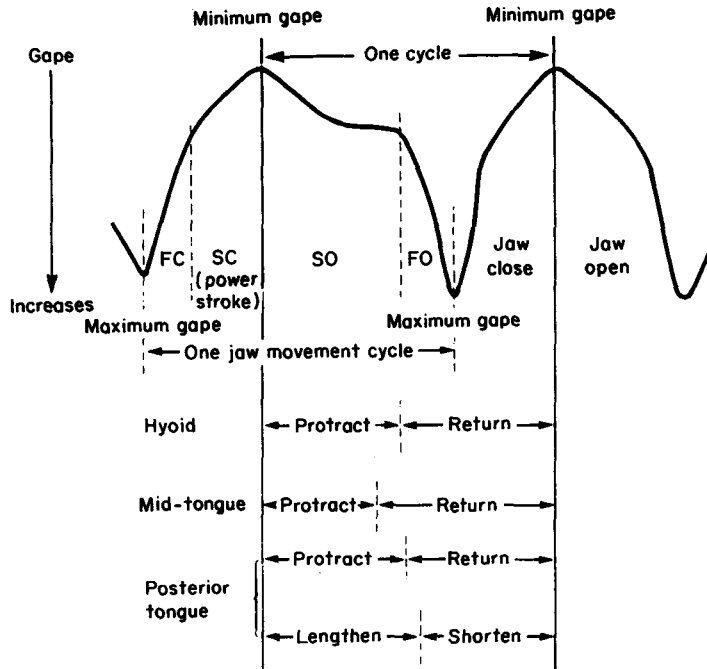


Figure 12. Basic mammalian transport/mastication cycle, characteristic of most non-primate mammals. Note the four-phase gape cycle and the general pattern of anterior movement (protraction) of the tongue and hyoid during the slow opening phase and the posterior movements during the fast open and closing phases. Abbreviations: FC, fast close; SC, slow close; SO, slow open; FO, fast open.' (Reprinted from Hiiemae & Crompton, 1985.)

and hyoid and tongue movements (e.g. Bramble & Wake, 1985; Hiiemae & Crompton, 1985; Hiiemae *et al.*, 1978; Schwenk & Throckmorton, 1989; Smith, 1984). During the slow opening phase the tongue and hyoid move forward; they move back during the fast opening phase and then begin to move forward again during closing phases (Figs 12, 13). A number of alternative transport patterns have been observed in amniotes, such as inertial feeding (e.g. crocodilians, varanid lizards, some birds; Busbey, 1989; Gans, 1969; Smith, 1982; Zweers, 1982) or the derived upper-jaw based transport of snakes (e.g. Cundall, 1983, 1987; Gans, 1961, 1983). While the four-phase cycle is common, it is by no means uniformly present. It is not clear whether tongue-based transport or some mechanism such as inertial feeding is primitive for amniotes (Olson, 1961).

One derived feature of mammals is that a relatively stereotyped power stroke or masticatory phase is incorporated into the cycle during slow closing. This power stroke most often involves lateral jaw movements. The addition of a lateral-to-medial power stroke is thought to be one of the most significant innovations of the mammalian masticatory apparatus and the functional explanation for much of the reorganization of the mammalian jaw muscles (e.g. Barghusen, 1973; Bramble, 1978; Crompton, 1989; Crompton & Hylander, 1986; Crompton & Parker, 1978; Davis, 1961). In mammals, food transport and processing are integrated into a continuous and relatively stereotyped process (Hiiemae, 1976, 1978). In contrast, in the reptiles studied, chewing or biting is

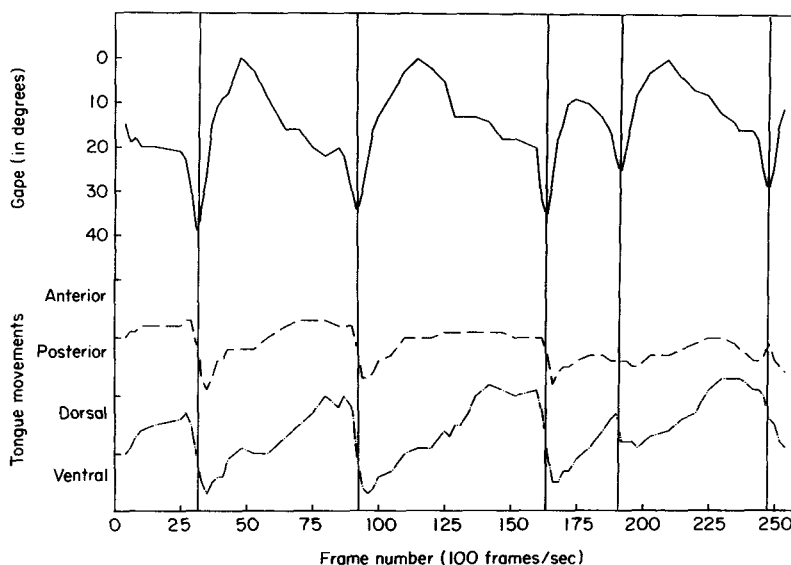


Figure 13. Jaw and tongue movements during food transport in *Utromastix aegyptius*. Cineradiographic film was taken at 100 frames per second. Small metal markers were placed in the tongue prior to filming to allow visualization of tongue movements (for details on method see Smith, 1984). Upper profile (solid line) shows jaw movement, dashed line represents tongue movement in anterior-posterior direction (protraction-return) and dotted line represents tongue movements in the dorsal ventral dimension (measured relative to a fixed upper jaw). Vertical lines indicate jaw movement cycles. Note the similarity to mammalian cycles in both gape profile and tongue coordination. The third full cycle represents a pharyngeal packing cycle. Note that the pharyngeal packing cycle follows a full gape cycle and that the difference between the full cycle and a packing cycle is apparent in the closing, slow opening and fast opening phases.

usually more irregular, generally taking place as independent chewing cycles that precede or interrupt the course of food transport.

