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A Comparative Study on the Masticatory Apparatus of a Rodent and a Lagomorph

Robert John Pollock

Loyola University Chicago

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A COMPARATIVE STUDY ON THE MASTICATORY APPARATUS
OF A RODENT AND A LAGOMORPH

by

Robert J. Pollock, Jr.

A Thesis Submitted to the Faculty of the Graduate School
of Loyola University in Partial Fulfillment of
the Requirements for the Degree of
Master of Science

June
1962
LIFE

Robert John Pollock, Jr. was born April 15, 1933 in Oak Park, Illinois.

He attended elementary school and high school in Oak Park being graduated from Oak Park-River Forest Township High School in January 1951. From March 1951 to August 1952 he attended Northwestern University, College of Liberal Arts. In September 1952 he entered Northwestern University Dental School and was graduated in June 1956 with a Doctor of Dental Surgery degree.

Upon graduation from dental school, he was appointed an Instructor in Prosthetic Dentistry at Northwestern University. From October 1956 to October 1958 he served in the United States Air Force.

Upon discharge he entered private practice in Oak Park and in January 1959 was appointed an Instructor in Operative Dentistry at Northwestern University. In September of 1959 he enrolled in the Graduate School of Loyola University to pursue a Master of Science degree in the Department of Oral Biology.

He was appointed a Teaching Fellow in Anatomy and Periodontia at Loyola University and entered the Teacher Training Program, sponsored by the National Institutes of Health, in January of 1960.
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Thanks are due Dr. John O'Malley and Dr. David Jones who with the above served on my advisory board. Mr. John Blickenstaff photographed and printed the roentgenograms and was always ready to advise me on photographic techniques.

Finally, special gratitude is due to my wife whose patience and understanding knew no bounds and whose help in typing the preliminary copies of the thesis is greatly appreciated.
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CHAPTER I
INTRODUCTION

For many years Lagomorpha were classified as a suborder of Rodentia under the name Duplicidentata, and contrasted with the other rodents, the Simplicidentata. It was not until 1912 that Gidley proposed that Lagomorpha be given ordinal status, and it was not until recently that this classification has become generally accepted. It is noteworthy that both classifications were based largely on structures of the masticatory apparatus. In spite of this no comparative study of the total masticatory apparatus of these two groups has been reported in the literature.

It was the purpose of this investigation to make an integrated study of the structure and function of the various parts of the masticatory apparatus, namely skeleton, teeth, mandibular articulation, and muscles, in a rodent and a lagomorph and to compare the two orders.
CHAPTER II
REVIEW OF THE LITERATURE

Although differences between rodents and lagomorphs were noted in the literature prior to 1912 taxonomists had considered these differences insufficient to give lagomorphs ordinal status and instead had simply set lagomorphs apart from other rodents by the subordinal designations Simplicidentata, including all of what is now considered the order Rodentia, and Duplicidentata, now classified as the order Lagomorpha. In 1912 Gidley first proposed that lagomorphs be given independent ordinal status and defined the following basic differences between them and rodents to support his viewpoint.

<table>
<thead>
<tr>
<th>Lagomorpha</th>
<th>Rodentia</th>
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<tr>
<td>1. Incisors, 4 above (functional) 6 in young individuals.</td>
<td>1. Incisors, 2 above, never more than 2 in young individuals.</td>
</tr>
<tr>
<td>2. Functional premolars, 3 above and 2 below.</td>
<td>2. Functional premolars, never more than 1 above and 1 below.</td>
</tr>
<tr>
<td>3. Dental Formula $I_1^2$, $Pm_{32}^3$, $M_{32}^3$, or $\frac{3}{2}$, rarely $\frac{2}{2}$.</td>
<td>3. Dental Formula $I_1^4$, $Pm_{10}^{102}$, or $\frac{0}{0}$, $M_{33}^{33}$, or $\frac{3}{2}$.</td>
</tr>
<tr>
<td>4. Palate broad, distance between upper tooth rows much greater than the lower.</td>
<td>4. Palate progressively narrow, distance between upper tooth rows less than lower.</td>
</tr>
</tbody>
</table>
Surfaces of glenoid fossa divided into two parts, an anterior ridge and a posterior pocket, thus limiting the jaws to lateral motion only in chewing.

Cheek tooth row in plane with ascending ramus of lower jaw.

Caecum in spiral fold.

Elbow joint modified, not permitting of rotary motion of the forearm.

Fibula fused with tibia, distally, and articulating with calcaneum.

Other differences than those given above might be added, but these, if properly weighed are sufficient to warrant separate orders.

This classification was not however generally accepted until recent years, and many prominent investigators such as Weber (1927), Forester (1928), Simpson (1931), and Becht (1953) continued to use the old classification long after Gidley's paper. Simpson (1931) in his first attempt at a classification of mammals stated that "The classification of rodents is one of the most vexatious of taxonomic problems" and that "the available classifications are based on conflicting taxonomic criteria, and diametrically opposed and largely unestablished views of evolutionary trends".

Simpson (1945) in his classic paper "The Principles of
Classification and a Classification of Mammals" placed lagomorphs and rodents in separate orders and stated, "Subsequent discoveries have supported Gidley even more than he could have anticipated". Thus it is now firmly established that rodents and lagomorphs comprise two distinct orders.

Considering the wide use of various lagomorphs and rodents as laboratory animals it is surprising how meager the literature is in the area of descriptive anatomy. Krause (1884) and Craigie (1957) dealt superficially with the anatomy of the head and neck of the rabbit. Flower (1885) discussed the osteology of the rodent skull superficially still including lagomorphs under rodents. Flower and Lydekker (1891) attempted to describe the many characteristics of rodents, often contrasting Duplicidentata with other rodents. Toldt (1905) described the lower jaw and the major muscles of mastication in numerous rodents. Broman (1919) described the transverse palatine muscle in rodents. Greene (1935) presented an excellent text on the detailed morphology of the rat. Papers dealing with the teeth and their supporting apparatus included Orban (1925) on the rabbit and Sicher (1923), Gottlieb and Greiner (1923), and Hunt (1959) on the guinea pig. Numerous papers, including Addison and Appleton (1915), Schour and Steadman (1935), Hoffman and Schour (1940), Herzberg and Schour (1941), and Schour and Massler (1942), deal with the continuously growing incisor in the rat.

Comparative anatomic studies of the teeth are numerous if
not always accurate and include Osborn (1907), deTerra (1911), Todd (1918), Thompson (1919), Simkins (1937), and Scott and Symons (1952). Few comparative studies have dealt with other parts of head and neck anatomy. Forester (1929) did a study using the guinea pig, rat, and rabbit, but he limited the study to the masseter and lateral pterygoid muscles and was hampered by the fact that he still considered the rabbit as a rodent. In 1949 DuBrul wrote an excellent paper relating posture and locomotion to skull morphology in lagomorphs and rodents. Becht (1953) investigated the relation of structure and function in the masticatory apparatus of Carnivora, Rodentia, in which he included the rabbit, and Ungulata, but treated the subject very generally. In 1955 Lonnerblad studied carnivores, rodents, and ungulates comparing their "mouth organs". The major emphasis of this paper was on the teeth and most of the text was a review of previous studies.
CHAPTER III
MATERIALS AND METHODS

For purposes of this study the squirrel was selected as an example of a rodent and the rabbit as an example of a lagomorph. Data from unpublished studies on the guinea pig and rat was used to supplement the findings in the rodent. The masticatory apparatus was studied in detail relating structure and function, and comparing the findings in the two animals. The following materials and methods were used:

1. Dry skulls were obtained and used to investigate the osteology of the head. Squirrel skulls\(^1\) included one of each the grey squirrel and the ground squirrel. Both of the rabbit skulls\(^2\) were from New Zealand white rabbits.

