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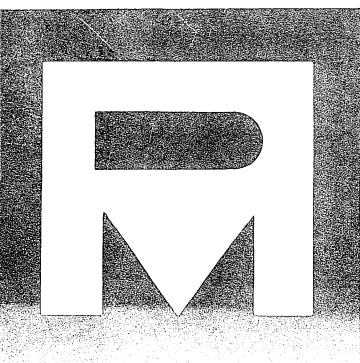
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THE ANATOMY AND INTERNAL ARCHITECTURE OF THE MUSCLES OF MASTICATION IN DIDELPHIS MARSUPIALIS

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ABSTRACT

The anatomy and internal architecture of the jaw musculature in *Didelphis marsupialis,* the American opossum, was studied using a combination of dissection and thick sectioning techniques. Since the purpose of this investigation was to provide detailed anatomical information as a basis for subsequent functional studies of jaw activity, all muscles associated with normal feeding and ancillary oral behaviour are described. These muscles are the temporal, masseter, pterygoids, digastric, mylohyoid, the remaining suprahyoid muscles and part of the extrinsic tongue musculature.

In mammals, the jaw muscles medial to the superficial masseter are classically regarded as the temporal, masseter and zygomatico-mandibular; however, no structural justification for such a division can be found in *Didelphis.* With the exception of the outermost layer of the adductor mass which is differentiated as a discrete superficial masseter, the temporal and masseteric part of the adductor musculature is a single unit converging from an extensive origin on bone and fascia to insert onto the coronoid process or its associated tendon. This musculature is described as consisting of three parts: an external adductor originating from the temporal fascia, the zygomatic arch and the masseteric fascia and inserting onto the external surface of the coronoid process, its tendon and the ramus of the lower jaw; an internal adductor originating primarily from the wall of the cranium and inserting onto the inner surface of the coronoid process; and a posterior adductor, the fibers of which pass anteriorly from the cranium posterior to the temporo-mandibular joint to insert onto the posterior border of the coronoid process and the most posterior part of its tendon. The fibers in each part have a different orientation but are not

separated into discrete muscles. This division is for descriptive purposes only and no homologies are implied with the similarly named muscles of reptiles.

The superficial masseter is a large, fan-shaped muscle extending from a tendinous origin on the maxilla to the inferior surface of the inflected mandibular angle where it has a thick, fleshy insertion.

The remainder of the adductor musculature in the opossum consists of a very small external and a thick internal pterygoid muscle. The former inserts into the articular capsule of the temporo-mandibular joint as well as into the condylar neck. The latter has a long, almost linear cranial origin extending posteriorly from the palate toward the temporo-mandibular joint. The fibers pass inferolaterally to insert on the upper surface of the inflected angle.

The anatomy of the suprahyoid muscles in the opossum is essentially the same as in eutherian mammals. All the muscles gain part, if not all, of their attachment to the hyoid through a thick, crescentic tendon formed by the fusion of the central tendons of both digastrics.

No definite conclusions can be drawn as to the exact function of these muscles on the anatomical evidence alone. However, their position, internal architecture and relative size are suggestive: the external and internal adductors probably have the dual function of suspending the lower jaw from the cranium and adducting the jaw against resistance. The nearly horizontal orientation of much of the posterior adductor is evidence that it can, in addition, act as an effective retractor, with the superficial masseter as its antagonist. In addition to protracting the mandible, the superficial masseter may have a role in producing lateral movement in conjunction with the pterygoids or the adductors. Finally, the suprahyoid musculature in *Didelphis* probably functions, as in other mammals, to control the movement of the hyoid apparatus, the larynx and epiglottis, and the lower jaw relative to the hyoid. In addition, the mylohyoid, geniohyoid and genioglossus have an important action in elevating and depressing the floor of the mouth and the tongue.

INTRODUCTION

Didelphis marsupialis belongs to an ancient family of marsupials that first appeared in Late Cretaceous time (Clemens, 1968). An understanding of both the anatomy and function of its jaw musculature may aid in interpreting this system in Mesozoic mammals and in reconstructing the basic plan from which the jaw musculature of Eutheria differentiated. The primary purpose of this paper is to provide a full description of the anatomy and internal architecture of the jaw musculature in *Didelphis* as a basis for later consideration of its functional and evolutionary contexts.

The group of muscles innervated by the fifth cranial nerve, the trigeminal, and often referred to as "the muscles of mastication", constitutes the greater part of the jaw musculature in mammals. These muscles are the M. temporalis (temporal), the M. massetericus (masseter, normally divided into two parts, the M. massetericus superficialis or superficial masseter and the M. massetericus profundus or deep masseter), the M. pterygoideus internus (internal or medial pterygoid), the M. pterygoideus externus (external or lateral pterygoid) and two smaller muscles, the M. mylohyoideus (mylohyoid) and the anterior belly of the M. digastricus (digastric). For practical purposes the whole digastric is regarded as a muscle of mastication. All these muscles act in the initiation and control of the movements of the lower jaw and so are responsible for most masticatory activity involving mandibular movement. However, the mechanisms of ingestion, mastication and deglutition are also dependent on other ("accessory") muscles of mastication. These can be broadly divided into two groups. The first includes the M. geniohyoideus (geniohyoid), the M. genioglossus (genioglossus), the M. buccinatorius (buccinator) and the M. orbicularis oris (orbicularis oris). All these muscles are attached to one or both jaws. The second group, the remaining supra- and infrahyoid muscles, have a less direct action but are particularly important in deglutition because they control the position of the hyoid complex and its attached soft tissues. Since this paper is primarily concerned with the functional anatomy of the jaw musculature, only the muscles of the first group are included in this account.

Although frequent references to *Didelphis* are found in the comparative anatomical literature and particularly where the

phylogeny of jaw musculature is discussed (Dobson, 1882; Adams, 1919; Edgeworth, 1935; Fox, 1964; Barghusen, 1968), the only available general description of this region in the opossum was published by Coues in 1872. This account, although comprehensive in its coverage, includes little detail on the attachments and internal structure of the muscles. More recently, Turnbull (in press) has prepared an account of the jaw muscles in *Didelphis* as a part of a general functional survey of jaw muscles in mammals.

Some explanation of the approach used in this study is necessary as it differs from that commonly adopted by anatomists. Fiedler (1952) and Frick (1957) regarded the jaw musculature in mammals as a single unit (M. adductor mandibulae) as did Adams (1919) and Lubosch (1938) although the latter two excluded the digastric. However, the musculature is rarely described as such despite Fiedler's and Frick's assertion that any division between the temporal, masseter and the pterygoids is both arbitrary and artificial. If Fiedler and Frick could be described as belonging to the "lumping" school, using Simpson's (1945) neologism, then many classical anatomists are "splitters". For example, the masseter has been described as having as many as four layers (Allen, 1880) one of which is often separately designated as the M. zygomatico-mandibularis (Parsons, 1899; Fiedler, 1952; Becht, 1954; Schumacher and Rehmer, 1962). The criteria on which these authors base this division of the masseter into "layers" or "parts" are rarely stated or justified. The large mass of muscle tissue extending from the zygomatic arch to the masseteric fossa on the lateral surface of the coronoid process and ramus of the mandible often seems to have been divided into a variable number of elements on the basis of vague fascial planes, intramuscular neurovascular bundles or on the arbitrary delineation of limits of origin or insertion. However, the deeper fibers of the masseter are often continuous with and adherent to those of the temporal (Allen, 1880; Parsons, 1896; Tullberg, 1899; Toldt, 1905; Adams, 1919; Becht, 1954) making separation difficult. While the recognition of parts within muscles or even within muscle masses may be valuable in purely anatomical or phylogenetic terms, it does not facilitate functional studies unless this division reflects changes in fiber orientation and therefore differences in action. In this respect description of the gross anatomy and internal architecture of the jaw musculature of *Didelphis marsupialis* constitutes a problem.

In *Didelphis* a large compact mass of muscle homologous with the temporal and masseter of other mammals fills the temporal fossa and ensheathes the coronoid process. This mass has a complex internal architecture but contains no natural divisions to justify recognition of separately named muscles. Such a muscle is difficult to describe, particularly in view of its complicated internal architecture. In this account the mass is called the adductor complex. Description of the internal architecture of the adductor complex is here facilitated by the use of the terms "posterior", "internal" and "external adductor"; these terms are intended solely in reference to parts of the adductor complex which have a characteristic fiber orientation. No homologies with the similarly named jaw muscles of reptiles are implied.

The large mass of muscle ensheathing the coronoid process of the lower jaw and taking origin from the lateral margin, roof and medial wall of the temporal fossa in mammals has been variously divided. The simplest and most usual division is into a M. temporalis and a M. massetericus which broadly correspond with the internal and external adductor musculature of mammal-like reptiles (Barghusen, 1968). Some authors (Parsons, 1898; Fiedler, 1952; and Davis, 1964, among others) recognize a third basic element, the M. zygomatico-mandibularis, described by Becht (1954) as "an independent member of the group with a history of its own." Within this basic division, further elements are sometimes recognized. The temporal is usually divided into deep and superficial parts separated in the plane of the coronoid process by its tendinous extension into the body of the muscle (Davis, 1964). Becht (1954) describes a separate anterior temporal muscle in Carnivora originating in the orbits and varying in size according to the development of the postorbital ligament. In addition, a pars supra-zygomaticus, passing horizontally forward over the zygomatic arch to insert into the anterior border of the coronoid process, is recognized by many authors. The divisions of the masseter are even more complicated. It is variously described as consisting of two, three or four layers depending on whether or not the author recognizes a separate M. zygomatico-mandibularis. The most external of these layers may or may not be regarded as a separate muscle, the superficial masseter, although its great development in the Rodentia has made this recognition usual in that group (Parsons, 1894, 1896). Sicher (1944) and Davis (1964) de-

scribe a distinct superficial masseter in several genera of bears and the giant panda, and Miller *et al.* (1964) describe a superficial layer of the masseter in the dog, as does Allen (1880). Many authors regard the deeper element as a single deep masseter but if the zygomatico-mandibular is also recognized, the deeper element is automatically divided into two layers. According to Becht (1954), who does distinguish the zygomatico-mandibular, the deep masseter consists of two layers in Rodentia and three in the "Ruminantia". Even if the deepest layer is not elevated to the status of a separate muscle, the deep masseter is still reported as having two layers in many mammals including the dog (Miller *et al.,* 1964).