Swallowing

Deglutition, or swallowing in its most general sense, consists of emptying the pharyngeal region or of passing food from the mouth into the oesophagus. Once in the oesophagus, peristalsis transports food into the stomach. In most reptiles pharyngeal emptying is accomplished by contraction of superficial throat musculature such as the *M. constrictor colli*, aided by other muscles of the neck and hyoid region (Smith, 1984, 1986). This activity pushes the hyoid apparatus up toward the braincase and cervical region and compresses the food posteriad through the pharynx to the oesophagus. A distinct stage, pharyngeal packing, transitional between typical transport cycles and pharyngeal emptying, is present in lizards (Smith, 1984, 1986). In this stage an upward and then backward motion of the posterior parts of the tongue and hyoid during slow opening serves to pack food sufficiently far back in the pharynx to ensure that the subsequent hyoid compression will drive food back rather than forward. Pharyngeal packing cycles are the only cycles in lizards where the tongue and hyoid move back during slow opening (Smith, 1984; Fig. 13). In *Varanus*, which lacks a free posterior portion of the tongue, pharyngeal packing is accomplished by distinct movements of the specialized hyobranchial apparatus (Smith, 1986).

Bramble & Wake (1985) describe swallowing in turtles, and although they use terminology different from that of Smith (1984, 1986), the behaviour is similar. In turtles, following intra-oral transport, the tongue sweeps up and then back along the roof of the mouth, pushing the bolus back into the pharynx during slow opening. This movement is followed by head elevation and pharyngeal compression via activity of external constrictors. Thus, both the pharyngeal packing and pharyngeal compression stages are present in turtles, but both are called swallowing by Bramble & Wake (1985). Emptying the pharynx by external constrictors aided by gravity is also observed in crocodiles (Busbey, 1989) and birds (Zweers, 1982) and must be considered primitive.

In mammals swallowing is a complex reflex, involving the coordination of a large number of muscles and nerves (Fig. 14; Bateman & Mason, 1984; Bosma, 1961; Crompton, 1989; Doty, 1968; Hiiemae & Crompton, 1985; Jean, 1984; Miller, 1982). Doty (1968) states that it is the most complex reflex that may be invoked by the stimulation of a single region in the central nervous system and that it is one of the first reflexes to develop *in utero* (at *c.* 10 weeks in humans). In non-primate mammals swallowing is incorporated into regular transport cycles as discrete additions to the masticatory cycle at the end of the slow open phase, leaving other parts of the masticatory cycle generally unchanged (Crompton, 1989; Hiiemae & Crompton, 1985). In *Macaca* swallowing occurs towards the beginning of jaw opening (Hylander & Crompton, 1986). In most mammals a swallow is preceded by an upward and backward movement of the tongue during slow opening, which, as in reptiles, drives the bolus back into the entrance of the pharynx (pyriform recess). The pyriform recess and pharynx are emptied by a reflex sequence of contraction of the palatal muscles, posterior tongue muscles and pharyngeal elevators and constrictors. The mammalian swallow is a stereotyped activity, involving the coordination of many tongue, hyoid and pharyngeal muscles (Fig. 14). The muscles most significant in actually producing "the swallow" are the unique mammalian pharyngeal elevators and

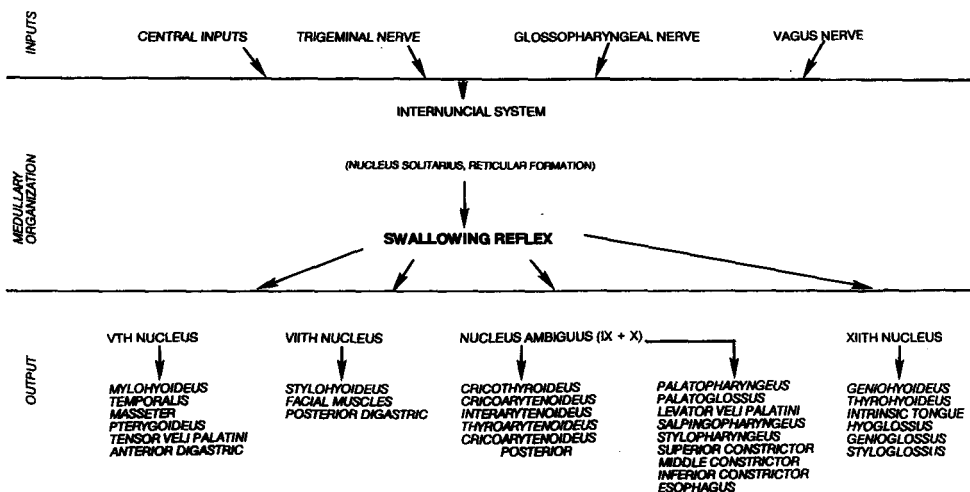


Figure 14. Diagram of nerves and muscles significant in the mammalian swallow. All the muscles listed are recruited during the swallowing reflex. Simplified and redrawn from Doty (1968).

constrictors. The swallowing muscles are for the most part innervated by nerves whose cell bodies lie in the nucleus ambiguus: cranial nerves IX and especially X.