2. The soft tissues were studied macroscopically by dissection of three grey squirrels and three New Zealand white rabbits. The animals used in dissection were obtained alive, killed, and preserved in 20% alcohol.

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1 I am indebted for the loan of these skulls to Mr. Dwight Davis of the Chicago Natural History Museum.

2 One skull was obtained on loan from Dr. A. J. Farchione and the other was purchased from the General Biologic Supply House, Chicago, Illinois.
3. Lateral roentgenograms of bisected heads were used to determine the morphology and position of the condyle in various functional positions of the mandible.

4. The mandibular joint of one squirrel and one rabbit was dissected and studied macroscopically.

5. Observations were made on living squirrels and rabbits during feeding to determine the normal pattern of mandibular movements. In addition close up motion pictures were made and studied of a rabbit during feeding.
CHAPTER IV

FINDINGS

A. RABBIT

1. Skull (Figs. 1-8)

In a study on "Posture, Locomotion and the Skull in Lagomorpha", DuBrul gave an excellent overall description of the rabbit skull as follows:

"The gross outline of the rabbit skull in norma lateralis is that of a relatively uniform deep oval. The greatest diameter passes from the height of contour of the upper incisor teeth on their outer surface immediately below the alveolar margin caudad to the tip of the external occipital protuberance. The vertical dimension is greatest just posterior to the molar teeth and runs from the anterior supra-orbital process ventrally to the inferior border of the mandible at its expansion immediately caudad to the pre-gonial notch.

Purely for purposes of convenience the long axis of the skull will be oriented in a horizontal plane. The vault of the skull will be designated as superior (upward), the lower border of the jaw as inferior (downward), the incisal area as anterior (forward), and the occipital region as posterior (backward). It will be seen clearly later that the true postures and planes of the head are highly susceptible to adaptive, functional and evolutionary influences and that this is an extremely arbitrary orientation. Further, and in accordance with the above, the skeleton of the head will be divided into three major components.

The basic posterior or cranial component is attached directly to the vertebral column. It is conical in form with the
base of the cone surrounding the foramen magnum facing downward and backward (posteroinferiorly). Its apex is directed sharply upward and forward and is terminated by a small truncating surface, the cribiform plate of the ethmoid. The anterior and inferior surface of this cone forms the true base of the skull and floor of the brain case. It affords attachment for the facial component.

The second or facial component assumes the shape of a four-sided pyramid. The nasal bones form the superior surface, the roof of the mouth forms the inferior, while the premaxilla and maxilla contribute to the formation of the flattened lateral walls. The base of this pyramid facing upward and backward toward the cranial floor is separated from the latter by a large depression on either side of the skull, the orbital fossae. Its apex terminates in the downward curving central incisors. The cranial and facial components are welded together at the central keel-like portion of the cranial base and are greatly strengthened by lateral buttresses, the zygomatic arches.

The third component of the head skeleton is the mandible, most conveniently thought of as two flattened irregular triangles joined at their apices and flaring outward toward their bases. The base of either side is directed posteriorly and is formed by the angular process below and the head of the articular condyle above by means of which it contacts the cranial portion at its lateral surface. The apex is formed by the upward-curving mandibular incisor which, together with the aid of the molar teeth, affords contact with the facial component."

Some details of the osteology of the masticatory apparatus have to be added.

The upper jaw (Figs. 1, 2, 4, 5) is composed of the premaxilla, the maxilla, and the palatine bone. The premaxilla consists of a body and three processes: the alveolar process, the palatine process, and the frontal process. The body of the premaxilla continues anteroinferiorly as
a short alveolar process forming the sockets of both the large anterior incisor and the small posterior incisor. Much more of the anterior and lateral enamel covered surface of the anterior incisor is exposed than of the medial and posterior surfaces of this tooth. The body of the premaxilla that houses the larger part of the incisor is smooth on its inferior and lateral surfaces. The inferior surfaces of the bodies of the premaxilla meet at the midline just behind the incisors but are separated more posteriorly by the incisive foramina. The palatine processes of the premaxilla project as thin and elongated bony plates posteriorly from the apposed portion of the bodies. They join in the midline and separate the anterior part of the incisive foramina. The long, narrow frontal process projects posteriorly and slightly superiorly from the posterosuperior part of the body and separates the nasal and maxillary bones ending in a suture with the frontal bone.

According to Craigie the maxilla consists of a body and five processes: the palatine process, the alveolar process, the zygomatic process, the orbital process, and the sphenoorbital process. The bodies of the maxillae bound laterally the posterior part of the incisive foramina. The lateral surface of the body is thin and fenestrated. It meets the body of the premaxilla anteriorly and the frontal process of the premaxilla superiorly. The palatine processes of the maxillae arising from the posterior part of the body, meet in the midline and form the anterior half of a stout bridge
of bone which connects the two sides of the upper jaw in the region of the premolars and first molars. The posterior half of this bony bridge is formed by the palatine process of the palatine bone. The anterior border of the palatine processes of the maxillae form the posterior border of the incisive foramina.

The alveolar process projects downward from the body and contains the sockets for the three premolars and three molars. The cheek teeth appear as two parallel, widely separated rows. Their distance is greater than that between the right and left mandibular teeth. The alveolar processes of the maxillae extend further downward on the lateral surfaces of the cheek teeth than on their medial surfaces.

The zygomatic process projects laterally from the base of the alveolar process and from the posteroinferior corner of the body. The zygomatic process forms the anterior root of the zygomatic arch. A bony prominence, the masseteric tubercle, appears on the inferolateral portion of the zygomatic process. The masseteric tubercle is flat but roughened below for the attachment of the anterior tendinous part of the masseter muscle. Posteriorly the zygomatic process is fused to the zygomatic bone. According to Craigie, "the position of the original suture being roughly identifiable as the point where the free horizontal portion of the zygomatic arch arises from the transverse zygomatic process".
The orbital process projects laterally from the posterior portion of the body of the maxilla and helps to form the anterior border of the orbit. The spheno-orbital process forms a small part of the medial wall of the orbit. A thin sheet of bone, a part of the maxilla, covers the basal end of the last premolar and three molars which project upwards into the anteroinferior part of the orbit.

The palatine bone is formed by two plates, a horizontal and a vertical, joined at right angles. The horizontal palatine plate is joined anteriorly to the palatine process of the maxilla. Together the horizontal plates of the palatine bones and the palatine processes of the maxillae form a stout horizontal bridge of bone which is narrow anteroposteriorly. The posterior border of the horizontal plate is concave. In the midline the two plates project backward as the posterior nasal spine. This bilaterally concave border is the posterior border of the hard palate and lies in line with the posterior surfaces of the first molars. The greater palatine foramen is found in the suture between the palatine bone and maxilla. The vertical plate of the palatine bone forms the smooth lateral wall of the nasopharyngeal duct. The medial plate extends posteriorly as a narrow bar that continues, bending downward into the strong pyramidal process. It fills the pterygoid notch between the medial and lateral pterygoid plates of the sphenoid bone.
The pterygoid process (Figs. 4, 5) of the sphenoid bone is formed by the medial and lateral pterygoid plates. The medial pterygoid plate lies in a sagittal plane and forms the lateral wall of the nasopharynx. The inferior end of the medial plate forms a sharp projection, the hamular process. The lateral pterygoid plate is thin and slants anteriorly and inferiorly at an angle of about 45°, presenting an anterosuperior and a posteroinferior surface. The two pterygoid plates form the pterygoid fossa. The root of the pterygoid process is perforated by a round foramen that leads from the pterygoid fossa into the temporal fossa. The pterygoid process lies medially and anteriorly to the cranial articular surface of the mandibular joint.