The plethora of terms, not all of which have been detailed above, used to describe the jaw musculature in mammals is not applicable to *Didelphis* where no real division exists. If *Didelphis* is a relatively generalized survivor of a Cretaceous marsupial radiation, then the anatomy of the jaw adductors may substantially represent the basic arrangement in early mammals. Moreover, if Adams (1919) is justified in stating that the anatomy of the muscles of mastication in mammals has remained remarkably uniform overall with only minor adaptive changes, then there are no reasonable grounds for maintaining or adding to the existing complex nomenclature.

MATERIALS AND METHODS

The anatomy of the jaw musculature of *Didelphis marsupialis* was examined by dissection of fresh, unfixed heads as well as heads fixed in 12% Formal-saline. The internal architecture of the muscles was studied by sectioning frozen heads with a band saw in either coronal, horizontal or sagittal planes; the sections were then stored in 10% Formal-saline before examination under a dissecting microscope. This method revealed the precise distribution and orientation of internal tendons and muscle fibers.

OBSERVATIONS

The greater part of the jaw musculature is confined within the area of the temporal fossa (Figs. 1, 2, 4, and Appendix 1). This musculature consists of three major components: the adductor

complex (broadly corresponding to the temporal and deep mas-
seter of Eutheria), the superficial masseter and the pterygoids.
The temporal and masseteric fascia, an intrinsic although non-
muscular part of the system, are described first in view of their
intimate relation to the adductor musculature.

THE TEMPORAL AND MASSETERIC FASCIA

The superficial surface of the adductor musculature both above
and below the zygomatic arch is covered by a well-defined layer
of fascia. Variable in thickness, it extends over the entire lateral
surface of the head from the nuchal and sagittal crests above to
the lower border of the mandible below. This fascia is divided into
two parts by the zygomatic arch; in mammals the upper is nor-
mally termed the temporal fascia and the lower, the masseteric
fascia. Although the underlying musculature in *Didelphis* is not
distinguished by these names in this paper, the terms temporal and
masseteric are retained in reference to the fascia in the comparable
position to that in mammals.

The Temporal Fascia

The temporal fascia extends from the sagittal and nuchal crests
to the zygomatic arch where it fuses with the periosteum. Ante-
riorly the fascia terminates as a thick band of fibrous tissue con-
necting the postorbital processes of the frontal and jugal bones,
thus defining the posterior superficial margin of the orbit. A thin,
inferior extension of this band separates the anterior wall of the
adductor musculature from the orbital tissues. With the excep-
tion of its anterior border, the temporal fascia is attached to bone
at all its margins.

Much of the temporal fascia is very dense, completely aponeu-
rotic and extremely difficult to separate from the underlying muscle
fibers that take origin from it. In its lower part (along the upper
border of the zygomatic arch and over a small area adjacent to
the postorbital process of the frontal) the fascia is an important
origin for adductor muscle fibers. The fact that a substantial pro-
portion of the adductor musculature takes origin from the fascia

is correlated with the relatively large size of the muscle and the relatively small area available for its attachment. The temporal fascia is a functional replacement of the original bony roof of the temporal fenestra but has the advantage of accommodating the expansion of the musculature accompanying contraction.

The Masseteric Fascia

The temporal fascia continues inferiorly as the masseteric fascia. Attached above to the periosteum of the outer surface of the zygomatic arch, it passes inferiorly over the adductor musculature and over the superficial masseter to merge with the connective tissue covering the digastric and suprahyoid muscles at the lower border of the jaw. With the exception of the upper one third, which overlies the adductor musculature, the fascia is neither thick nor aponeurotic. Anteriorly its border merges with the periosteum of the maxilla immediately in front of the tendinous origin of the superficial masseter and with the fascia surrounding the buccinator. Below the buccinator, the fascia continues toward the lower border of the jaw but is less distinct and fades out close to the anterior free border of the superifical masseter behind and below the last molar. Posteriorly, in the region of the temporo-mandibular joint, the fascia blends with the joint capsule over its lateral surface.

The greater part of the masseteric fascia represents the thin layer of connective tissue normally covering muscles. In its thick and predominantly aponeurotic upper third, the fascia provides an attachment for the lower external fibers of the adductor musculature and is difficult to separate from them.

THE ADDUCTOR COMPLEX

The adductor complex has a multiple origin from both bone and fascia which can be divided into medial, lateral, superior and inferior areas relative to the temporal fossa.

The medial origin covers the lateral wall of the cranium (Fig. 4A, C) extending from the posterior margin of the orbit to the nuchal crest behind, and from the sagittal crest above to the

alisphenoid and the root of the zygomatic process of the squamosal below (Appendix II).

The lateral origin of the adductor complex can be divided into three areas. The largest of these is the entire medial surface of the zygomatic arch from immediately behind its postorbital process to the point at which its squamosal element curves medially to join the cranium. The second area is on the inferior border of the zygomatic arch and extends from the jugo-maxillary suture to the posterior tip of the jugal. This area faces slightly outward as well as downward (Fig. 3). Finally, fibers take origin from the masseteric fascia as it extends ventrally toward the upper border of the superficial masseter.

The superior origin is from the lateral half of the temporal fascia and from a triangular area overlying the postorbital constriction of the cranium.

The inferior origin is the smallest and most clearly delimited. It corresponds exactly with the upper surface of the zygomatic process of the squamosal and with the superior surface of the bone overlying the temporo-mandibular joint.

The areas of insertion of the adductor complex are on the coronoid process and mandibular ramus (Fig. 4A, B). The medial insertion extends downward over the entire inner surface of the coronoid process as far as a near horizontal line connecting the alveolus of the last molar, the upper border of the inferior dental foramen, and the junction of the posterior border of the coronoid process with the condylar neck. The lateral insertion is only slightly more extensive. It covers the lateral surface of the coronoid process and the masseteric fossa on the ramus of the mandible and continues posteriorly onto the outer, slightly forward-facing surface of the condylar process below the sigmoid notch (Fig. 4A). In addition, many fibers originating from the posterosuperior area of the lateral wall of the braincase insert on the aponeurotic continuation of the coronoid process. This is a tendon of insertion, the "planum tendineum temporalis" or tendo m. temporalis (Davis, 1964), extending upward within the body of the muscle to a point approximately level with the base of the sagittal crest, and extending posteriorly almost to the nuchal crest. In its shape this tendinous sheet corresponds to a continuation both posteriorly and superiorly of the recurved upper portion of the coronoid process.

The Internal Architecture of the Adductor Complex

The adductor complex can be regarded as consisting of three basic parts on the basis of fiber orientation: an internal adductor, an external adductor and a posterior adductor. The first two are also more or less demarcated by the sites of origin of their fibers; the delineation of the posterior adductor on this criterion alone is somewhat arbitrary. However, the internal architecture of the of the muscle mass as shown in Figures 8, 9 and 10 demonstrates the basically dissimilar orientation of the posterior fibers as compared with the internal and external adductor groups.

The Internal Adductor

This part broadly corresponds to the deep temporal of other authors and includes, in its anterior part, a small element of the superficial temporal. Almost all its fibers pass laterally and inferiorly from their origin on the lateral wall of the cranium anterior to the temporo-mandibular joint (IA, Fig. 4A, C) to insert either into the medial surface of the internal tendon or onto the medial surface of the coronoid process (Fig. 4A, B). The orientation of these fibers (in the parasagittal plane) as they pass to their insertion is not uniform. Fibers originating anterior to the coronoid process pass slightly posteriorly, those arising in the central area pass vertically downward, and those behind the process pass slightly forward to their insertion. (For a detailed account see Appendix II). In some but not all specimens, the organization of the most superior fibers included in the internal adductor is complicated by a mesh of internal tendon plates (Fig. 8C). Short fibers insert into these plates which then insert into the internal tendon, giving this part of the muscle a multipennate structure.

The External Adductor

In many respects the internal architecture of the external adductor is a mirror image of the fiber pattern of the internal adductor. The external adductor takes origin from the temporal

fascia (but not its aponeurotic area posterosuperior to the orbit), the zygomatic arch and the masseteric fascia. All external adductor fibers pass medially and more or less inferiorly to insert onto the coronoid process or the internal tendon. Those fibers originating from the temporal fascia are arranged in substantially the same pattern as those of the internal adductor except that their course is, in general, shorter and nearer the horizontal. Anteriorly, fibers of the external and internal adductors form the muscular posterior wall of the orbit and here the two muscles have about the same bulk (Figs. 8D, 9A, B). Occasionally small tendon plates are found in the posterosuperior part of the external adductor and serve as both origin and insertion for the muscle fibers (Figs. 8C right, 10E).

A gradual change in the orientation of the external adductor occurs between the fibers from superior and inferior limits of the muscle (Fig. 8). The majority of fibers which arise from the temporal fascia above the zygomatic arch, pass inferomedially with a slight anterior inclination. The block of fibers attached to the medial surface of the zygomatic arch pass directly inferomedially to their insertion into the masseteric fossa (Fig. 8C, D) as do most of those originating from its inferior border. However, the fibers attached to the posterior third of the inferior border of the zygomatic arch pass posteriorly as a thick band to attach to the condylar process and lower border of the mandible just anterior to the temporo-mandibular joint (Figs. 6, 8B left). The most external fibers, originating from the masseteric fascia, also have a slightly posterior as well as inferomedial orientation. The external and internal adductors almost fuse anteriorly where they form the dense, muscular posterior wall of the orbit (Figs. 9A, B, 10B, C). Such separation as is anatomically recognizable is provided by a small tendon extending the coronoid process anteriorly and fusing, in part, with the postorbital fascial wall.