Four behavioural synapomorphies distinguish swallowing in the Mammalia from that reported for reptiles, and indeed from all non-mammalian tetrapods. First, swallowing results primarily from the activity of the internal pharyngeal elevators and constrictors, none of which exist in non-mammalian amniotes. Second, mammals swallow by means of a highly coordinated and stereotyped reflex contraction of the palatal, tongue, pharyngeal and hyoid muscles rather than by a gradual and prolonged contraction. Third, the primary nerve effecting swallowing in mammals is cranial nerve X (although other nerves are involved). In reptiles it is primarily nerve VII. And fourth, swallowing is integrated into the basic transport cycle, which is integrated with the chewing cycle. In reptiles, pharyngeal compression is a distinct stage, following a number of transport and packing cycles. These morphological, behavioural and neurological differences might provide a rationale for restricting the term 'swallowing' or 'deglutition' to mammalian behaviour and referring to the analogous action in other tetrapods as 'pharyngeal emptying'.

DISCUSSION

Transformation of the mammalian oral-pharyngeal region

Morphological studies of homology

Three categories of structure emerge in a comparison of the mammalian and reptilian oral-pharyngeal region. First are the structures that are clearly homologous in reptiles and mammals, with little transformation of function and minor to moderate changes in form. These include the muscles and bones of the masticatory system, some extrinsic tongue muscles, and the supra- and infra-hyoid muscles. Second are structures for which homology may be postulated on the basis of innervation or development, but which have undergone major morphological and functional changes. This group includes, for example, the facial musculature, the tensor tympani and tensor veli palatini muscles and two of the three auditory ossicles. The above two kinds of structure have received the most attention from previous workers. The third category includes a large group of structures, primarily muscles, that have no obvious homologues in the Reptilia on the basis of innervation, developmental form or positional criteria. These structures include virtually all the palatal and pharyngeal muscles (and the facial muscles, according to Edgeworth, 1935). The evolution of this third category of structures has received virtually no previous attention, yet the origin of seemingly neomorphic structures raises the most general questions about the evolution of form. The pharyngeal apparatus of mammals is truly a distinguishing feature and is one of the few examples in vertebrate morphology of the differentiation of an entirely new neuromuscular apparatus. The origin and significance of these latter structures will form the topic of much of the discussion to follow.

There are a few structures in the mammalian oral-pharyngeal region whose homology has not previously been considered in detail. For example, three kinds of data indicate that the stylopharyngeus muscle in mammals and the

branchiohyoideus muscle in reptiles may be homologous. This homology is suggested on the basis of innervation, as the two are among the few muscles in either taxa innervated by cranial nerve IX, the glossopharyngeal. Furthermore, developmental data on marsupials (Jouffroy *et al.*, 1971) show that the stylopharyngeus is similar to the branchiohyoideus in position and connections early in development. Although Edgeworth (1935) does not recognize this particular homology, he does state that the stylopharyngeus muscle in mammals develops from a muscle primordium that is different from other pharyngeal muscles. In reptiles the branchiohyoideus runs between the second and third branchial arches. The stylopharyngeus in mammals originates from the styloid process, which is derived from a portion of the second arch. Thus, positional data also suggest homology. If this hypothesis of homology is correct, it further illustrates the uniqueness of the mammalian musculature innervated by the vagus nerve: the stylopharyngeus is the single pharyngeal muscle not innervated by X and is also the only pharyngeal muscle with an apparent homologue in reptiles.

Homologies of structures in the central nervous system are more complicated. A number of authors have traced neurons of the vagus nerve to ventral or lateral nuclei in reptiles and birds. These are typically named the nucleus ambiguus, following the terminology defined for the Mammalia. However, in most of these studies homology of efferent components and targets has not been demonstrated. The nucleus ambiguus received its name because of its relatively poorly defined morphology in mammals. The presence of this nucleus is even more ambiguous when non-mammalian tetrapods are considered. Because the primitive condition of the branchial motor nerves is an undifferentiated column of cell bodies, and there is variability in the subdivision of this column in the Reptilia, it is possible that motor nuclei containing cell bodies of nerves forming either IX or X became differentiated independently in the different tetrapod groups. Until the homology of targets and components has been demonstrated, the use of the term nucleus ambiguus is probably unwarranted for non-mammalian tetrapods.

The variation in tongue form and movement pattern is so large within tetrapods that it is difficult to determine the primitive condition of the tongue on the basis of comparison among extant vertebrates. Schumacher (1973) and Sewertzoff (1929) suggest that the condition in crocodylians, with little tongue musculature and a reduced hyoid apparatus, is primitive. But in most amniote groups, including birds and some lizards, chelonians and amphibians, the tongue is supported significantly by the hyoid apparatus. In some of these animals virtually all tongue movements are produced entirely by movements of or within the hyoid apparatus. This condition is quite distinct from that of mammals where the tongue base is supported by the hyoid, but the tongue body is itself structurally and to some extent functionally independent. The widespread occurrence in tetrapods of the tongue as a structure with significant hyoid support suggests that this condition is primitive (Davis, 1961).