The zygomatic arch (Figs. 3, 4, 5) serves for the attachment of the masseter muscle. The anterior root is formed by the zygomatic process of the maxilla. The greater posterior part of the arch is formed by the zygomatic bone, a roughly rectangular plate which lies in a sagittal plane. Anteriorly it is fused to the zygomatic process of the maxilla. Posteriorly the zygomatic bone projects beyond the posterior root of the arch which is formed by the zygomatic process of the squamosal bone. The zygomatic process of the squamosal bone is made up of a triangular plate of bone in a sagittal plane and a horizontal base with a smooth inferior surface which forms the cranial portion of the mandibular articulation. The
articulat surface (Fig. 9) is short and convex anteroposteriorly, much longer and concave mediolaterally.

Two faint horizontal ridges are seen on the posterior wall of the orbit at about the level of the mandibular articulation. These ridges are marked by numerous small bony projections and serve for the attachment of part of the temporal muscle. A smooth sulcus, which Craigie calls the temporal fossa, just above the posterior root of the zygomatic arch serves for the passage of a portion of the temporal muscle from its origin on the neurocranium into the orbit where it merges with the rest of the muscle. This sulcus is bridged by the posterior supraorbital ligament which attaches to the posterior supraorbital process above and the posterior root of the zygomatic process below.

The mandible (Figs. 6, 7, 8) is a V-shaped bone made up of two halves immovably joined at the apex, symphysis, by fibrous connective tissue. Each half consists of a strong, thick body which bears the incisors and the cheek teeth, and a thin, largely translucent ramus which serves for the attachment of the major muscles of mastication and carries the condyle for the articulation of the mandible to the cranium.

The symphysis is long anteroposteriorly and extends posteriorly to the plane of the third premolar. The superior aspect of the symphysis is marked by a shallow groove which deepens posteriorly and is bounded
by the anterior part of a sharp but low ridge which continues on the otherwise smooth superior surface of the body. This ridge runs to the level of the third premolar and serves to attach the supramandibular muscles. The lower incisors project from the anterior end of the mandibular body on each side of the symphysis. On the inferior surface the symphysis appears as a suture in a median ridge.

Viewed from the lateral aspect the body is triangular. The inferior border forms a gentle curve with the convexity facing inferiorly and continuing smoothly with the labial surface of the incisors. The mental foramen is seen just below the superior border and just anterior to the cheek teeth. The cheek teeth and their alveolar process project from the superior aspect of the body in its posterior half. Whereas the two halves of the body diverge posterior from the symphysis, the cheek teeth form two parallel rows, and thus the alveolar process and the mandibular body are not situated in the same plane. The posterior portion of the body continues into the ramus being demarcated from it on the lateral surface by the mas­setteric ridge. The ramus continues in the same plane as the divergent portion of the body. The ramus extends into three processes: the angular process, the coronoid process, and the condylar process. The ramus is a thin, translucent plate of bone being reinforced by a thickening of its borders.

Viewed from the lateral aspect the outline of the ramus is
irregular. The inferior border is convex and projects somewhat below the inferior border of the body. This convexity continues into the inferior third of the posterior border ending in the angular process which is approximately in the same plane as the superior border of the body. A J-shaped notch completes the contour of the posterior border and separates the angular process from the condylar process which forms the blunt superior end of the ramus. The anterior border of the ramus then slopes anteriorly and inferiorly to end just posterior to the last molar. The masseteric ridge which separates the ramus from the body continues along the inferior and posterior convexity to the angular process and makes the whole lateral surface of the ramus appear slightly depressed. The depression is the area of attachment of the masseter muscle.

The anterior border of the ramus is thickened by two ridges separated by a groove, the sulcus ascendens, which serves for the attachment of the temporal muscle. The inferior end of the groove is perforated by a foramen through which passes a vein. The lateral ridge carries the short coronoid process which curves somewhat medially over the sulcus ascendens. The medial ridge projects medially as well as anteriorly giving to medial surface of the ramus an even more depressed appearance than the lateral surface shows.

Medially the inferoposterior convex border of the ramus is
raised and even hooks slightly over the depression for the attachment of the medial pterygoid muscle. The mandibular foramen is found at the junction of the ramus and body just below the superior border of the body. A low ridge runs obliquely posterosuperiorly from the inferior border of the mandibular foramen to the posterior concave border of the ramus and divides the medial surface into two fields. The medial pterygoid muscle inserts into the posteroinferior field, and the temporal muscle inserts into the greater part of the anterosuperior field.

The condylar process (Fig. 10) continues the ramus posteriorly and superiorly and is divided into an anterior part that carries the articular surface and a posterior part that ends in a rounded corner. The superior border of the condylar process behind the articular surface is a rather sharp ridge that bends slightly medially. The posterior border of the condylar process continued downward into the posterior border of the ramus. The articular surface is shaped somewhat like a comma if viewed from above. The body of the comma lies anteriorly, the tail posteriorly curving slightly laterally. The entire articular surface is convex in all directions.

2. Dentition (Figs. 1, 2, 4, 6, 11, 12)

The dental formula of the rabbit is $I_1^2$, $C_0^0$, $P_3^3$, $M_3^3$. The incisors are located in the atrium of the oral cavity while the premolars
and molars are located in the oral cavity proper. Both the incisors and the cheek teeth of the rabbit are continuously growing teeth.

The incisors form a segment of a logarithmic spiral. The upper large incisor forms a greater segment of a smaller spiral while the lower incisor forms a smaller segment of a larger spiral. The large incisors are approximately twice as wide mediolaterally than anteroposteriorly. The lower incisor is slightly wider mediolaterally than the upper anterior incisor. The small posterior incisor is elliptical in transverse section with a slightly longer mediolateral than anteroposterior axis. The upper large incisor has a vertical groove on its anterior surface. The upper posterior incisor and the lower incisor are not grooved. The bulk of the incisal end of the tooth is composed of dentine. The large pulp cavity can be seen only as a pinpoint opening at the center of the incisal bevel. The anterior surface of the incisor is covered with unpigmented enamel while the medial, lateral, and posterior surfaces are covered with cementum. The basal end of the upper incisors (Fig. II) lie in the body of the premaxilla. The basal end of the lower incisor (Fig. II) lies in the body of the mandible medial to the third premolar.

The exposed portion of the large gnawing upper incisor curves downward and slightly backward while that of the smaller upper posterior incisor curves downward and slightly forward. The exposed
portion of the lower incisor curves forward and slightly upward. Due to lack of enamel on posterior, medial, and lateral surfaces of the large incisors the back of the tooth wears more rapidly than the front. Thus, large, concave, but short wear facets bevel the posterior surface in such a way that a sharp edge of enamel is maintained. The bevel of the upper large incisor faces backward and very slightly downward while the bevel of the lower incisor faces upward and slightly backward. The upper posterior incisor is only slightly beveled. Its bevel faces inferiorly and slightly anteriorly.

The cheek teeth are continuously growing and folded, ptychodont, in form. The premolars and molars are morphologically similar. The occlusal surfaces are marked by high, sharp, transverse ridges and deep transverse grooves. The upper cheek teeth are all of approximately equal size except for the second premolar which is slightly smaller and the third molar which is rudimentary. The lower premolars and molars are also of equal size except for the diminutive third molar.

3. Mandibular Articulation (Figs. 9, 10, 11, 12)

Mandibular articulation is formed by the articular surface of the squamosal bone (Fig. 9) and the articular surface of the mandible (Fig. 10). A disc is interposed between the two bony articular surfaces and separates the joint into an upper and a lower compartment.
The smooth articular surface of the squamosal bone (Fig. 9) is situated on the inferior surface of the posterior root of the zygomatic process and is slightly raised from the surrounding bone. It faces backward and downward. The mediolateral dimension of the articular surface is approximately twice that of the anteroposterior dimension. The articular surface is oval with an indented posterior border. The articular surface is convex in its anteroposterior dimension but strongly concave mediolaterally. This concavity makes the articular surface appear almost tent shaped. A depression is seen above the articular surface on the posterior surface of the root of the zygomatic process. Craigie calls this the mandibular fossa, but it takes no part in the joint.