The architectural differences between the external and internal adductors relate to the more extensive insertion of the external adductor and to its two small internal tendons. These tendons could be used to demarcate a zygomatico-mandibular or two layers of a deep masseter, although neither extends completely through the muscle. The larger and the better developed of these tendons extends inferiorly from its origin at the junction of the medial and inferior surfaces of the central part of the zygomatic arch

(Fig. 8C). The other tendon is less distinct; it projects laterally
and superiorly from the sharp lower border of the masseteric
fossa below and anterior to the condylar process (Figs. 8C right,
9C). As the superficial fibers of the external adductor insert by
means of this tendon, it separates the outer surface of the adductor
from the deep surface of the superficial masseter in this area.

The Posterior Adductor

The posterior adductor has its main axis in the horizontal
rather than in the vertical plane. Unlike the other parts of the
adductor complex, the posterior area of insertion of the adductor
is much smaller than its origin so that its fibers converge on their
insertion. The bulk of the posterior adductor takes origin from the
posterosuperior area of the temporal fossa and the adjacent parts
of the sagittal and nuchal crests. These fibers pass outward, for-
ward, and either downward or horizontally to converge on the
internal tendon or the posterior border of the coronoid process
(including the sides of its recurved tip). There are two small slips
of this muscle, the suprazygomatic and the fibers originating from
the bony roof of the joint, which pass horizontally forward
(see Appendix II).

As is shown in Figures 8A and 10E, the internal architecture of
the major part of the posterior adductor is, in some specimens,
complicated by a dense mesh of internal tendon and aponeuroses.
The posteroexternal fibers are more clearly organized and pass
predominantly anteroinferiorly to insert into the internal tendon
of the coronoid process. Near the anterior margin of the posterior
adductor, above the joint, the fibers run more evenly anteroin-
feriorly to attach to the tendon and so to the coronoid process
(Fig. 8B right).

The posterior adductor is not divisible into true "superficial"
and "deep" parts. Although the coronoid process and its extension
tendon separate the insertion of the muscle into outer and inner
areas, this division does not completely divide the muscle. The
fiber orientation of this muscle mass suggests that it is a single
functional unit and one basically different from either the internal
or external adductors.

Discussion

The question arises as to whether a relatively undifferentiated muscle mass such as the adductor complex in *Didelphis* can exhibit the same type and range of movement as a group of recognizably separate muscles. Anatomical evidence alone cannot provide an answer but the internal structure of the adductor complex is suggestive. Although there are no distinct anatomical boundaries to distinguish the internal, external and posterior adductors, the substantial shift in fiber orientation is indicative of a basic difference in their effect on contraction.

The adductor musculature functions to maintain the integrity of the jaw apparatus and to initiate and control movements of the lower jaw. The first is achieved in conjunction with tendons and ligaments and particularly of the joint capsule. However, the major factor in regulating the position of the lower jaw is the activity of the tonic musculature. The anterior temporal and the deep masseter were found to suspend the lower jaw from the cranium in the rat (Hiiemäe, 1966) and to be in large part responsible for the stability of the system. As can be readily seen in the coronal sections in Figure 8, the external and internal adductors in *Didelphis* also "sling" the mandible between them by ensheathing almost the entire mandibular ramus and the coronoid process in muscle.

The most important phasic action of the adductor complex is elevation or adduction of the lower jaw. In addition, since both internal and external adductors have a substantial transverse component, contraction of the external adductor of one side with relaxation of the other could produce lateral movement. This action is unlikely to be the main mechanism for producing lateral jaw movement in *Didelphis* although such an action may be synergistic.

The precise function of the posterior adductor is less readily elucidated on purely anatomical grounds. In many mammals, including man, the analogous musculature is regarded as primarily a mandibular retractor and elevator and in addition as a synergist in the production of lateral movements (Kawamura, 1964; Hiiemäe, 1966). Mandibular elevation and retraction are very probably functions of the posterior adductor in *Didelphis* also. In addition, the posterior adductor in *Didelphis* has a small transverse component which may be capable of pulling the

coronoid process of the same side posteromedially, so moving the lower jaw toward the contralateral side. Such an action could be of considerable importance in the production of "Bennett movements"[1], if they occur.

THE SUPERFICIAL MASSETER

Phylogenetically the superficial masseter is derived from the adductor complex (Barghusen, 1968), and in *Didelphis* it is sufficiently differentiated from the external adductor to justify its recognition as a separate muscle. However, some intermingling of fibers is found and in many specimens the separation of the upper part of the deep surface of the superficial muscle from the outer surface of the adductor is somewhat arbitrary. Nevertheless, the two are different functional entities in view of their fiber length and orientation.

The superficial masseter is a fan-shaped, unipennate muscle (Fig. 5) with an effective length some three times that of the external adductor and with a long axis near the horizontal. It takes origin as a thick but slightly flattened tendon from a small prominence on the maxilla immediately below and in front of the lower border of the jugo-maxillary suture. This tendon passes posteroinferiorly and after a short course broadens out into a triangular aponeurosis. The upper border of the aponeurotic area more or less coincides with the upper border of the muscle and is almost straight, passing posteriorly toward the external auditory meatus and fading out on the superficial surface of the muscle below the temporo-mandibular joint. The lower border is very much shorter; it passes more sharply downward, exposing muscle fibers anterior to it (Fig. 5) and again fades out on the outer surface of the muscle. This aponeurosis serves as the origin for the superficial masseter which arises from its deep surface and fans out to wrap around the lower border of the jaw. The muscle inserts on the expanded lower surface of the jaw and onto the fascial layer separating the internal pterygoid from the superficial masseter. A few fibers, however, take origin from the tendon or even from

[1] Bennett (1908) stated that the mandibular condyle in man would, in certain circumstances, be translated laterally (or medially) across the glenoid fossa. Any such linear movement is known as a Bennett movement.

the maxilla and pass directly downward to insert on the medial surface of the lower border of the mandible where they are closely related to the insertion of the anterior belly of the digastric. These fibers are clearly seen in Figures 5 and 13. This part of the muscle overlies, but does not attach to, the convex, smooth area separating the masseteric fossa and the lower border of the jaw. It appears that this area functions as a pulley around which the superficial masseter contracts.

The bulk of the fibers insert into the broad medial expansion of the lower border of the jaw and the inflected angle (Fig. 4A, B, D). A few fibers insert into the fascial layer linking the medial border of the condylar process with the angle and so pass around the joint immediately external to the lower part of the joint capsule. A number of the most superficial fibers insert onto the fascial plane formed by the fusion of the fascia covering the internal pterygoid and the superficial masseter, which is itself attached to the extreme medial edge of the angular process. As the muscle approaches its insertion it becomes extremely thick and gives a rounded appearance to the angular region of the jaw.

Discussion

By virtue of its nearly horizontal orientation the superficial masseter probably functions as a protractor of the lower jaw and therefore could act as an antagonist to the posterior adductor. However, the superficial masseter also wraps around the lower border of the jaw and the inflected angle. This relationship indicates the possibility that the superficial masseter rotates the jaw about its long axis (i.e., moves the lower border laterally and dorsally). Conversely, it is possible that the torque of the superficial masseter is balanced by an opposing torque of the pterygoids. Experimental data, rather than anatomical evidence, is necessary to solve this problem.

THE PTERYGOID COMPLEX

The two muscles which form the mammalian pterygoid complex, the internal pterygoid (M. pterygoideus internus or medialis) and the external pterygoid (M. pterygoideus externus or lateralis)

have probably had quite different phylogenetic histories. Crompton (1963) has shown that the former, together with the M. tensor tympani, is derived from the anterior pterygoid musculature of reptiles, while the external pterygoid developed from a slip which separated from the deep surface of the medial part of the reptilian adductor mass.

The Internal Pterygoid

The internal pterygoid is a thick, short muscle that appears almost trapezoid in shape when viewed from the interomedial aspect (Fig. 11). It originates from a long, approximately triangular area on the cranium (Figs. 4A, 8B, C) below the lower border of the origin of the internal adductor and is separated from it by the first and second divisions of the trigeminal nerve. The triangle has its base anteriorly on the palatine bone behind the sphenopalatine foramen and extends onto the pterygoid and its wide transverse process (Figs. 4A, 8C left). The remaining area of origin is much narrower and extends posteriorly from the pterygoid process along a ridge of the alisphenoid.

In contrast, the area of insertion is large. The limit of its attachment is along the condylar notch to immediately above the inferior dental foramen and from there down onto the medial surface of the lower jaw. The superior limit of its attachment is along a line extending from the base of the condylar process to immediately below the inferior dental foramen; from there the line passes down to the lower border of the ramus where the inflected angle narrows to become a rounded margin (Fig. 4B). From this line the insertion extends inferiorly and medially over the entire surface of the angle and the angular process as well as the adjacent area of the fascia linking the angular and coronoid processes. In addition, some fibers insert into the common fascial plane shared by the internal pterygoid and the superficial masseter. It should be noted, however, that anteriorly the attachments of the two larger muscles diverge, leaving a small area of bone for the attachment of the mylohyoid (Fig. 11).

The fibers of the internal pterygoid pass downward, laterally and posteriorly to their insertion. Those fibers originating on the palatine or pterygoid process insert near the anterior limit of the

inflected angle and those originating posteriorly from the alisphenoid insert onto the angular process. In fact the muscle has a partly fibrous, partly tendinous origin. The thick, free anterior border of the internal pterygoid is fleshy but posteriorly the deeper fibers (superficial in Figs. 11 & 12) take origin from an aponeurosis extending over the upper and posterior quarters of the muscle surface (Fig. 10C). In this area, the origin of the muscle is never entirely aponeurotic; some fibers take origin from the alisphenoid but the considerable bulk of the internal pterygoid can be partly attributed to the additional area for fiber attachment afforded by the tendon. In addition to this aponeurosis, the body of the muscle is more or less divided along its length by an internal tendon of variable extent and position (Figs. 8B, C, 9D, 10C). As the orientation of the muscle fibers superficial and deep to the tendon is essentially the same, it seems likely that the tendon serves as an internal area of origin and insertion rather than dividing the muscle into two different functional units.