In mammals and most lizards the tongue is a muscular-hydrostatic organ. For the most part, movements and especially changes in shape are produced by interactions between various intrinsic and extrinsic tongue muscles, with little direct influence of the hyoid apparatus (Kier & Smith, 1985; Smith & Kier, 1989). If the primitive condition in amniotes is a tongue with little independent movement, then an independently mobile tongue may have evolved

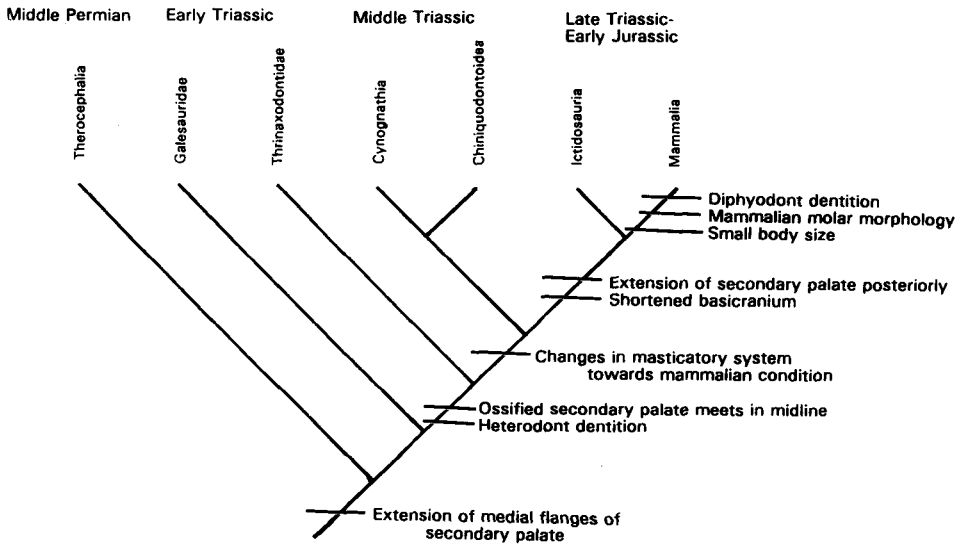


Figure 15. Evolution of some features of interest in reconstructing the morphology and function of the oral-pharyngeal region in mammal-like reptiles. Phylogeny from Hopson & Barghusen (1986); characters from that paper and from Barghusen (1986).

convergently in mammals and lizards*. This question is important in testing hypotheses of conserved neuromuscular patterns (see below).

The fossil record

With the exception of the ossified secondary palate, the fossil record provides little direct evidence on the evolution of any of the structures discussed above. However, a number of inferences about the evolution of the oral-pharyngeal region can be made on the basis of the fossil record of mammals and their ancestors (Fig. 15). A partially ossified secondary palate appears early and a number of times in parallel in therapsid evolution, in many cases before the specifically 'mammalian' masticatory apparatus appears (i.e. in some therocephalians and cynodonts in the early Triassic; Hopson & Barghusen, 1986). A complete, ossified secondary palate, heterodont dentition and jaw adductors apparently similar to those of mammals are seen in the cynodont *Thrinaxodon*. On functional grounds it would be expected that a highly mobile tongue and some kind of cheek muscle also evolved with mastication (Brink, 1956; Davis, 1961). Pharyngeal anatomy is more difficult to reconstruct, but the evolution of mammalian pharyngeal muscles might be correlated with changes in the cranial base. The most important of these may be the shift in morphology of the pterygoid region from a reptilian to a mammalian arrangement (i.e. loss of pterygoid flanges, development of a pterygoid hamulus), the shortening of the basicranium (reduction of length of basisphenoid and basioccipital) and the evolution of a styloid process and mammal-like mastoid region. The shortening of the basicranium and changes in the pterygoid region do not begin to appear

*In this context it is important to recognize the distinction between homology of structure and homology of state. It is undeniable that the tongue is homologous in mammals and lizards; but the tongue as an independently mobile organ may not be. In this case the situation is similar to that of the bird and the bat wing. They are undeniably homologous as forelimbs, but are not homologous as wings.

until the late Triassic (with the unnamed group comprising the Ictidosauria + Mammalia; Hopson & Barghusen, 1986). Finally, mammalian tooth occlusion, diphyodont dentition (suggesting suckling of young; Brink, 1956; Guillette & Hotton, 1986; Hopson, 1973; Long, 1972; Pond, 1977, 1983) and small body size (suggesting very high metabolic rate and the possible requirement of breathing while masticating or suckling, Crompton *et al.*, 1978; Guillette & Hotton, 1986) appear with the origin of the Mammalia, also in the Late Triassic.

Although much work is required to correlate the evolution of soft tissues with hard tissues, some inferences on the evolution of the oral-pharyngeal region may be made from these data. First, because the evolution of the hard palate occurs early and in parallel in numerous therapsid lineages, it appears to be independent of specific changes in the masticatory apparatus. More importantly, it develops long before changes appear in the basicranium that may be associated with the pharynx. It is unlikely that the development of the hard palate is necessarily associated with the pharyngeal reorganization of mammals. Second, because a number of the pharyngeal muscles arise from the base of the skull or pterygoid region, it might be hypothesized that the evolution of these pharyngeal muscles accompanied the changes in the base of the skull occurring in the common ancestor of the Ictidosauria + Mammalia (cited by Hopson & Barghusen, 1986, as synapomorphies of these two groups). It is usually hypothesized that suckling arose with the Mammalia (and the small body size and diphyodont dentition; e.g. Hopson, 1973; Pond, 1977). If the above inference is correct, reorganization of the pharyngeal region may have, in part, preceded suckling. These hypotheses are tentative, and require further reconstruction of fossils with particular attention paid to this region. Some areas for focus would include the styloid and mastoid process area, the points of origin of several important pharyngeal muscles in mammals, and the hyoid apparatus. Additionally, although hyoid bones are rare in the fossil record, the hyoids of mammal-like reptiles or archosaurs might help in assessing the transformation of lingual support. For example, some type of relatively robust entoglossal process, projecting anteriorly from the hyoid bone, may be indicative of a tongue with significant hyoid support.