The smooth, comma shaped articular surface of the mandible (Fig. 10) is situated on the superior aspect of the condyle and is slightly raised above the posterior part of the superior surface. The body of the comma lies anteriorly, the tail posteriorly curving slightly laterally. The articular surface is convex anteroposteriorly and mediolaterally. It faces upward and slightly forward. The border of the articular surface is sharp anteriorly, medially, and laterally.

The disc divides the joint into two compartments. If the disc is cut in a sagittal plane it appears thin near its center and progressively thickens both anteriorly and posteriorly. Cut in a frontal plane the
The disc is more uniform in thickness and thickens only slightly at its edges. The disc is fused to the capsule anteriorly, medially, and laterally, but posteriorly it is connected to the capsule by loose connective tissue. The lateral pterygoid muscle inserts into the anteromedial edge of the disc.

The capsule is very thin. It attaches superiorly to the border of the articular surface of the squamosal bone and inferiorly to the condyle just below the edge of the articular surface. The capsule is quite loose between the squamosal bone and the disc and much tighter between the disc and condyle but still allows some movement of the disc in all directions.

The relation of the articular surfaces of the mandibular joint is seen roentgenographically in Figures 11 and 12.

4. Musculature (Figs. 13-21)

Masseater Muscle

The masseter muscle (Figs. 13, 14, 15) is a large, powerful muscle. It arises by three heads from the zygomatic arch and inserts into the ramus of the mandible. The anterior superficial head arises from the outer surface of the anterior two-thirds of the zygomatic arch and from the inferior surface of the masseteric tubercle at the anterior root of the arch. The anterosuperior portion of the lateral surface of the muscle is tendinous. The fibers run posteroinferiorly to be inserted into the inferior border of
the medial surface of the ramus. A distinct bundle which forms the anterior border of the muscle wraps around the inferior border of the ramus and then turns posteriorly and inserts into the raised inferior margin of the ramus and the tendinous plate on the medial surface of the medial pterygoid muscle.

The anterior deep head is separated from the anterior superficial head posteriorly, but they are fused along the anterior border of the muscle. The anterior deep head arises from the medial surface of the zygomatic arch anterior to the mandibular articulation and from the anterior surface of the posterior root of the arch. The fibers arising from the anterior two-thirds of the zygomatic arch run inferiorly and insert into the lateral surface of the ramus below the occlusal plane of the cheek teeth. The more posterior fibers run inferiorly and medially or anteroinferiorly and medially to insert into a narrow anterior strip of the lateral surface of the ramus above the occlusal plane of the cheek teeth. These more posterior fibers fuse with the adjacent part of the temporal muscle. Toldt considers this part of the anterior deep head and the posterior head to be a separate muscle, the zygomatico-mandibular muscle.

The posterior head arises from the medial surface of the zygomatic arch lateral and posterior to the mandibular articulation. The fiber direction is anteroinferiorly and medially. The posterior head inserts
into the lateral surface of the ramus above the occlusal plane of the cheek teeth.

The anterior superficial head elevates and protrudes the mandible. The anterior deep head elevates the mandible. The posterior head elevates and retrudes the lower jaw.

Medial Pterygoid Muscle

The medial pterygoid muscle (Figs. 15, 16) is easily separated into a medial and a lateral portion. The medial portion arises from the pterygoid fossa and the medial half of the roughened inferior surface of the pyramidal process of the palatine bone and passes inferiorly to insert into the raised inferior border of the medial surface of the ramus. To the superficial tendon near the inferior border of the ramus inserts a bundle of the masseter muscle. The lateral portion arises from the lateral half of the inferior surface of the pyramidal process of the palatine bone and spreads fan-like inferoposteriorly to insert into the posteroinferior portion of the medial surface of the ramus.

The anterior fibers of both heads are nearly vertical while the more posterior fibers of the lateral head run posteroinferiorly. The medial pterygoid muscle functions mainly in closing the jaws. The medial pterygoid muscle acts synergistically and simultaneously with the masseter. Contraction of either the masseter or the medial pterygoid individually
would put a bending force on the ramus, but acting together their bending forces balance each other. The weaker medial pterygoid muscle attaches at a greater angle to the mandible than the stronger masseter muscle with a resultant balance of the bending forces.

Lateral Pterygoid Muscle

The lateral pterygoid muscle (Fig. 17) arises from the lateral surface and posterior edge of the lateral pterygoid plate and from the portion of the pterygoid fossa formed by the pyramidal process of the palatine bone. The muscle passes posteriorly, laterally, and superiorly to insert into the anterior and medial surface of the ramus adjacent to the condyle, the medial edge of the condyle, and the intra-articular disc.

It functions bilaterally in protrusion of the mandible and unilaterally in lateral excursions.

Temporal Muscle

The temporal muscle (Figs. 18, 19) may be divided somewhat artificially into three parts. The first part arises from an irregularly diamond shaped area on the superior surface of the neurocranium. This head passes anteriorly under the posterior supraorbital ligament into the orbit where it becomes tendinous and bends inferiorly to insert into the medial surface of the coronoid process. The other two parts of the muscle arise as two muscular sheets from two parallel ridges on the posterior wall.
of the orbit. These muscular sheets fuse and insert into the upper part of the sulcus ascendens, the whole length of the medial ridge of the sulcus ascendens, and the greater part of the anterosuperior field of the medial surface of the ramus.

The temporal muscle closes the jaws and retrudes the mandible.

Transverse Palatine Muscle

The transverse palatine muscle (Fig. 20) arises from a median ridge which runs along the suture joining the bodies of the pre-maxillae. The most anterior fibers run laterally, but the more posterior fibers angle increasingly posteriorly. The muscle inserts into the upper lip, especially at the corner of the mouth. The muscles function bilaterally to draw the hair covered infoldings of the upper lip (Fig. 22) into the diastema to separate the atrium and the main part of the oral cavity. They seem to act in conjunction with the supramandibular muscles.

Supramandibular Muscle

The supramandibular muscle (Fig. 21) arises from a sharp ridge which runs from a point just posterior to the lower incisors to a point just anterior to the first premolar on the superior surface of the body of the mandible. The muscle fibers run laterally and posteriorly to insert into the infolding of the lower lip and the cheek. (Fig. 22)
The supramandibular muscles function in conjunction with the transverse palatine in closing off the atrium from the main part of the oral cavity.

**Digastric Muscle**

The digastric muscle (Fig. 15) arises by a tendon from the jugular process of the occipital bone. The fleshy anterior portion of the muscle inserts into a roughened field on the medial surface of the body of the mandible below the mylohyoid line and adjacent to the symphysis.

Contraction of the digastric muscle retrudes and depresses the mandible.

**Mylohyoid Muscle**

The mylohyoid muscle (Fig. 23) arises from a line on the upper part of the medial surface of the body of the mandible, extending from the base of the alveolar process below the third molar to the symphysis. The muscle is divided by connective tissue into anterior and a posterior part. The fibers of the anterior part meet those of the opposite side in a median raphe which runs from the symphysis to the hyoid bone. The posterior one-third of the muscle inserts into the inferior surface of the body of the hyoid bone.

Contraction of the anterior fibers raises the floor of the mouth while contraction of the posterior fibers raises the hyoid bone or,
if the hyoid bone is fixed, may depress the mandible.

Geniohyoid Muscle

The geniohyoid muscle arises with a fine tendon from the medial surface of the body of the mandible in the groove at the posterior end of the symphysis. The muscle passes posteriorly and forms a fleshy, fusiform belly which contacts that of the opposite side and inserts into the upper part of the body of the hyoid bone.

The geniohyoid muscle pulls the hyoid bone upward and forward, or if the hyoid bone is fixed, it retrudes and depresses the mandible.