The External Pterygoid

This muscle, barely more than a slip, originates from a small area on the alisphenoid above and behind the foramen rotundum (Fig. 4D). It then passes posteriorly, laterally and slightly downward to insert into a small depression on the superomedial surface of the condylar process and into the capsule of the squamodentary joint (Figs. 4B, 10B). When dissected from the inferomedial approach (Fig. 12) it is seen as a thin, rounded fasciculus with a thin aponeurosis on its (deep) surface. Removal of this deep belly exposes a second, thinner, fasciculus partly separated from the first. The larger belly inserts into the condylar process and the smaller into the joint capsule.

Discussion

While the anatomical relations of the internal pterygoid can be clearly seen (Figs. 8B, C, 9C, D, E, 10C, E), the functional relationships of the muscle to the superficial masseter is not clear. Although the two occupy similar positions in *Didelphis* and in eutherian mammals, the inversion of the angular process must alter

their functional relationships. First, the actual length of the super-
ficial masseter in *Didelphis* is thereby increased and that of part of
the internal pterygoid reduced. Second, part of the attachment of
the internal pterygoid is moved medially. On contraction this mus-
cle will tend to invert the lower border of the mandible (as well
as pull it medially and forward) and is thus capable of inducing a
rotation of the mandible about its long axis. It has already been
suggested that the superficial masseter might be capable of produc-
ing lateral movement of the mandible coupled with a similar type
of rotation. Whether or not this is the case, it remains likely that
the two muscles act as mutual antagonists and also probably as
synergists, i.e., the internal pterygoid of one side acting in concert
with the contralateral superficial masseter.

In *Didelphis,* the external pterygoid may initiate mandibular
depression by rotating the condyle forward, thus tilting the lower
jaw downward. It also may act with the internal pterygoid in
producing lateral jaw movement. Positive experimental confirma-
tion of these actions is not yet available; however, its very small
size suggests that no powerful action can be produced by its con-
traction and that its role in the generation of mandibular move-
ment is probably supplementary to that of the other muscles.
The position of both internal and external pterygoids in mammals
has led to the suggestion that they both act primarily to produce
lateral movement of the lower jaw. Whether or not this is their
principal function in *Didelphis* is not known, but the development
of the "marsupial flange" and the consequent alteration of the
position of the internal pterygoid must reflect some functional
difference.

THE SUPRAHYOID MUSCULATURE

There are three important muscles linked to the hyoid apparatus
and functioning as muscles of mastication: the M. digastricus
(digastric), the M. mylohyoideus (mylohyoid) and the M. genio-
hyoideus (geniohyoid). In addition, two muscles of the tongue,
the M. genioglossus (genioglossus) and the M. hyoglossus (hyo-
glossus) can be included in this group as they are attached to the
lower jaw and the hyoid, respectively, and are functionally asso-
ciated with the other accessory muscles.

The Digastric

As in most, but not all, mammals the digastric in *Didelphis* is formed of two fleshy bellies linked by a central tendon. This tendon, arising as an aponeurosis on the deep surface of the posterior belly, forms part of the "expansion aponeurotique de digastrique" described by du Châine (1914). Du Châine demonstrated a tendinous arcade, formed largely by the paired central tendons of the digastric but with contributions from the mylohyoid and geniohyoid, which serves as a common attachment for all these muscles and is itself attached to the hyoid bone. In effect, the major suprahyoid muscles have a common insertion into the median expansion of the central tendons of the paired digastric. This arcade is well developed in *Didelphis* as a narrow, almost crescentic band of tendon, convex anteriorly, which crosses the midline in front of the trachea and arches posteriorly toward the angles of the lower jaw at each side.

The posterior belly of the digastric in *Didelphis* has a fleshy origin from the paraoccipital process and is closely related to the cranial attachments of the M. styloglossus and M. stylohyoideus. As it passes anteriorly it lies in a gutter between the fibers of the superficial masseter laterally and the internal pterygoid dorsomedially and in fact overlies the common fascial insertion of these muscles. At about the level of the angular process the posterior belly begins to change from an entirely fleshy mass of ovoid cross-section into a narrow, tendinous band. The fibers of the posterior belly insert either into the aponeurosis on its deep surface, which forms the most posterior extension of the central tendon, or directly into that tendon.

The anterior belly of the digastric has a long origin from the central tendon and a long linear insertion into the lower jaw (Fig. 4B, D). It is a thin sheet of muscle, broadly triangular in shape with its origin and insertion forming the base and one side of the triangle (Fig. 13), the other side being its long medial free border. The fibers of the anterior belly run directly anteroposteriorly so that the more lateral the fiber, the shorter its course. The medial fibers pass anteriorly for a considerable distance to attach to the jaw just below the first molar. The medial edge of the anterior belly is bound down to the underlying mylohyoid and to its pair on the other side by a fairly dense layer of fascia.

The digastric in *Didelphis* is similar to that of most mammals and in all probability serves the same functions.

The Mylohyoid

The mylohyoid, like the digastric, is a paired muscle but is fused in the midline to form a single functional unit. It is a thin sheet arching downward and medially from one half of the lower jaw, across the midline and up to its attachment on the other. The bony insertion of this muscle is linear and lies on the medial aspect of the lower border of the jaw (Fig. 4B, D). The posterior fibers of the mylohyoid take origin from a narrow area of bone below the inferior dental foramen and on the medial surface of the inflected angle between the insertion of the internal pterygoid and the superficial masseter. At the level of the anterior border of the internal pterygoid, the attachment of the mylohyoid curves upward (dorsally) and then passes anteriorly. Over the anterior half of its length the attachment of the mylohyoid is closely related to the insertion of the anterior belly of the digastric (Fig. 4B) but is always separated from it by smooth bone. The anterior limit of mylohyoid origin is at approximately the level of the first molar.

There is no obvious central raphe in the mylohyoid of *Didelphis*. The majority of fibers seem to pass directly across the midline. Not all, however, have a straight course; those originating near the inferior dental foramen pass slightly anteriorly as well as medially. Over the central third of the posterior border, the mylohyoid is attached to the tendinous arcade and so gains insertion into the hyoid apparatus. The short anterior border of the mylohyoid is bound down by fascia.

The Geniohyoid

This muscle is the largest of the supra-hyoid group. A powerful, unipennate muscle, the geniohyoid originates from the inferior lip of the genial depressison on each half of the lower jaw and immediately behind the symphysis as a tough but flattened tendon. This passes posteriorly for a short distance and then is continued as the thick, rounded fleshy belly which inserts into the deep part

of the tendinous arcade and into the hyoid bone itself. There is no constriction of the belly of the geniohyoid as it approaches its insertion. The muscles of the right and left sides are in contact medially but do not fuse. Throughout its length the belly of the geniohyoid is covered superficially by the mylohyoid. The geniohyoid in turn covers the genioglossus (Fig. 14).

Discussion

The digastric, mylohyoid and geniohyoid are regarded as accessory muscles of mastication for two reasons. First, they control (with the assistance of the remaining supra-and infra-hyoid muscles) the position of the hyoid bone and its associated structures in relation to the cranium and the lower jaw. In swallowing, the hyoid moves upward carrying the larynx with it so that the epiglottis can effectively seal the airway. On completion of deglutition, the hyoid apparatus drops or is pulled back. The stylohyoid and the posterior belly of the digastric suspend the hyoid from the cranium; the mylohyoid, geniohyoid and the anterior belly of the digastric control its position in relation to the lower jaw and the infra-hyoid muscles connect it with the sternum and the scapula. Second, the anterior belly of the digastric, the mylohyoid and the geniohyoid can all lift the floor of the mouth and so act as elevators of the tongue. The mylohyoid, in view of its orientation, is probably the most effective of the group in this respect; however, their common tendinous insertion coupled with their close fascial connections means that all three muscles are likely to be involved.

The Genioglossus

This muscle is one of the larger extrinsic muscles of the tongue and has an important action in controlling its shape and position. Taking origin as a fleshy bundle from the genial depression, it passes posteriorly beneath the geniohyoid as a progressively widening band, fading out in front of the hyoid apparatus. Its most superficial fibers curve upward to their insertion into the dorsum of the tongue (Fig. 14). Viewed in sagittal section (Fig. 10D) the genioglossus can be seen as a broad fan of muscle fibers pas-

sing posterosuperiorly into the body of the tongue from their origin on the lower jaw. The genioglossus can pull the tongue bodily forward or can depress its middle or posterior thirds.

The Hyoglossus

Like the genioglossus, the hyoglossus is a large muscle. It originates as a fleshy mass from the hyoid bone deep to the insertion of the geniohyoid and then passes forward, laterally and upward around the posterior part of the genioglossus (Fig. 14) to insert as a fan of fibers into the lateral part of the body of the tongue in its posterior two-thirds. This muscle acts to retract the tongue, or, like the genioglossus, to alter its shape.

Discussion

The tongue is an extremely mobile organ and has an essential role in ingestion, mastication and deglutition. These two muscles, together with the styloglossus and its intrinsic musculature, are responsible for movement of the tongue and for producing the local changes in shape essential to efficient mastication.

THE FACIAL MUSCULATURE

In addition to the muscles which initiate and control mandibular movement, there are other smaller muscles which function in normal feeding activity. The most important of these is the buccinator (M. buccinatorius) which, with the orbicularis oris (M. orbicularis oris), forms the body of the lips and the cheek. The opossum, like many mammals, has very short functional lips. The angle of the mouth is approximately level with the second molar; at this point the labial sulcus has considerable depth but this diminishes anteriorly until the sulcus is eliminated just in front of the third premolar. The mobile length of the lips is therefore about one third the length of the tooth row; the remainder is closely tied down to the underlying bone and to the rhinarium. It seems unnecessary to recognize both a buccinator and orbicularis

oris in *Didelphis*. A thick, well-defined muscle homologous with the buccinator of other mammals is present and this fades out in the anterior premolar region, leaving only traces of muscle in the lip surrounding the anterior teeth.