Development

One key to understanding the evolution of mammalian pharyngeal muscles may lie in studies of development. Are mammalian pharyngeal muscles derived from the branchial muscle plate and therefore homologous with amphibian muscles, or are they, as claimed by Edgeworth (1935), developed from an entirely new primordium and therefore neomorphic? The answer to these questions must await detailed comparative studies of the development of pharyngeal muscles in mammals, which, relative to structures of the craniofacial skeleton, have received minimal attention. Data on the source of the tissues forming pharyngeal muscles or the mechanism of patterning of the pharyngeal muscles might provide general information on the evolution of craniofacial patterning and the generation of morphological novelties.

Birds possess the primitive condition of the oral-pharyngeal region, so experimental work utilizing avian chimeras cannot resolve the issue of the origin of pharyngeal muscles. One result of avian chimera experiments makes the issue of the embryonic origin of pharyngeal muscle tissues particularly intriguing. In

birds it appears that muscle patterning is provided by the connective tissues rather than by the muscle tissue (Noden, 1983a, b). In birds the larynx and the area with efferent innervation from X marks the transition between the portion of the head where the connective tissues are derived from neural crest cells and the portion where the connective tissues arise from somites (Noden, 1983a, b, 1984). In birds, all muscles anterior to the larynx receive their connective tissues from the neural crest and are therefore patterned by the neural crest. The pharynx in mammals develops from tissues that lie close to or on this boundary. Is one of the sources of pharyngeal muscle patterning in mammals the neural crest? Speculations on the possible role of the neural crest in the innovations of the mammalian pharynx are interesting, given its apparently major role in other cranial novelties in vertebrates (Gans & Northcutt, 1983; Northcutt & Gans, 1983).

Nervous system evolution

One of the notable features that distinguishes mammals from other tetrapods is the reorganization of the motor nuclei of the brainstem. The major characteristic of mammals is the development of discrete motor nuclei to 'special visceral' muscles, the striated muscles of the branchial arches (Kappers, Huber & Crosby, 1936; Sarnat & Netsky, 1981). In other tetrapods, these motor nerves are in a broadly overlapping column with a variety of functional components. In mammals the motor nucleus of the facial nerve and especially the nucleus ambiguus are spatially distinct nuclei with a large series of striated muscles as their efferent targets. The reorganization of the cranial motor nuclei of mammals is often attributed to the increased complexity of the mammalian larynx (e.g. Kappers *et al.*, 1936), but there is relatively little elaboration of laryngeal musculature in most mammals. Furthermore, the larynx receives innervation from the less elaborate caudal portion of the nucleus ambiguus (the caudal portion is well developed in bats, with their elaborate larynx; Kobler, 1983). The larger, more rostral, compact division of the nucleus ambiguus innervates the pharynx (Lawn, 1966a, b). The evolution of the nucleus ambiguus is most likely related to the differentiation of the pharyngeal apparatus. Ulinski (1986: 155) argues that general functional changes in the organization of motor systems occurred during the reptile-mammal transition. He claims that "well-developed specific motor nuclei may be characteristic of mammals" (p. 155). Ulinski relates these changes in the mammalian motor system to increased modulation of movement and elaboration of sensory feedback and central control pathways. The pattern of reorganization observed in the nerves innervating the swallowing apparatus may also be part of a more general neuromuscular transformation.

Conservatism of neuromuscular control

The similarity of jaw and tongue movement profiles in a number of tetrapods has led to suggestions that there is a basic vertebrate pattern of feeding that reflects retention of a primitive pattern of neural control. For example, Bramble & Wake (1985: 242) state "the many similarities shared by the transport cycles of mammals and reptiles prompt the specific question, could the mammalian masticatory cycle have evolved from the primitive chewing cycle of reptiles with relatively little overall change in neuromotor programming? We suspect that the

answer may be yes. A demonstration that the mammalian and reptilian transport cycles are based on similar motor programming would be of considerable theoretical importance. It would suggest that the evolution of the complex mammalian masticatory system was accomplished through minimal change in associated neuromotor mechanisms but relatively enormous alterations in the peripheral feeding structures (bones, muscles, dentition). Whether this could be a more general pattern in the functional transformation of morphological complexes is of obvious interest."

As summarized by Bramble & Wake (1985), there is great interest in the ways in which neural control systems evolve in vertebrates. Several recent studies discuss the conservatism in the neuromuscular system in both locomotor and feeding behaviour (e.g. Bramble, 1980; Bramble & Wake, 1985; Jenkins & Goslow, 1983; Lauder & Schaffer, 1988; Peters & Goslow, 1983; Roth & Wake, 1989; Schwenk & Throckmorton, 1989). Rarely do hypotheses of conserved neuromuscular control patterns contain specific predictions that would distinguish the hypotheses from an alternative hypothesis, positing convergence due to similar functional requirements. Indeed, few discussions of conservative motor patterns contain explicit alternative hypotheses. In the case of the primitive feeding mechanism, the alternative hypothesis of functional convergence would propose that in animals with lingual-based food transport, the tongue moves forward and under the food during the closed and slow opening phases because the teeth and palate hold the food in place at this time, allowing the tongue to slide forward relative to the food. The tongue and bolus move back during a fast opening phase because this is the time when the oral cavity is enlarged to allow unimpeded backward movement of a food item. The similarities in jaw and tongue movement profiles observed between reptiles and mammals are explained by simple functional requirements.