5. Observations on Living Animals During Feeding

In biting off pieces of food the rabbit protrudes the lower jaw and then opens and closes in a hinge-like movement. This brings the sharp edges of the incisors into contact and cuts off bits of food. The food particles are then shifted from the atrium to the oral cavity proper by the tongue.

The chewing movement is initiated by opening of the jaws and a lateral shift of the mandible. The jaws are then closed and the mandible is shifted medially grinding the food between the cheek teeth.

The biting movements are slow and deliberate while the chewing movements are rapid and repetitive. It also appeared that the rabbit uses predominantly one side for chewing during any one feeding.
B. SQUIRREL

1. Skull (Figs. 24-33)

The gross outline of the squirrel skull in norma lateralis (Fig. 24) is that of an ellipse the length of which is approximately twice the width. For the purposes of description the skull will be oriented in a plane running through the external occipital protuberance and the inferior margin of the external nares.

The neural component (Figs. 26, 27, 28) of the cranium is roughly pyramidal in form and articulates with the vertebral column. The base of the pyramid and the foramen magnum face posteriorly. The latter is located in the lower half of the posterior surface of the neurocranium. The apex of the pyramid is directed anteriorly and slightly superiorly and terminates as the cribriform plate of the ethmoid above and medial to the anterior border of the orbits. The base of the skull forms the inferior surface of the pyramid. The facial component attaches to the apex and anterior half of the inferior surface of the neurocranium.

The facial component (Figs. 25, 26, 27, 28) of the cranium assumes the shape of a four sided pyramid with a blunted apex which is formed by the external nares below which the upper incisors project inferiorly. The base of the pyramid faces backward and upward. The roof of the mouth forms the inferior surface, the premaxillae and the maxillae
form the lateral walls, and the nasal bones, the premaxillae, the maxillae, and the frontal bones all contribute to the superior surface. The facial component is separated from the neural component on either side by the orbits and joined to the neurocranial component laterally by the zygomatic arches.

The mandible (Figs. 29, 30, 31) consists of two halves joined anteriorly by a movable symphysis. Viewed from above the mandible appears V-shaped. The lower incisor curves forward and upward from the anterior end. The angular process forms the posteroinferior corner. The condyle forms the posterosuperior corner and articulates with the cranial portion of the skull. The coronoid process hooks upward and backward anterior to the condyle. To this general outline a detailed description of the osteology of the masticatory apparatus must be added.

The upper jaw (Figs. 25, 27, 28) is composed of the premaxillae, the maxillae, and the palatine bones. The premaxilla consists of a body and three processes: the alveolar process, the palatine process, and the frontal process. The short alveolar process projects downward from the anterior end of the body of the premaxilla. The alveolar process forms the anterior portion of the socket of the upper incisor. The superior portion of the socket resides in the body of the premaxilla and the basal end is in the body of the maxilla. The alveolar process covers more of the
medial, posterior, and lateral cementum covered surfaces of the incisor and less of the anterior enamel covered surface.

The body of the premaxilla forms the anterior part of the lateral surface of the facial skeleton and contains the greater portion of the socket of the upper incisor. The medial surface of the body forms the lateral wall of the nasal cavity. The lateral surface of the body is smooth and carries in its posterosuperior corner a slight depression, the anterior part of the masseteric fossa. A sharp ridge which forms the upper margin of the masseteric fossa separates the body and the frontal process.

The frontal process projects posteriorly in a horizontal plane. It lies between the nasal bone and the frontal process of the maxilla, and ends in broad contact with the frontal bone.

The palatine process of the premaxilla curves inferomedially from the inferior edge of the body and meets the palatine process of the opposite premaxilla in the midline. Just lateral to the midline is an anteroposterior slit, the incisive foramen, which is closed posteriorly by the palatine process of the maxilla. The fine lateral palatine ridge runs posteriorly from a point just posterior to the incisor passing just lateral to the incisive foramen and continues on the palatine process of the maxilla to a point just anterior to the third premolar. The lateral palatine ridge serves as the origin of the transverse palatine muscle.
The maxilla consists of a body and five processes: the palatine process, the alveolar process, the zygomatic process, the orbital process, and the frontal process. The body contains the basal end of the socket of the upper incisor. The medial surface of the body forms part of the lateral wall of the nasal cavity. The lateral surface is depressed and with the anterior surface of the zygomatic process forms the greater posterior portion of the masseteric fossa, bounded superiorly by a sharp ridge, the masseteric crest of the maxilla. The slit-like infraorbital foramen is located near the lower edge of the body. The roughened masseteric process or spine forms the lower border of the infraorbital foramen.

The palatine process projects medially in a horizontal plane. It meets the palatine process of the premaxilla anteriorly, the palatine process of the palatine bone posteriorly, and joins the opposite palatine process of the maxilla in the midpalatine suture. The palatine process forms part of the roof of the mouth and the floor of the nasal cavity.

The alveolar process projects inferiorly lateral to the horizontal plate of the palatine bone and the posterior half of the palatine process of the maxilla. The alveolar process forms the sockets of the two premolars and three molars. The superior surface of the posterior part of the alveolar process forms the floor of the orbit.

The zygomatic process projects laterally from the postero-
lateral edge of the body and the base of the alveolar process. The anterior end of the zygomatic bone extends as a rather thin bar forward and upward and joins the posterosuperior surface of the zygomatic process of the maxilla. Together they form the anterior root of the zygomatic arch.

The orbital process is a thin sheet of bone which projects posterosuperiorly from the body and forms part of the medial wall of the orbit. The orbital opening of the infraorbital canal is located at the junction of the zygomatic, orbital, and alveolar processes.

The short, almost square, frontal process projects posteriorly above and behind the masseteric crest of the maxilla and meets the frontal bone posteriorly and the frontal process of the premaxilla medially.

The palatine bone consists of a horizontal and a vertical plate joined at right angles. The horizontal plate forms the posterior part of the hard palate. The horizontal plates meet in the midline and border on the palatine process of the maxilla anteriorly, and the alveolar process of the maxilla laterally. The greater palatine foramen is located in the suture joining the palatine bone, and the maxilla. The posterior border of the horizontal plate is concave. In the midline, the two plates project as the posterior nasal spine. This doubly concave border is the posterior border of the hard palate and lies posterior to the third molars. The vertical
plate forms part of the lateral wall of the nasal cavity and nasopharyngeal duct, and part of the medial wall of the orbit laterally. The smooth stout pyramidal process projects posterolaterally from the posterolateral and inferior corner of the palatine bone and fits into the pterygoid notch between the medial and lateral pterygoid plates of the sphenoid bone.

The pterygoid process of the sphenoid bone (Figs. 27, 28) consists of a large medial and an almost vestigial lateral plate. The medial pterygoid plate is a thin triangular plate of bone posterior to the palatine bone and forms the greater part of the bony lateral wall of the nasopharyngeal duct. The hamular process projects far posteriorly from the posteroinferior corner of the medial pterygoid plate. It reaches to the medial surface of the tympanic bulla. The lateral pterygoid plate in the squirrel is reduced to a low, sharp ridge and runs posterolaterally from the pyramidal process of the palatine bone. The pterygoid fossa lies between the medial and lateral pterygoid plates. The pterygoid process lies directly medial to the cranial articular surface of the mandibular joint.

The zygomatic arch (Figs. 25, 26, 27) serves along with the masseteric fossa for the origin of the masseter muscle. The anterior root of the zygomatic arch is formed by the zygomatic process of the maxilla and the anterior end of the zygomatic bone. The arch curves inferiorly and laterally from its anterior root and then straightens out running
posteriorly and very slightly laterally at the level of the inferior border of the orbit. The posterior root of the arch is formed by the zygomatic process of the temporal bone which projects first laterally then curves inferiorly to join the free part of the arch on its superior edge. The posterior half of the superior edge of the arch is made up of an anterior projection of the zygomatic process of the temporal bone while the rest of the free part of the arch is formed by the zygomatic bone.