Buccinator

The buccinator in *Didelphis* is a thick muscle, basically cres-centic in shape with the "horns" pointing anteriorly and the "body" lying across the angle of the mouth and forming the cheek posteriorly (Figs. 5, 6 and 13). The attachments are to soft tissue, to fascia and to bone. The inner, labial attachment is anterior to the angle of the mouth, merging with the soft tissue of the lip and gradually fading out anterior to the second premolar. The outer border is attached to the maxilla just above the last premolar and the first and second molars, as the muscle sweeps round to its midpoint, where the attachment leaves bone (Fig. 4A). The fibers regain a bony attachment parallel to the upper along the body of the lower jaw below the cheek teeth. This edge can best be described as "rolled" (Fig. 13). The muscle is at its thickest near the angle of .the mouth where there is a somewhat tendinous raphe. As it passes upward and forward or downward and forward, the fibers sweep round and then turn under to reach their attachment. At the angle of the mouth the muscle is covered by the fascia overlying the anterior part of the superficial masseter and its tendon.

Discussion

The function of the buccinator in man and in those mammals in which this muscle has been examined is one of food control. Contraction of the buccinator serves to assist the tongue in repositioning the material on the occlusal surfaces of the cheek teeth. It is worth noting that *Didelphis* frequently drops the lower jaw through an arc of thirty degrees or more. When this occurs the buccinator is under considerable tension and stands out within the cheek. Indeed, the full depth of the labial sulcus becomes clearly visible only in these circumstances as the cheek pulls away from the teeth.

CONCLUSIONS

The conclusions of this study, in addition to the basic descriptive text, are as follows:

Previous descriptions of the muscles of mastication in *Didelphis* have failed to appreciate the undifferentiated nature of the adductor musculature within the infratemporal fossa. This muscle mass has been variously subdivided into separately named muscles. In fact, there is no evidence for such subdivision, although for *descriptive purposes* only the terms "internal", "external" and "posterior" adductors are convenient in reference to major parts of this single muscle muscle mass which have distinctive fiber orientations.

The anatomy of the superficial masseter in *Didelphis* is unlike that of its homologue in the eutherian carnivores. In the latter group this muscle usually inserts onto the small angular process of the lower jaw and in some cases into a common raphe with the internal pterygoid (Becht, 1954). The arrangement in *Didelphis* differs due to the medial inflection of the angular process. The nature of the superior attachment of the superficial masseter also differs. In the carnivores this muscle takes origin from the inferolateral surface of the zygomatic arch as a wide fibrous band and is, therefore, a rectangular muscle with an upward and forward inclination. In *Didelphis* the superficial masseter originates from a narrow tendon attached to a boss on the maxilla just below and anterior to the zygomatic process of that bone. The muscle then fans out to become a powerful unipennate fleshy belly with a nearly horizontal line of action. The superficial masseter is the only part of the adductor mass to have achieved anatomical and, apparently, functional separation.

We are cautious about the possible paleobiological significance of the arrangement of adductor musculature in *Didelphis*. We are aware, on the one hand, that *Didelphis* is one of the most generalized of living marsupials; its dentition is basically similar to that of Late Cretaceous marsupials, although Clemens (1968) has demonstrated certain distinct dental differences. On the other hand, there is as yet no direct evidence that *Didelphis* retains the basic adductor pattern of Late Cretaceous marsupials. With reservations, therefore, some speculative remarks may be made. The basic pattern of mammalian jaw musculature was established in advanced

cynodonts (Crompton, 1963; Barghusen, 1968). At this phylogenetic stage, the adductor musculature had attained a position and relative size comparable with the temporal and masseter of mammals. Assuming that the adductor muscle pattern of *Didelphis* retains the basic pattern of Late Cretaceous marsupials, it would appear that an advanced degree of morphological differentiation of the adductors was a comparatively late event in therian phylogeny. However, fiber groupings characterized by distinct orientation are present in *Didelphis* and this condition probably simulates the first stage in the development of the differentiated jaw muscles of eutherians.

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APPENDIX I

THE ANATOMY OF THE DIDELPHIS SKULL AS RELATED TO THE JAW MUSCULATURE

As can be seen in Figures 1, 2 and 3, the actual cranium of *Didelphis* is small both absolutely, reflecting the limited cerebral development of the opossum, and relatively when compared with the snout. The extent to which the facial bones dominate the skull is partly attributable to the long tooth row which, in the figured specimen, approximates 69% of the total skull length. In order to accommodate the molar series, the maxilla has an extensive poste-

rior extension which completes the floor of the orbit (Figs. 1, 2).
The corresponding length of the mandibular tooth row coupled
with the posterolateral position of the jaw joint (Figs. 2, 3) result
in a relatively long lower jaw. With such a small cranium and a
large lower jaw, the available area for bony origin of the adductor
musculature is disproportionately small. However, the development
of nuchal and sagittal crests as well as the deep zygomatic arch
compensate for the limited surface area of the cranium.

The greater part of the adductor musculature in *Didelphis* takes
origin from the bony surfaces limiting the temporal fossa. In the
absence of a postorbital bar the fossa is delimited anteriorly by the
postorbital processes of the frontal and the jugal above (Fig. 2)
and by the posterior extension of the maxilla and the alveolus
of the third molar below (Figs. 1, 3). The fossae of both sides
share a common superior border, the sagittal crest. This is formed
by the frontals, the parietals and the fused postparietals and supra-
occipitals. The latter also contributes, with the squamosal, to the
nuchal crest which delimits the temporal fossa posteriorly. Strictly
speaking, the fossa has no inferior border but the origin of the
adductor musculature extends downward to include the thin
triangular pterygoid processes and the lower limit of the wing of
the alisphenoid. Posteriorly, the inferior border of the temporal
fossa is formed by the squamosal root of the zygomatic arch which
continues anteriorly to form the lateral wall of the fossa.

The zygomatic arch of *Didelphis* is a very deep and robust bar
of bone, formed by the zygomatic process of the squmosal, the
jugal and the zygomatic process of the maxilla. The latter makes
a very limited contribution to the outer, lateral surface of the arch
anteriorly but on its medial surface extends backward as far as the
postorbital process and forms the lateral wall of the orbit. The
zygomatic arch of *Didelphis* not only curves outward and back-
ward from its anterior root but also outward and downward. The
extreme lateral margin of the skull is formed by the inferior rather
than the superior border of the arch (Figs. 1, 2). The width of
the temporal fossa is greatest at the level of the postorbital con-
striction of the cranium and the pterygoid processes (Figs. 1,
3). The widening of the fossa is also more or less coincident
with the anterior border of the coronoid process of the lower jaw.
Posteriorly, the zygomatic arch changes orientation as it curves
medially toward the cranium. At the level of the squamoso-

alisphenoidal suture the lower border curves medially through a right angle to become the anterior border of the squamosal root of the zygomatic arch. The superior margin curves more gently medially to merge with the body of the squamosal (Fig. 1) and to continue toward the nuchal crest as a thick ridge of bone above the external auditory meatus (Fig. 2). This "twisting" of the arch brings the originally external surface into a downward-facing position as the glenoid fossa. The internal surface forms an upward and forward-facing bony floor to the posterior part of the temporal fossa (Fig. 1).

The oval articular fossa is largely formed by the squamosal but with a small contribution from the jugal near its anterolateral margin. Its long axis is transverse to that of the skull. In its short axis the fossa is shallowly concave. A robust postglenoid process extends downward and slightly posteriorly (Fig. 2).

In its general form the mandible of *Didelphis* closely resembles that of some eutherian carnivores. There are large coronoid and angular processes; the latter is inflected medially, a marsupial specialization. The lower border of the mandibular ramus widens posteriorly, giving it an elongated triangular shape (Fig. 3) and providing a large area for muscle attachment. Above its expanded lower border the mandibular ramus is excavated on its lateral surface by a well-developed masseteric fossa and on its inner medial surface by a pterygoid fossa. The former extends from the lower border of the lateral surface of the ramus to the apex of the coronoid process and posteriorly to the condylar process. The pterygoid fossa, much smaller, extends from the medial margin of the inflected angle to the lingula. The lateral margin of the lower border of the mandibular is smoothly curved from the level of the second molar to below the middle of the masseteric fossa (Figs. 2, 3). Posteriorly, this smoothly curved margin merges with the inferior surface of the inflected angle. The masseteric fossa is closely related anteriorly to the thickened border of the coronoid process which arises inferolateral to the first molar and extends upward for about two-thirds of the length of the process to fade out at the junction of its anterior and superior borders. The posterior border of the fossa which forms the sigmoid notch with the short condylar process is very much thinner.

In lateral view (Fig. 2), the stout condylar process is continuous with the lower border of the mandible. The short condylar

neck expands into the transversely orientated condyle which is more sharply convex in its anteroposterior (short) axis than in its transverse (long) axis. Much of the articular surface is flat. The articular condyle is on a level slightly above the occlusal plane.

In the articulated skull the lower jaw bisects the temporal fossa at an angle of approximately 15° to the long axis of the skull (Fig. 1). The coronoid process, which in lateral view (Fig. 2) projects above the upper border of the zygomatic arch, lies almost equidistant from the arch and the outer wall of the braincase when the mandible is in centric position.