The hypothesis of neuromuscular conservatism focuses on the most basic component of the feeding cycle, vertical movements of the jaws in opening and closing. The variety of medio-lateral and antero-posterior movements during chewing strokes are generally ignored. There is much more variation and complexity in the total orbit of jaw movements in tetrapods than simple jaw opening and closing, and these complex movements require neuromuscular control patterns that are complex, specific and derived (e.g. Crompton & Hylander, 1986; Crompton & Parker, 1978; de Vree & Gans, 1975; Franks *et al.*, 1985; Gans *et al.*, 1985; Gans, de Vree & Gorniak, 1978; Gorniak, 1977; Gorniak *et al.*, 1982; Herring, 1976; Hiimae, 1978; Kallen & Gans, 1972; Smith & Redford, 1990; Thexton, 1984; Weijs & Dantuma, 1975, 1981). It is the medio-lateral power stroke that is, in fact, the hallmark of mammals and responsible for the "relatively enormous alterations in the peripheral structures" referred to by Bramble & Wake (1985: 242). It has undoubtedly involved major and significant changes in neuromotor mechanisms (Székely & Matesz, 1989).

The two competing hypotheses—retention of a primitive motor pattern versus convergence due to functional demands—are not distinguishable solely on the basis of comparison of movement patterns or electromyographic activity, but instead must be tested by examining the phylogenetic distribution of features of the neural and muscular system. For example, if the primitive pattern in amniotes is some form of inertial feeding, then lingual-based transport is independently derived in mammals and extant reptiles. If so, the similarity of

behaviours beyond jaw opening and closing cannot be traced to a conservative neuromuscular pattern but instead must be explained by functional convergence. The primitive mechanism of tongue movement—via intrahyoid movements or via intrinsic lingual musculature—is also of importance. In these two patterns of movement, fundamentally different muscles, and in some cases mediation through different motor nerves, produce the same tongue movements. If hyoid-produced lingual movements are primitive for tetrapods, the similarity of tongue movement patterns in mammals and lizards cannot be attributed to retention of a primitive neuromuscular pattern but again must be the result of functional convergence. Confirmation of the hypothesis of neuromuscular conservatism will require, like any other hypothesis of homology, rigorous analysis of characters and the mapping of these characters on a phylogeny.

Leaving aside questions concerning the masticatory system and food transport, it is undeniable that the evolution of swallowing involved enormous changes in neuromuscular mechanisms of mammals. The swallowing apparatus has undergone a virtual revolution in mammals that involves the evolution of a set of new striated muscles of unique function, a complete change in the pattern of innervation by cranial nerve X, and the reorganization of the motor nuclei of the brainstem. Thus, a major and unique neuromuscular innovation has been imposed upon a primitive system.

Are reptiles the appropriate outgroup?

In discussions of the evolution of the mammalian feeding apparatus, the condition found in modern reptiles is used typically as the outgroup condition for reconstruction. Where obvious similarities in hard parts exist in the therapsid ancestors of mammals and living reptiles the practice can readily be justified. However, several lines of evidence indicate that the condition of the hyobranchial and pharyngeal region in the living Reptilia (including birds) and Mammalia is so divergent that they may have arisen independently from an amphibian-like condition.

One of the most important features pointing to an independent derivation of the hyopharyngeal region in mammals and reptiles from an amphibian-like condition is the fact that no reptile possesses internal pharyngeal musculature, whereas such musculature does exist in both mammals and amphibians. Pharyngeal muscles, innervated by the vagus nerve, are present in larval amphibians (Piatt, 1938) and adult salamanders such as "*Amblystoma*" *punctatum* (cephalo-dorso-subpharyngeus; Piatt, 1935, 1938) and *Thorius dubius* (dorso-pharyngeus; R. E. Lombard, personal communication). These muscles are similar to those of mammals in that they lie between the hyoid apparatus and pharyngeal wall, are innervated by the vagus nerve (X), and have two layers—a more or less longitudinal (oblique) layer and a circular muscle layer. They differ in form from those of mammals but do provide a potential muscular precursor for the mammalian condition. If these are homologous muscles, then the extant Reptilia are derived in having lost the striated pharyngeal musculature innervated by X. It should be noted that some authors, such as Edgeworth (1935), claim that there are no homologues of the mammalian pharyngeal muscles in any non-mammalian tetrapod.

Jouffroy *et al.* (1971) also argue that the hyoid and laryngeal regions of reptiles

and mammals are derived independently from an amphibian-like condition rather than a reptile-like condition. They advance two major lines of evidence to support this argument. First, in monotremes the branchial apparatus consists of four arches: the hyoid and three branchial arches. No extant reptile possesses more than three arches: the hyoid and two branchial arches. They conclude that the primitive mammalian condition is more primitive than that of reptiles and approaches the condition observed in extant amphibians. Second, they point out that the laryngeal muscles of mammals and amphibians are innervated by two homologous branches of cranial nerve X, the superior and inferior (or recurrent) laryngeal nerves. In contrast, in reptiles the innervation of the larynx is via a single laryngeal nerve that is a branch of cranial nerve IX.