The inferior surface of the posterior root of the zygomatic arch forms the cranial articular surface (Fig. 32) of the mandibular articulation. The articular surface is a smooth, sagitally disposed, semicylindrical groove with approximately equal anteroposterior and mediolateral dimensions.

Above the posterior root of the zygomatic arch is a smooth, broad depression, the posterior orbital notch (Figs. 26, 28) in the posterior margin of the orbit which is bridged over by a ligament attaching to the supraorbital process above and the root of the zygomatic arch below. The posterior orbital notch serves for the passage of the major portion of the temporal muscle from its origin on the neurocranium into the orbit.

A low crest, the temporal line, runs posteriorly on the superior surface of the neurocranium from the superior end of the posterior orbital notch to the superior nuchal line which separates the superior and
lateral surface of the neurocranium from its posterior surface. The tem-
peror line and the superior nuchal line outline the superior and posterior
orders respectively of the temporal fossa from which arises the greater
part of the temporal muscle.

The lower jaw (Figs. 29, 30, 31) consists of two halves
joined at their anterior ends by fibrous connective tissue which forms a
moveable symphysis or syndesmosis. Each mandible consists of a stout
body which bears the incisors and cheek teeth and a thin, largely trans-
lucent ramus which serves for the attachment of the major muscles of
mastication, and carries the condyle for the articulation of the lower jaw
to the cranium. However, the body and ramus in the squirrel are not too
well separated.

The lower incisor curves anteriorly and superiorly from the
anterior end of the mandibular body. The bone projects furthest anteriorly
on the medial surface of the incisor in the area of the symphysis and least
on the enamel covered anteroinferior surface. The socket of the incisor
curves posteriorly and then posterosuperiorly into the anterior part of the
ramus behind and lateral to the cheek teeth.

The symphysial surface of the mandible is irregularly ear-
shaped. The mandibles are in close approximation at the superior border
but diverge posteroinferiorly. The inverted V-shaped symphysial space
allows the inversion of the mandibles and thus the spreading, abduction, of the lower incisors.

Just posterior to the symphysis on the medial surface is a small depression to which attaches the geniohyoid muscle. A fine crest, the supramandibular ridge, runs from the posterosuperior corner of the symphysis on the superior border of the mandible posteriorly to a point just anterior to the premolar. The supramandibular ridge serves for the attachment of the supramandibular muscle.

The smooth border of the mandibular body continues the convexity of the incisor posteriorly to the junction of the body and ramus. The lateral surface of the body is marked posteriorly by a forward encroachment of the masseteric fossa. Anteriorly, midway in the diastema and just below the superior surface is the mental foramen.

The anterior portion of the superior border is smooth lateral to the supramandibular crest forming a wide diastema between the incisor and the cheek teeth. Posteriorly the surface of the diastema bends sharply upward into the anterior surface of the alveolar process supporting the cheek teeth. The alveolar process projects superiorly from the upper surface of the body but in a sagittal plane while the body diverges from the midline posteriorly. Thus the posterior end of the alveolar process projects medially over the medial surface of the body.
The ramus is low, irregularly shaped, and has three processes: the angular process, the coronoid process, and the condylar process. The ramus continues in the plane of the body and is therefore lateral to the plane of the alveolar process of the cheek teeth.

The angular process forms the convex posteroinferior corner of the ramus. The posterior part of the convex border is raised laterally into the masseteric tubercle. A wide notch separates the angular process from the condylar process which forms the posterosuperior corner of the ramus. The condylar process is separated from the coronoid process by another notch which is deepest near its anterior end. The coronoid process forms the hook-like anterosuperior corner of the ramus.

The anterior border of the ramus is convex and curves anteroinferiorly from the coronoid process to a point just lateral to the third molar where it continues into an oblique line on the lateral surface of the body. The oblique line continues forward and slightly downward into the masseteric crest below the premolar. The masseteric ridge loops posteroinferiorly to the inferior border of the mandible below the third molar. The oblique line and the masseteric ridge outline the anterior extent of the masseteric fossa.

Viewed from the medial aspect the ramus is distinguished from the body by a general thinning of the bone. Two ridges cross the
medial surface. The temporal crest\(^1\) is nearly vertical and starts at the tip of the coronoid process and extends to the posterior end of the alveolar process. The triangular area between the temporal crest and the anterior border of the ramus serves for the attachment of the temporal muscle. The ridge of the mandibular neck\(^2\) runs obliquely anteroinferiorly from the condyle over the condylar process to the posterior end of the alveolar process of the body. The mandibular foramen lies between the lower ends of these two ridges. The inferior border is raised and bent mediadly. This together with the thick mandibular body anteriorly and the ridge of the mandibular neck superiorly bounds a depressed area in the lower half of the medial surface of the ramus which serves to attach the medial pterygoid muscle and a small bundle of masseter muscle.

The condyle (Fig. 33) forms the mandibular part of the mandibular articulation. The smooth convex articular surface faces upward and slightly backward. It is slightly longer anteroposteriorly than it is wide mediolaterally. The edge of the articular surface is sharp.

2. Dentition (Figs. 24, 25, 27, 29, 34)

The dental formula of the squirrel is \(I^1, \ C^0, \ P^2, \ M^3\).

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\(^1\) The term temporal crest was first used by P. Eisler in describing the area of attachment of the human temporal muscle.

\(^2\) The term ridge of the mandibular neck was first used by H. Sicher in describing the human mandible.
The incisors are located in the atrium of the oral cavity, while the pre-molars and molars are located in the oral cavity proper. The incisors are continuously growing while the premolars and molars are teeth with limited growth.

The continuously growing incisors form a segment of a logarithmic spiral. The upper incisor is the greater part of a smaller spiral while the lower incisor is the lesser part of a larger spiral. The incisors are elliptical in cross section with the anteroposterior dimension being approximately twice the mediolateral dimension. The bulk of the incisal end of the tooth is composed of dentine. The large pulp chamber shows a pinpoint sized opening at the center of the incisal bevel. The anterior surface of the incisor is covered by reddish brown pigmented enamel while most of the medial and lateral, and the entire posterior surfaces are covered by cementum. Approximately three quarters of the length of the cementum covered surfaces are embedded in bone. The basal end of the upper incisor (Fig. 34) lies in the body of the maxilla a short distance anterosuperior to the upper third premolar while the basal end of the lower incisor (Fig. 34) lies in the ramus of the mandible posterior and lateral to the lower third molar.

The exposed portion of the upper incisors curves downward and slightly backward while that of the lower incisors curves forward and
slightly upward. Due to the lack of enamel on the posterior, medial, and lateral surfaces, the back of the incisor wears more rapidly than the front. Thus large, concave wear facets form the entire posterior surface of the exposed portion of both the upper and lower incisors. The wear facets bevel the incisal end of the tooth so as to form a sharp edge of enamel at the junction of the anterior surface and the bevel. The shorter upper facet curves upward and slightly posteriorly from the incisal edge while the longer lower facet curves posteriorly and slightly inferiorly.

The cheek teeth are all tuberculate with short enamel covered crowns exposed to the oral cavity and cementum covered roots embedded in bone. The upper third premolar is very small and rudimentary. It has a conical crown and a single root. The upper fourth premolar is well developed. It is slightly smaller than the molars but otherwise closely resembles them. The molars are approximately uniform in size. Their occlusal surfaces are marked by two transverse crests connecting the two buccal cusps to the single lingual cusp. The occlusal outline of the first two molars is rectangular while that of the third molar is triangular. The fourth upper premolar and all the upper molars have three roots.

The lower cheek teeth closely resemble each other in crown morphology. All of them are rectangular in occlusal outline with cusps at each corner, a central depression, and a marginal ridge. They are uni-
form in size except that the premolar is slightly smaller. The lower premolar has two roots and the lower molars four.