APPENDIX II

THE ANATOMY AND INTERNAL ARCHITECTURE OF THE ADDUCTOR COMPLEX

The adductor complex has four main areas of origin: medial, lateral, superior and inferior. The first is the most extensive. Anteriorly, the medial origin is limited by a slight ridge on the frontal bone which passes posteroinferiorly to the fronto-alisphenoidal suture above the ethmoidal foramen. Passing above the optic-orbital fissure and the anterior alar foramen, the ridge continues (although less well-marked) posteriorly as the inferior margin across the wing of the alisphenoid. The ridge terminates at the anterior root of the zygomatic process of the squamosal. Like the anterior and anteroinferior margins, the superior and posterior limits of the medial origin are continous. The superior extends from the postorbital process of the frontal as a slightly marked ridge curving medially towards the midline (Figs. 1, 4C). It then passes along the top of the sagittal crest to the junction of the sagittal and nuchal crests. The posterior border corresponds with the tip of the nuchal crest until its junction with the posterior root of the zygomatic process. The margin then runs anteriorly along the dorsal surface of the zygomatic process to the alisphenoid where it joins the slight ridge marking the inferior border of the area of attachment. The lateral wall of the braincase enclosed by these margins is concave anteriorly and convex posteriorly (Figs. 1, 2).

The Internal Architecture of the Adductor Complex

THE INTERNAL ADDUCTOR. The internal adductor is of fairly simple structure. As can be seen from Figures 8, 9 and 10, its fibers pass laterally and more or less inferiorly to their insertion on the medial surface of the coronoid process. However, the orientation of these fibers in the parasagittal plane is not uniform. Those taking origin from the anterior part of the medial wall of the fossa and from the small fascial area above pass inferiorly, laterally and slightly posteriorly. They insert either into a small tendinous area in front of and continuous with the anterior border of the coronoid process (Fig. 9B) or onto the anterior border of the process itself (Figs. 8D, 9C, D). Fibers originating from the medial wall of the fossa at the level of the postorbital constriction of the cranium pass almost directly laterally and inferiorly (Fig. 8C left) to insert on the entire medial surface of the coronoid process (Fig. 4B). The most posterior fibers taking origin from the wall of the cranium just anterior to the squamo-dentary joint pass laterally, inferiorly and anteriorly to their insertion on the posterior part of the medial surface of the coronoid process (Figs. 8B left, 10B).

The course of fibers originating from the medial wall of the fossa above its maximum convexity is slightly different. In general, they are all orientated anteriorly and pass more horizontally and laterally than do the deeper and inferior fibers (Figs. 8B left, C). They insert into either the apex of the coronoid process or into the internal tendon. Anteriorly, the fibers originating from the dorsum of the cranium just behind the postorbital process of the frontal form the upper anterior part of the muscular postorbital wall and have a complicated course. Instead of inserting into the medial surface of the coronoid process near its anterior edge, they pass over this edge and insert onto the lateral surface of the process.

THE EXTERNAL ADDUCTOR. The fibers of the external adductor pass more or less directly inferiorly and medially to their insertion. However, there is a variable degree of antero- or posteromedial inclination depending upon the site of fiber origin. Anteriorly, for example, fibers originating from the fascia near the upper border of the zygomatic arch pass slightly posteriorly as well as medially before inserting into the central part of the masseteric fossa (Fig. 9B). As the fibers elongate towards the anterior and inferior

parts of the muscle mass, their direction changes from the near horizontal to the near vertical (Figs. 8, 9). The part of the adductor originating from the medial surface of the zygomatic arch has no significant change in fiber orientation; it inserts into the inferior part of the masseteric fossa. The fibers passing to the anterior of the coronoid process are almost vertical (Fig. 8D left). There is, however, a more marked change in orientation of the fibers which take origin from the inferior border of the zygomatic arch. Just in front of the squamo-dentary joint, a band of fibers passes inferomedially to link the inferior border of the zygomatic arch and the concave posteroinferior area of the masseteric fossa (Fig. 8B left, C right). This band is continued anteriorly as fibers originating from the expanded lower border of the zygomatic arch (Fig. 8D left). These gradually fade out as the lower border of the mandible narrows anteriorly and curves inferiorly, thus increasing the vertical distance between the arch and the lower border of the masseteric fossa. In general, the outermost layers of fibers, which originate from the masseteric fascia below the arch, parallel the deeper group but are inclined slightly posteriorly (Fig. 10A).

THE POSTERIOR ADDUCTOR. The internal architecture of the posterior adductor is basically simple, as can be seen from Figures 8, 9 and 10. Two small blocks of muscle are worth further comment.

The suprazygomatic slip is a thin band of fibers passing almost horizontally on the external surface of the adductor immediately above the posterior root of the zygomatic arch. They insert into the posterior border of the coronoid process immediately below its apex. Removal of this slip exposes fibers of the posterior adductor passing horizontally and in some cases even upwards to insert into the internal tendon.

The inferior limit of the origin of the posterior adductor, the "roof" of the squamo-dentary joint, provides attachment for a thick band of fibers without internal tendons. Enclosed on three sides by bone (Fig. 8A right), these fibers pass horizontally forward to insert onto both the medial and lateral surfaces of the posterior part of the coronoid process as well as its posterior border below the recurved apex. This small block of muscle is closely related to the external pterygoid which passes superolaterally to its insertion on the condylar neck immediately below.

LITERATURE CITED

Adams, L. A. 1919. A memoir on the phylogeny of the jaw muscles in recent and fossil vertebrates. Ann. N. Y. Acad. Sci. **28**: 51-166.

Allen, H. 1880. On the temporal and masseter muscles of mammals. Proc. Acad. Nat. Sci. Philad. **1880**: 385-396.

Barghusen, H. R. 1968. The lower jaw of cynodonts (Reptilia, Therapsida) and the evolutionary origin of mammal-like adductor musculature. Postilla **116**: 1-49.

Becht, G. 1954. Comparative biologic-anatomical researches on mastication in some mammals. I and II. Proc. K. Ned. Akad. Wet., Series C, **56**: 508-527.

Bennett, N. G. 1908. A contribution to the study of movements of the mandible. Proc. R. Soc. Med. **1**: 79-85.

Clemens, W. A. 1968. Origin and early evolution of marsupials. Evolution **22**: 1-18.

Coues, E. 1872. The osteology and myology of *Didelphys virginiana*. Mem. Boston Soc. Nat. Hist. **2**: 41-154.

Crompton, A. W. 1963. On the lower jaw of *Diarthrognathus* and the origin of the mammalian lower jaw. Proc. Zool. Soc. Lond. **140**: 697-753.

Davis, D. D. 1964. The giant panda: a morphological study of evolutionary mechanisms. Fieldiana, Zool. **3**: 1-339.

Dobson, G. E. 1882. On the digastric muscle, its modifications and functions. Trans. Linn. Soc. Lond., (Zool.), 2nd Ser., **2**: 259-267.

du Châine, J. 1914. Le digastrique (abaisseur de la mandible des mammifères). J. Anat. Physiol., Paris, **50**: 248-319, 393-417,

Edgeworth, F. H. 1935. The cranial muscles of vertebrates. Cambridge University Press, Cambridge. 493 p.

Fiedler, W. 1952. Zur Gliederung der Kaumuskulatur bei den Säugetieren. Verhandl. Anat. Ges. **50**: 354-361.

Fox, R. C. 1964. The adductor muscles of the jaw in some primitive reptiles. U. Kans. Publs. Mus. Nat. Hist. **15**: 657-680.

Frick, H. 1957. Über die Trigeminusmuskulatur und die tiefe Facialmuskulatur von *Orycteropus aethiopicus*. Z. Anat. Entwgesch. **116**: 202-217.

Hiiemäe, K. M. 1966. The development, structure and function of the mandibular joint in the rat. Ph. D. Thesis, unpubl., Univ. Lond.

Kawamura, Y. 1964. Recent concepts of the physiology of mastication, p. 77-109. *In* P. H. Staple [ed.], Advances in Oral Biology. Vol. I. Academic Press, New York.

Lubosch, W. 1938. Muskeln des Kopfes: Viscerale Muskulatur (Fortsetzung). D. Säugetiere, p. 1065-1105. *In* Bolk, Göppert, Kallius and Lubosch [eds.], Handbuch der vergleichenden Anatomie der Wirbeltiere 5. Urban and Schwarzenberg, Berlin and Vienna.

Miller, M. E., G. C. Christensen and H. E. Evans. 1964. Anatomy of the dog. W. B. Saunders Co., Phil. 941 p.

Parsons, F. G. 1892. Some points on the myology of rodents. J. Anat. Physiol., Lond., **26**: x-xiii.

——————— 1896. Myology of rodents. Part II. Proc. Zool. Soc. Lond. **1896**: 159-192.

——————— 1898. The muscles of mammals with special relation to human myology. J. Anat. Physiol., Lond., **32**: 428-450.

————— 1899. The joints of mammals compared with those of man. J. Anat. Physiol., Lond., **34**: 41-68.

Schumacher, G. H. and H. Rehmer. 1962. Über einege Unterschiede am Kauapparat bei Lagomorphen und Rodentia. Anat. Anz. **111**: 103-122.

Scott, J. M. 1955. Growth changes in the glenoid fossa. Dent. Practnr. Dent. Rec. **6**: 117-120.

Sicher, H. 1944. Masticatory apparatus in the giant panda and the bears. Field Mus. Nat. Hist., Zool. Ser., **29**: 61-73.

Simpson, G. G. 1945. The principles of classification and a classification of mammals. Bull. Am. Mus. Nat. Hist. **85**: 1-350.

Toldt, C. 1904, 1905. Der Winkelfortsatz der Unterkiefer beim Menschen und bei Säugetieren und die Beziehungen der Kaumuskulatur zu demselben. Sber. Acad. Wiss. Wein., Abt. 2, **113**: 43-108; Abt. 3, **114**: 315-376.

Tullberg, T. 1899. Uber das System der Nagethiere: eine phylogenetische Studie. Nova Acta R. Soc. Scient. Upsal., Ser. 3, **18**: 1-514.

Turnbull, W. D. [in press]. The mammalian masticatory apparatus. Fieldiana, Geol.