The arrangement of the nuclei of the brainstem of amphibians, reptiles + birds, and mammals may also point to a greater divergence between reptiles and mammals than has been assumed in previous discussions. The most complete tracings of the brainstem nuclei in amphibians are those of salamanders (Roth *et al.*, 1988; Wake *et al.*, 1988). The cell bodies of nerve X to striated muscles lie in a brain stem nucleus that resembles the nucleus ambiguus of mammals in position and composition. But, in salamanders, like reptiles and unlike mammals, there remains extensive overlap between the motor nuclei of VII, IX and X.

The combined evidence of the nervous system, hyobranchial skeleton and pharyngeal musculature lends support to the hypothesis that the hyobranchial and laryngeal apparatus (muscles, nerves and bones) diverged from a common condition more closely resembling extant Lissamphibia than any extant member of the Reptilia. If so, in the primitive condition, pharyngeal muscles innervated by both IX and X were present. The Reptilia did not incorporate musculature innervated by the vagus nerve into the pharynx or larynx of adults, whereas in the line leading to mammals, pharyngeal musculature innervated by the vagus nerve was retained in adults. If correct, it is possible that an early dichotomy in the swallowing mechanism was established, with internal constrictors in the line leading to mammals and external constrictors present in the "Reptilia". If so, it is possible that the muscles of the second arch of mammals may never have been swallowing muscles, but may have been associated with the facial region early in evolution*. If the dichotomy in terrestrial feeding mechanisms between the Reptilia and the line leading to mammals was this early and this fundamental, then behavioural comparisons with living reptiles may tell us little about the primitive condition in mammals.

Three evolutionary hypotheses may be derived from these data, which can only be resolved by further study: (1) that the Mammalia (and their therapsid ancestors) and the Reptilia are independently derived from amphibian ancestors (therefore violating the Amniota); (2) that the Mammalia and Reptilia are a monophyletic group, but the pharynx of this ancestor resembled the amphibian condition and the Reptilia lost pharyngeal musculature, most motor branches of X, and a branchial arch, whereas the Mammalia retained and elaborated the primitive muscular condition; or (3) that the loss of the pharyngeal musculature accompanied the transition to land in the common ancestor of reptiles and the

*It is important to note that no living amphibian has been shown to possess a mammal-like swallowing mechanism and that, even if mammals arose from an amphibian-like pharyngeal condition, the mammalian pharynx and swallowing apparatus are still characterized by major neuromuscular innovations.

mammalian ancestor. Living reptiles retain the primitive condition, whereas mammals have re-evolved a new series of structures, perhaps out of embryological remnants of the pharyngeal musculature. This latter view is the most prevalent, but may, in fact, be the least plausible.

The hypothesis of an independent origin of the mammalian and reptilian oral-pharyngeal condition resembles in some respects the conclusions of Lombard & Bolt's (1979) analysis of the evolution of middle ear structures in tetrapods. In this paper Lombard & Bolt argue that the tympanic membranes and tympanic process in recent mammals, reptiles + birds, and frogs are not homologous and that the complex middle and inner ear apparatus evolved at least three times, most importantly in parallel in the two amniote lines we are most concerned with here: reptiles + birds, and mammals. Lombard and Bolt's analysis is also noteworthy in the present context because of its methodology. In this paper a careful morphological assessment and cladistic analysis of the characters of the middle and inner ears have provided a compelling hypothesis of the evolution of this complex morphological apparatus, largely in the absence of fossil data. It may be that a similar detailed morphological and cladistic analysis of the neuromuscular components of the oral-pharyngeal apparatus in tetrapods will resolve questions about the evolutionary transformation of this region.

Functional significance

The morphological innovations of the mammalian pharynx are more extensive and more distinctly mammalian than the modifications and reorganization of the jaws, teeth and masticatory muscles. The basic features discussed here are present in all extant mammals: monotremes, marsupials and placentals. The fact that monotremes possess these features is significant and supports a claim that this neuromuscular reorganization is one of the most fundamental mammalian adaptations. The common condition in monotremes, marsupials and placental mammals shows that these adaptations are either ancient or that monotremes share a relatively recent common ancestry with therians (e.g. Kielan-Jaworowska, Crompton & Jenkins, 1987).

What are the possible functional or adaptive bases for the reorganization of the pharyngeal apparatus? In extant mammals the oral and pharyngeal regions are functionally significant in at least four distinct behaviours: (1) separation of the air and food passages, (2) mastication, (3) swallowing and (4) suckling. In addition, vocalization and thermoregulation are significant functional features of the mammalian arrangement in many extant groups, but are not as closely tied to the pharyngeal region as to other areas of the oral cavity and larynx.

The separation of the airway and foodway, conferring the ability to breathe and feed simultaneously, is the most often cited hypothesis for the development of the palatal/laryngeal complex in mammals (e.g. Biewener, Soghikian & Crompton, 1985; Davis, 1961; MacLean, 1986; Romer, 1970). Negus (1931, 1949), in his monumental studies on the evolution of the larynx, claims that the separation of the air and food passages had little to do with respiration *per se*, but instead relates to the ability to retain olfactory acuity during mastication. To counter the views that see the palate largely relating to respiration, Thomason & Russell (1986) discuss the mechanical effects of the development of the hard palate. They present a convincing argument for the mechanical advantages of

partial as well as complete closure. Although the above functional relations may be important, and are not mutually exclusive, two points suggest that they have little to do with the neuromuscular innovations discussed here. First, the functional requirements of the separation of the airway and foodway do not explain the extensive neuromuscular reorganization of the pharynx. Second, fossil evidence indicates that the partial and then complete closure of the palate occurred in many lines in parallel and preceded other aspects of oral-pharyngeal reorganization by millions of years. The evolution of the hard palate is an important topic, but it appears to be independent of pharyngeal evolution.