3. Mandibular Articulation (Figs. 32, 33, 34, 35)

The mandibular articulation is a complex joint in that it is divided into a large upper compartment and a smaller lower compartment by an articular disc that is interposed between the squamosal bone and the mandible. The articular surface of the squamosal bone (Fig. 32) is a smooth, sagittal, semicylindrical groove with approximately equal anteroposterior and mediolateral dimensions. The anterior border of the articular surface is concave. The articular surface blends with the zygomatic arch laterally and the lateral surface of the neurocranium medially. The posterior border of the articular surface runs anterolaterally from the lateral surface of the neurocranium to the zygomatic arch, thus the lateral border of the articular surface is shorter than the medial border.

The articular surface of the condyle (Fig. 33) is roughly elliptical in outline with its longer anteroposterior axis in a sagittal plane. The outline is pointed anteriorly and posteriorly. The articular surface has a sharp edge around its entire circumference except at its anterior end. The posterior edge is slightly lower than the anterior edge and thus the surface faces slightly backward as well as upward. Though convex both anteroposteriorly and mediolaterally the highest point is slightly posterior
and medial to the center of the articular surface.

The articular disc is oval in outline. It is thickened around the periphery and very thin in the center over the prominence of the condyle. The disc is fused to the joint capsule around its entire circumference. The capsule, however, does not bind the disc tightly to the condyle but allows a limited movement in all directions.

The joint capsule attaches to the sharp edge of the articular surface of the condyle below and the periphery of the articular surface of the temporal bone above, medially, and laterally. The capsule is very thin posteriorly, medially, and laterally but thickens anteriorly. Posteriorly it is apposed to the temporal muscle, laterally to the masseter muscle, medially to the lateral pterygoid muscle, and anteriorly it bulges forward between the temporal muscle above and the lateral pterygoid muscle below. The capsule is extremely loose between the disc and the temporal bone especially anteriorly and posteriorly thus allowing considerable gliding movement in the upper compartment.

The relation of the articular surfaces of the mandibular joint is seen roentgenographically in Figures 34 and 35.

4. Musculature (Figs. 36-48)

Masseter Muscle

The large, powerful masseter muscle (Fig. 36) arises
from the lateral surface of the maxilla and the zygomatic arch and inserts mainly into the lateral surface of the ramus. The masseter muscle can, though incompletely, be separated into three parts. The anterior superficial head (Fig. 37) arises as a narrow and thin tendon from the masseteric tubercle or spine on the lateral surface of the maxilla and spreading, passes posteriorly and slightly inferiorly to insert into the inferior border of the ramus and the angular process. Anteroinferiorly a bundle separates from the main body of the anterior superficial head and curves around the lower border of the body of the mandible (Fig. 38). Most fibers of this bundle insert into the anterior part of the depression on the medial surface of the ramus upward almost to the level of the alveolar process, but a few fibers turn posteriorly and insert into a narrow strip of the tendon of the medial pterygoid muscle adjacent to the inferior border of the ramus.

The anterior deep head arises from the masseteric fossa on the premaxilla and the maxilla, and the inferior border and a triangular area on the lower part of the lateral surface of the zygomatic arch. The fibers are directed posteroinferiorly to insert into the depressed lateral surface of the ramus and by tendinous fibers into the masseteric crest of the mandible.

The posterior deep head can only be separated from the rest of the muscle at its superior end and then with some difficulty. It arises
from the entire length of the medial surface of the zygomatic arch and passes anteroinferiorly to insert into the oblique line, and a narrow strip of the lateral surface of the ramus adjacent to the attachment of the temporal muscle. Toldt calls this head the zygomatico-mandibular muscle.

The masseter muscle elevates and protrudes the lower jaw. That part of the muscle that wraps around the lower border of the mandible to insert into the medial surface of the ramus and into the medial pterygoid muscle also acts to evert that half of the mandible to which it attaches and thus adducts, closes, the lower incisors. This bundle, therefore, is antagonistic to the transverse mandibular muscle.

Medial Pterygoid Muscle

The medial pterygoid muscle (Fig. 38) in the squirrel is well developed. Arising from the pyramidal process of the palatine bone and the pterygoid fossa the fibers pass inferiorly and slightly posterolaterally to insert into a large oval depression on the medial surface of the angular process of the ramus (Fig. 39). The angular process is bent medially, thus extending medially almost under the pterygoid plate. This relation causes the medial pterygoid muscle to be almost vertical.

The medial pterygoid muscle functions with the masseter muscle in elevating the mandible.

Lateral Pterygoid Muscle
The lateral pterygoid muscle (Fig. 39) is fairly well developed despite the poor development of the lateral pterygoid plate. The muscle runs laterally and only slightly posteriorly from the pterygoid process to the mandible. The muscle is thicker anteroposteriorly than superoinferiorly. It arises from the inferior edge and lateral surface of the pterygoid plate and from an adjacent roughened triangular area of the sphenoid bone just superior to the pterygoid plate. The anterior fibers run laterally and slightly posterosuperiorly to insert into the anterior surface of the mandibular neck. The posterior fibers run posterolaterally and slightly superiorly to insert into the neck of the mandible and the capsule and disc of the mandibular joint on their anterior and medial surfaces.

Because of its direction the lateral pterygoid muscle does not seem to be able to protrude the mandible. In exerting a medial pull on the mandible and the articular disc it acts to stabilize the condyles during inversion of the mandible.

Temporal Muscle

The temporal muscle (Figs. 40, 41) arises from the temporal fossa on the superior and lateral surfaces of the neurocranium, the temporal fascia, the posterior orbital notch, and the orbital surface of the sphenoid bone above the level of the posterior root of the zygomatic arch. The muscle runs anteroinferiorly to insert by tendinous attachment into the
posterior border of the coronoid process and the anterior border of the ramus from the coronoid process to a point just lateral to the mandibular third molar, and by fleshy attachment into the temporal crest and the medial surface of the ramus between the temporal crest and the anterior border of the ramus.

The temporal muscle elevates and retracts the mandible.

**Transverse Palatine Muscle**

The transverse palatine muscle (Fig. 42) arises from the entire length of the lateral palatine ridge and runs laterally. The most anterior fibers curve forward lateral to the upper incisor. The transverse palatine muscle inserts into the upper lip and cheek. The muscles function bilaterally to draw inward the hair covered folds of the upper lip and cheek (Fig. 44). Synergistically with the supramandibular muscles they separate the atrium from the main part of the oral cavity.

**Supramandibular Muscle**

The supramandibular muscle (Fig. 43) arises anteriorly from a median raphe superior to the mandibular symphysis and posteriorly from the supramandibular ridge. Most of the fibers run laterally but the most anterior bundles curve anteriorly around the lateral surface of the incisor. The muscle inserts into the lower lip and cheek.

The supramandibular muscles act synergistically with the
transverse palatine muscles to draw in the hair covered infoldings of the lip and cheek (Fig. 44) that divide the oral cavity into the atrium and oral cavity proper.

Digastric Muscle

The digastric muscle (Fig. 45) consists of two bellies. The posterior belly arises from the lateral surface of the jugular process and ends in an intermediate tendon from which part of the anterior belly arises. The anterior belly arises from the intermediate tendon and from the inferior surface of the hyoid bone and inserts into the inferior border of the mandible at the posterior end of the symphysis. The anterior belly is fused with its counterpart on the opposite side separating only close to their insertions.

The digastric muscle acts to position the hyoid bone and to depress and retract the mandible.

Transverse Mandibularis Muscle

The unpaired transverse mandibularis muscle (Fig. 46, 47) attaches bilaterally to the inferior border of the body of the mandible posterior to the symphysis thus coursing transversely between the two halves of the mandible. Contraction of the muscle inverts the two halves of the lower jaw and abducts, spreads, the lower incisors. The transverse mandibularis muscle is innervated by branches of the mylohyoid branch of
the inferior alveolar nerve (Fig. 46).