FIGURE SECTION

The following abbreviations refer to Figures 4, 8, 9 and 10.

MUSCLES

External adductor, EA; Internal adductor, IA; Posterior adductor, PA; Superficial masseter, SM; Internal pterygoid, IP; External pterygoid, EP; Digastric, posterior belly, Dpb; anterior belly, Dab; Mylohyoid, Mh; Geniohyoid, Gh; Genioglossus, Gg; Hyoglossus, Hh; Buccinator, B.

FASCIA AND TENDONS

Temporal fascia, Tf; Masseteric fascia, Mf; Adductor tendon, At; Internal tendon, It (of either external adductor or internal ptery-goid as shown); Tendon of superficial masseter, Smt.

Figures 8, 9 and 10

Serial coronal (C$_{A-D}$), horizontal (H$_{A-E}$), and sagittal (S$_{A-E}$) sections of the heads of adult *Didelphis* to show the internal archi-tecture of the masticatory musculature at various levels. The orien-tation and labeling of each section is shown in the key diagram.

The following symbols are used:

	Bone
– –	Thick fascia
—	Internal tendons
●	Fibers cut transversely
—●	Fibers cut longitudinally
◢	Fibers cut obliquely, the "head" rep-resents the cut surface, the "tail" shows the direction and approximate angle of the fiber.

FIG. 1. *Didelphis marsupialis:* dorsal view of the articulated skull and lower jaw. Young adult, actual size.

FIG. 2. *Didelphis marsupialis:* lateral view of articulated skull and lower jaw. Actual size.

FIG. 3. *Didelphis marsupialis:* inferolateral view of articulated skull and lower jaw to show the position of the squamo-dentary joint and the inflected angle of the lower jaw. Actual size.

FIG. 4. The bony attachments of the masticatory muscles in *Didelphis:*
A) lateral view of the skull and lower jaw; B) medial view of the lower
jaw; C) dorsal view of the articulated skull and jaw; D) inferolateral view
of the articulated skull and lower jaw.

C

D

FIG. 4. cont.

FIG. 5. Lateral view of a *Didelphis* head after removal of the skin and dermal musculature to expose the temporal and masseteric fascia, the underlying adductors and the superficial masseter.

FIG. 6. Lateral view of a dissected head of *Didelphis* after reflection of the external adductor, exposing the internal tendon continuous with the coronoid process. Reflection of the superficial masseter shows the position of the lower part of the external adductor.

FIG. 7. Lateral view of the head of a dissected specimen of *Didelphis* to show the relationships of the coronoid process, the internal tendon and the adductors.

FIG. 8. Coronal sections of a head of *Didelphis*. The posterior surface of each section is figured. The left hand side of each section is in a plane slightly anterior to the right hand side. For position of sections, see p. 33.

FIG. 8. cont.

FIG. 9. Horizontal sections of a head of *Didelphis* viewed from below. The upper half of each section is in a plane slightly ventral to the lower. For position of sections, see p. 33.
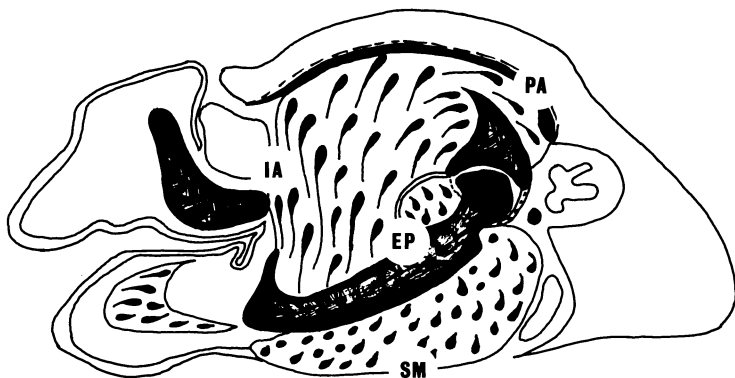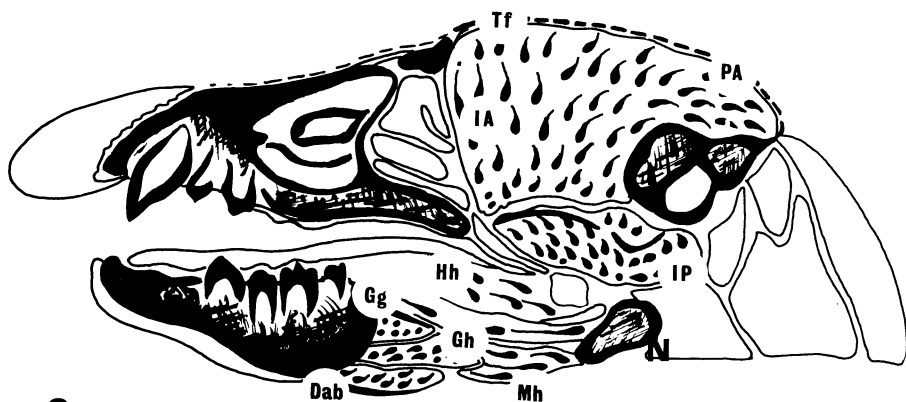
D

E

FIG. 9. cont.

FIG. 10. Sagittal sections of a head of *Didelphis*. Sections A-D show the outer (lateral) surface of each section, section E the inner (medial) surface of a section from the other side of the head. For position of sections, see p. 33.
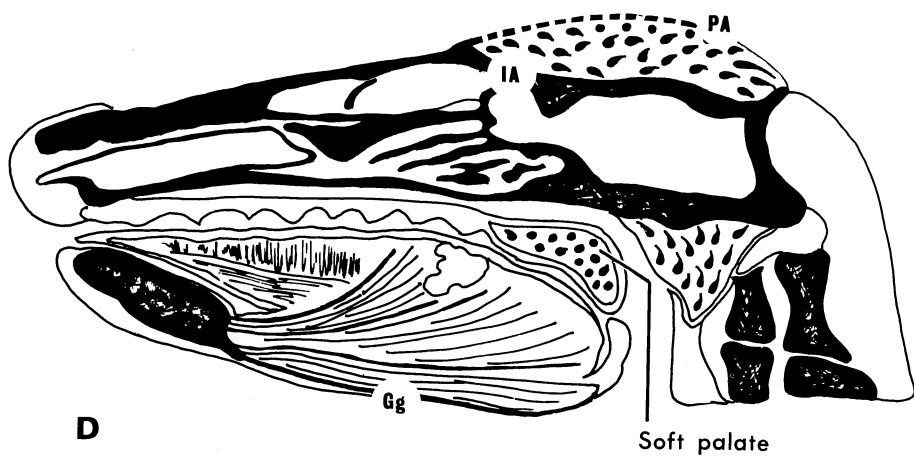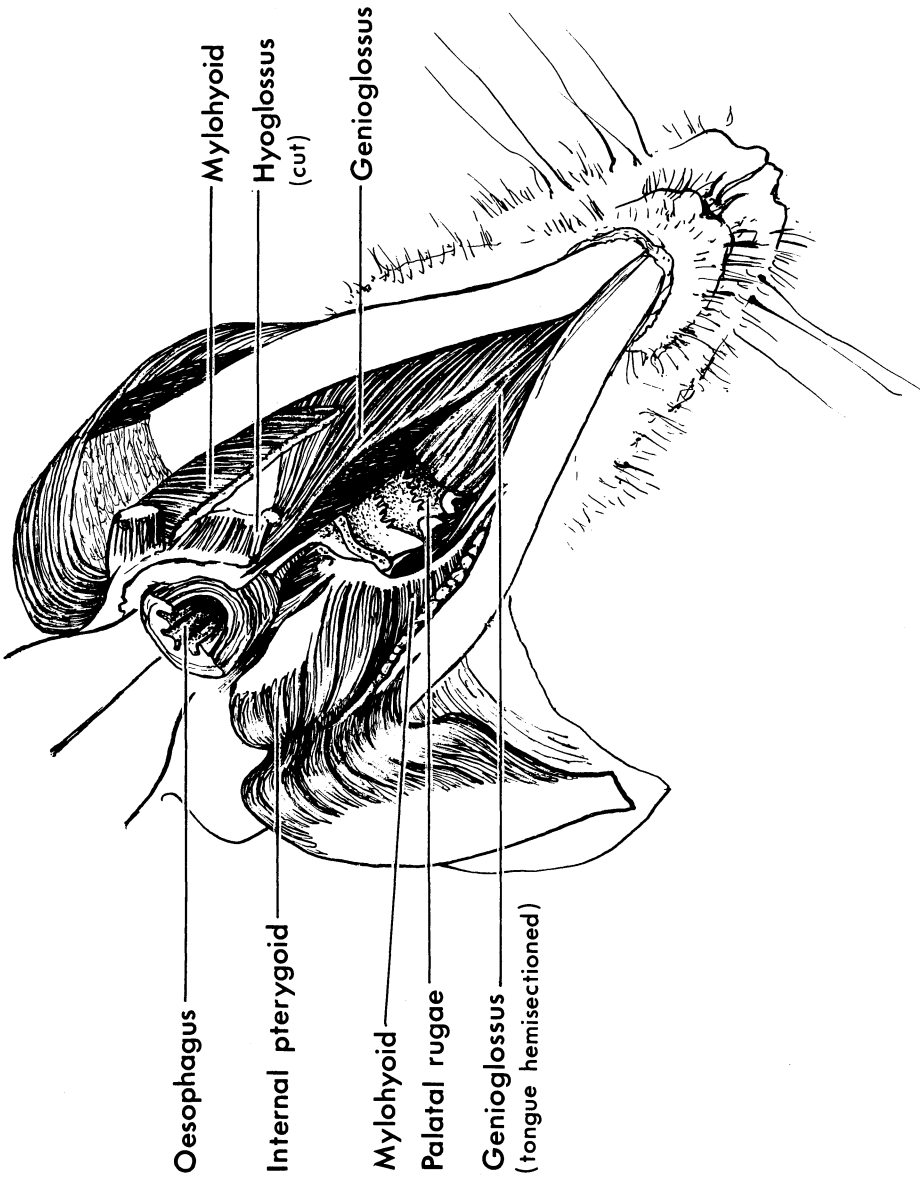
FIG. 10. cont.