In extant mammals, a number of aspects of the pharynx appear to relate to functional requirements of mastication and intra-oral food breakdown. Mastication utilizes muscular cheeks to keep food in the oral cavity and to return food to tooth surfaces. The evolution of facial musculature, in particular the buccinator muscle, might be largely attributed to these demands. Additionally, mastication involves mechanical breakdown of food into small pieces and mixing the food with saliva. It is probably of some advantage to keep this food/saliva mix from coating the nasal and middle ear cavities (Davis, 1961). Whereas these two cavities are continuous with the oral cavity in reptiles (except crocodylians), the mammalian palate separates the oral from the nasal and middle ear cavities.

The mammalian swallowing process is one of the most important functional consequences of the reorganization of the neuromuscular complex discussed here. Swallowing best explains the sum of the neuromuscular innovations of the mammalian pharynx, but the reason for the origin and evolution of the specialized swallowing complex in mammals is obscure. Mastication and swallowing are in some sense functionally related. The configuration of the mammalian pharynx, which results in a narrow foodway, may require the breakdown of food into relatively small packets before swallowing (in contrast to the reptilian condition where large packets may be consumed whole—Smith, 1984). Reciprocally, the development of mastication may have allowed the pharynx to take on the mammalian configuration and function effectively during swallowing. The differences between mammals and non-mammalian tetrapods centre on the difference between an apparatus that rapidly propels small food portions into the oesophagus (mammals) and one that can propel large items, albeit slowly (non-mammalian forms).

Finally, nourishment of the young by the female (suckling) is one of the most characteristic mammalian adaptations. The ability to suckle is present in monotremes as well as marsupials and placentals (Griffiths, 1988; Griffiths, McIntosh & Leckie, 1969; Griffiths & Slater, 1988) and is a characteristic shared by all mammals. For suckling to occur, a seal must be present between the airway and oral cavity and the teat and the mouth, and a mechanism must exist to create suction or expression of milk. The oral-pharyngeal configuration provides for these requirements, in particular the lips and cheeks, the hard and soft palate, the upper pharynx and the tongue, and the specialized crossing of the airway may be more important in suckling than in adult feeding. While it may be reasonable to hypothesize that many of the innovations of the pharynx may relate to suckling, the entire series of pharyngeal constrictors and elevators are probably more important in swallowing. Few experimental studies on the functional morphology of suckling exist (Ardran, Kemp & Lind, 1958; Brake, Wolfson & Hofer, 1979; Crompton & German, in preparation; Gordon &

Herring, 1987) and it is difficult to document the precise significance of oral-pharyngeal reorganization for suckling behaviour patterns. Further, although it is clear that there is diversity of suckling mechanisms within mammals, the primitive condition of the suckling apparatus is not obvious. Because of the differences in the form of the neonate, it would be particularly interesting to compare adaptations for suckling in monotreme, marsupial and placental mammals.

CONCLUSIONS

Despite the fact that a specific scenario of evolution of the oral-pharyngeal region is difficult to produce, this reorganization in mammals is more far reaching in effect than the separation of the oral and nasal cavities. The resultant morphology is central and crucial in virtually all mammalian oral behaviours: respiration, vocalization, mastication, suckling and swallowing. The integration is so complex that the identification of a single sequence of causality is probably impossible. The most useful type of data to aid in distinguishing the important factors in the evolution of the system would be cases where some parts of the complex are present in the absence of others. Unfortunately no such conditions have been identified among living organisms. Monotremes, the most primitive living mammals, possess all the essential elements of the mammalian oral-pharynx; no living reptiles show intermediate conditions, and no fossils provide clear cut evidence on the evolution of the behavioural, muscular or neural structures of interest. For these reasons the exact evolutionary events important in the evolution of the mammalian oral-pharynx remain elusive.

Four types of data would contribute significantly towards understanding the evolution of this system, and it is hoped that this review will stimulate such work. First, further examination of fossils for data on the origin of some of the structures discussed above would be of interest. Hyoid bones provide some evidence on the condition of the tongue, and studies of the cranial base might allow inferences on pharyngeal musculature (e.g. Barghusen, 1986). Second, detailed comparative and cladistic analyses of the form and innervation of structures such as the pharynx, tongue and hyobranchium and their muscles would produce more precise hypotheses on homologies versus homoplasies (e.g. Lombard & Bolt, 1979). It appears particularly important to include members of the Lissamphibia in such analyses. Results of such analyses would be significant in distinguishing functional patterns that are conservative from those that are independently derived. Third, comparative embryological and neurological studies of this region would assist in identifying potential homologous structures. Fourth, more functional studies of oral behaviours such as food transport, suckling and swallowing in a variety of vertebrates would provide data on the functional significance of the morphological differences between mammals and non-mammalian tetrapods.

The oral-pharyngeal region is of central functional significance in mammalian feeding, and without an appreciation of the transformations of this system there are major gaps in our understanding of the important events in mammalian evolution. The muscular and neuromuscular reorganization in mammals is tremendous, producing an entirely neomorphic apparatus. A resolution of the question: what development processes produced this muscular reorganization?

might lead to new hypotheses on the generation of morphological innovations. And finally, entirely new neuromotor patterns have evolved. This neural reorganization has involved the appearance of new muscles, new patterns of peripheral innervation and central nervous system reorganization. It is a dramatic case of radical innovation in the neuromuscular system and bears on recent discussions of the ways that neuromuscular systems evolve.

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