FIG. 11. Ventral view of a head of *Didelphis* after removal of the supra-hyoid musculature to show the relationships of the superficial masseter, the internal pterygoid, and the mylohyoid.
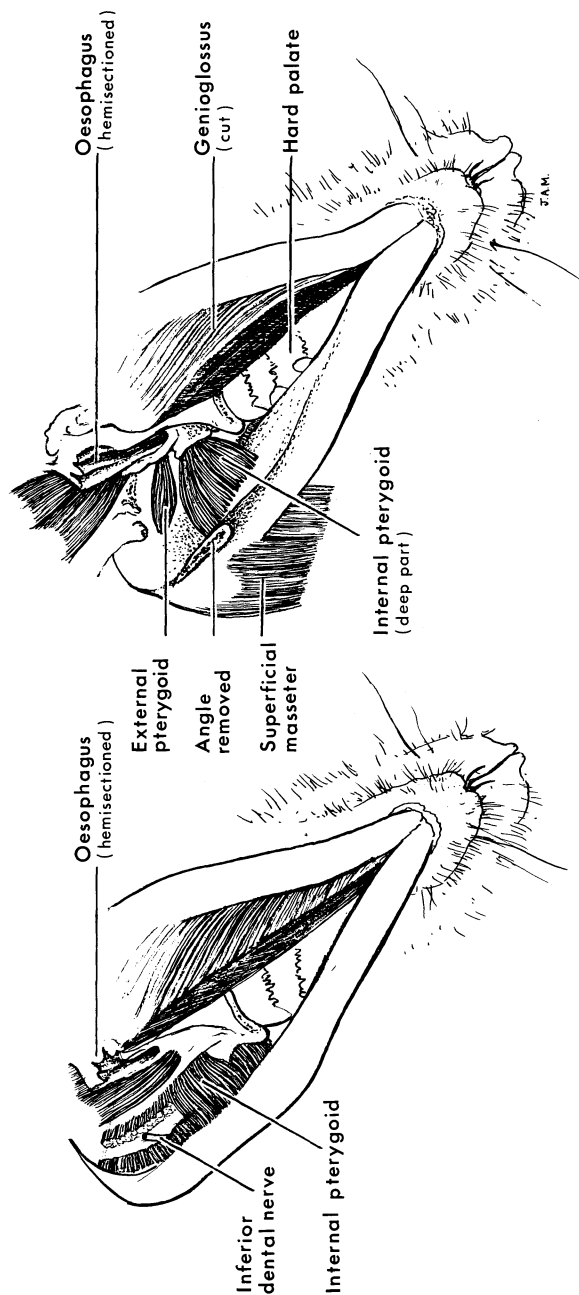
FIG. 12. Ventral views of the head after removal of: a) the posterosuperficial part of the internal pterygoid to show its relation to the inferior dental nerve, and b) after removal of the greater part of the internal to expose the external pterygoid.

Oesophagus
and trachea

Post. belly of
Digastric

Tendinous arcade
overlying hyoid

Superficial
masseter

Ant. belly of
Digastric

External
adductor

Mylohyoid

Buccinator
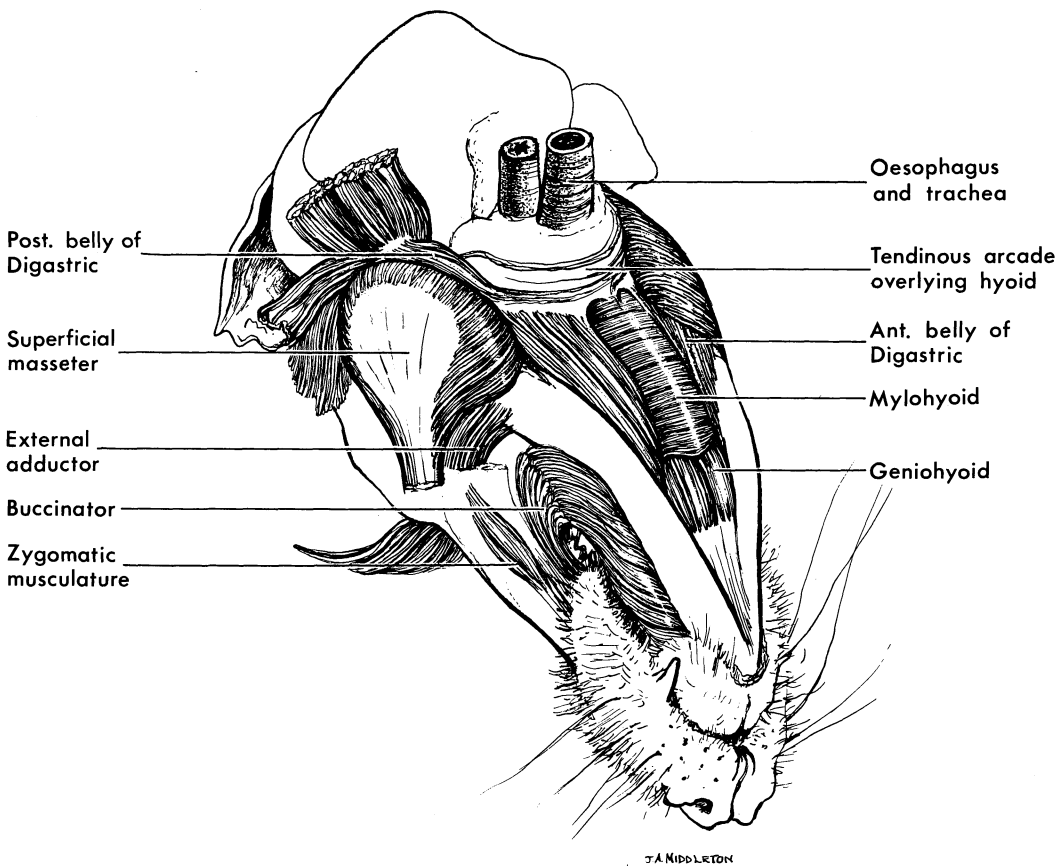
Geniohyoid

Zygomatic
musculature

J.A. MIDDLETON

FIG. 13. Ventral view of the head, after removal of the skin and superficial fascia, to show the relationships of the suprahyoid muscles.
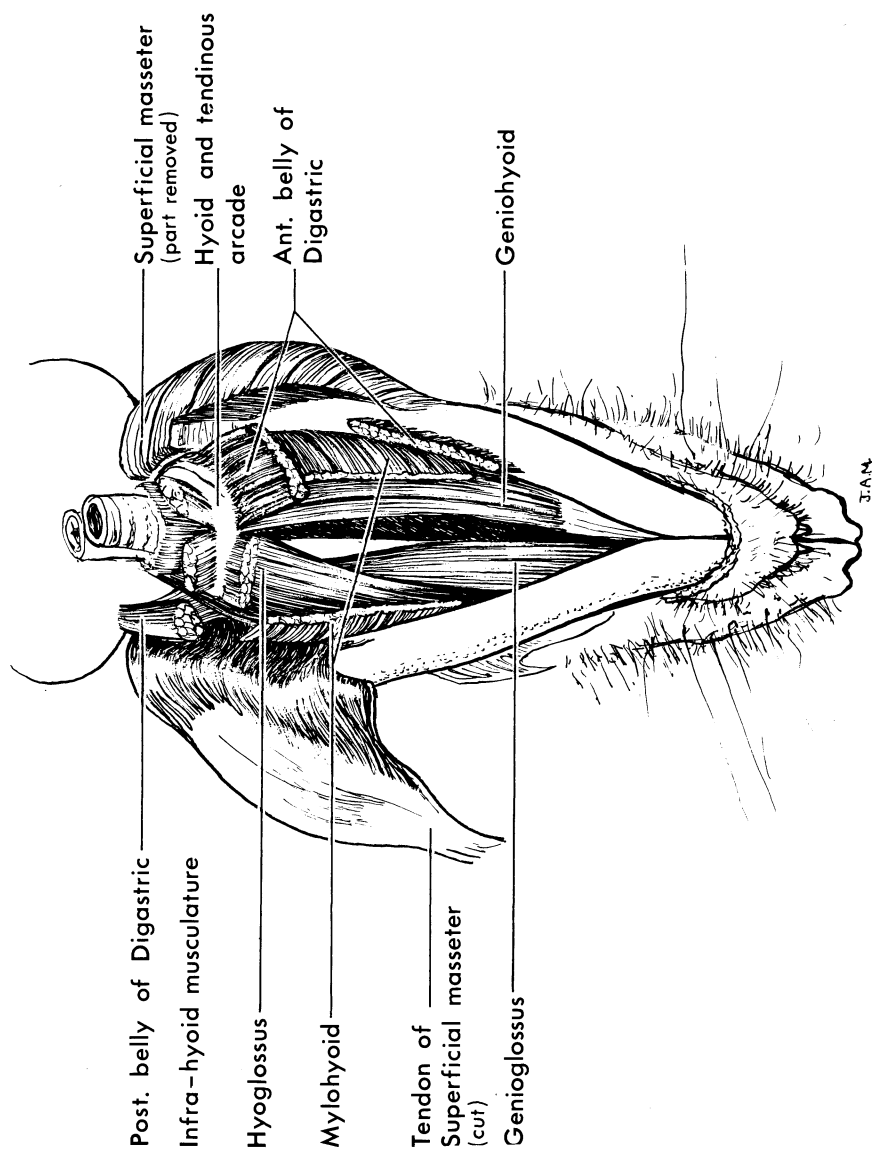
FIG. 14. Ventral view of the head, after removal of parts of the digastric and mylohyoid, to show the arrangement of the hyoid and tongue musculature.

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