Mylohyoid Muscle

The mylohyoid muscle (Fig. 47) arises from the upper part of the medial surface of the body of the mandible below the cheek teeth but not extending forward into the area of the diastema. The anterior three-fourths of the fibers meet those of the opposite side in a median raphe while the posterior one-fourth insert in the body of the hyoid bone. The mylohyoid muscle is incomplete anteriorly extending forward only to the posterior border of the transverse mandibularis muscle.

The mylohyoid muscle passes medioinferiorly from its origin to its insertion and thus acts to elevate the floor of the mouth and the hyoid bone. If the hyoid bone is fixed then those fibers attaching to it may act to depress the mandible.

Geniohyoid Muscle

The geniohyoid muscle (Fig. 48) arises from a small, oval depression on the medial surface of the body of the mandible just posterior to the symphysis above the attachment of the transverse mandibularis. The muscle, in contact with that of the other side, passes posteriorly above the mylohyoid muscle and inserts into the upper part of the anterior surface of the body of the hyoid bone.

The geniohyoid muscle pulls the hyoid bone forward, or if
the hyoid bone is fixed, it depresses the mandible.

5. Observations on Living Animals During Feeding

In gnawing the squirrel protrudes the lower jaw and then opens and closes in a hinge-like movement. When the upper and lower incisors come into an edge to edge position the mandible may shift forward so that the enamel of the upper incisors abrade the lingual facets of the lower incisors or backward so that the enamel of the lower incisors abrade the lingual facets of the upper incisors. This mechanism maintains the sharpness of the incisal edges. The hinge-like closing may bite off a bit of food or, more often, rapid, repetitive opening and closing shaves away a portion of the surface of the food. The food particles are then shifted from the atrium to the oral cavity proper by the tongue. The lower incisors may also be abducted, spread, and adducted, closed, to crack nuts.

The chewing movement is difficult to determine with certainty, however, it seems to be primarily a lateral movement.
CHAPTER V
DISCUSSION

In considering the results of this study extreme care must be taken to avoid making erroneous generalizations based on findings in a single species. However, with due caution, the data presented, and supplemented by information obtained in unpublished investigations on the guinea pig and rat are sufficient to allow certain observations to be made concerning the species studied and the two orders, Rodentia and Lagomorpha, to which they belong.

Though time has proven Gidley right and the separate ordinal status of lagomorphs is now generally accepted, certain similarities between rodents and lagomorphs do exist. Since common ancestors of the two orders are unknown the similarities seen must be considered to be the result of convergence.

The evergrowing, chisel-shaped incisors are the most obvious similarity. Their presence in all species of both orders would seem to indicate that, though lagomorphs are taxonomically separated from rodents, lagomorphs are functionally rodents, "gnawers". However, observations on living animals during feeding seemed to make this doubtful.
The rabbit made slow, deliberate biting movements with its incisors while the squirrel made rapid shaving movements. In observations on rats and mice it was noted that they would gnaw at large, hard pellets of food, slowly reducing them by repeatedly planing the surface of the pellet with their sharp incisors. Rabbits, however, require food that is easily incised, such as lettuce from which small pieces are easily bitten off.

A correlation could be made in contrasting the wide medio-lateral dimension of the rabbit incisor, which thus has a long biting edge, with the narrow mediolateral dimension of the rodent incisor, which thus has a short biting edge. It may well be that the short biting edge of the rodent incisor would concentrate force and thus be more effective on hard substances while the long cutting edge of the lagomorph incisor would be more efficient in biting off food that is penetrated easily.

Whether differences in the functional characteristics of the incisors of the rabbit are correlated to their relative shortness (the basal end of the upper incisor is in the premaxilla, the basal end of the lower incisor in the body of the mandible medial to the third premolar) is questionable. In squirrels the basal end of the lower incisor is in the ramus of the mandible, posterior and lateral to the third molar, and in guinea pigs it is medial to the first molar. In all rodents the basal end of the upper incisor is in the maxilla usually just anterior to the cheek teeth.
Thus, though the position of the basal end of the incisors may vary somewhat, the incisors are always relatively longer in rodents than in lagomorphs.

It should be noted that the incisors of rodents and lagomorphs also differ in that a vertical groove is found on the anterior surface of the large upper incisors of rabbits while this is not present in any rodents and the enamel on the incisors of rodents is pigmented, while in lagomorphs it is not. Though the continuously growing, chisel-shaped incisors are seen in all rodents and lagomorphs and are thought to be so characteristic for them, similar incisors are seen in other groups of animals, such as some marsupials (Diprotodon) and primates (Daubentonia).

Continuously growing, chisel-shaped incisors need an extensive anterior-posterior movement of the mandible to position these teeth to function. When the jaws are closed and the incisors come into an edge to edge position the mandible may shift forward so that the enamel of the upper incisor abrades the lingual facet of the lower incisor or backward so that the enamel of the lower incisor abrades the lingual facet of the upper incisor. This constant abrasion of the lingual facets, compensated by continuous growth and eruption of the incisor, results in a continuous sharpening of the enamel edge. The wear facets on the incisors, especially the lower incisor, of the squirrel, guinea pig, and rat are much longer and form a more acute angle with the enamel covered anterior surface than do the wear facets on
the rabbit incisors. This difference in the length and angle of the lingual slope can be correlated with the greater range of anterior-posterior movement seen in the rodents and the somewhat more restricted anterior-posterior movement seen in the lagomorph.

The anterior-posterior movement requires the adaptation of both muscles and mandibular joints. This is accomplished in different ways in rodents and in lagomorphs. In both groups there has been a forward migration of the origin of the masseter muscle, however, this muscle is restricted in its origin to the zygomatic arch in rabbits, while in rodents it also arises from the lateral surface of the maxilla and premaxilla. This forward migration of the origin of the masseter muscle brings some parts of the muscle into an increasingly oblique and in the case of the rodent nearly horizontal plane. In the squirrel the anterior superficial head of the masseter muscle arises from the masseteric tubercle on the maxilla and is nearly horizontal in direction while the anterior deep head arises from the masseteric fossa on the lateral surface of the maxilla and premaxilla and is markedly oblique in direction. Thus both of these heads are well positioned to pull the lower jaw forward. The lateral pterygoid muscle in the squirrel is mediolateral in direction and thus is unable to play any part in protruding the mandible. In the rabbit the anterior superficial head of the masseter muscle arises from the anterior two-thirds of the zygomatic
arch and from the masseteric tubercle on the anterior root of the arch and runs obliquely posteroinferiorly thus asserting an anterior pull on the mandible. The anterior deep head of the masseter muscle of the rabbit plays no part in protrusive movements. However, the lateral pterygoid muscle runs obliquely posterolaterally and thus is able to pull the condyles forward and to protrude the mandible.

Some major differences can also be seen in the muscles serving to retrude the lower jaw. In the squirrel the temporal muscle and the coronoid process are well developed, while they are poorly developed in the rabbit. Their poor development in the rabbit seems to be at least partially offset by a well developed digastric muscle whose retrusive pull is enhanced by its insertion into the mandible without attachment to the hyoid bone. In addition the zygomatic bone projects backward posterior to the posterior root of the zygomatic arch and serves as attachment of the posterior head of the masseter muscle which angles anteroinferiorly to insert into the mandible and functions to retrude the lower jaw.

Extensive anterior-posterior movements of the mandible seem to require a mandibular joint in which a short articular surface of one bone glides over a long articular surface of the other bone. In the rodent the cranial articular surface is a sagittally disposed, semi-cylindrical trough with a long anteroposterior axis which provides ample surface for
the small condyle to move forward and backward. In the rabbit the arrange-
ment is reversed. The articular surface of the squamosal bone is bar-
like with a long mediolateral and a short anteroposterior axis. It is the
articular surface of the condyle that is long anteroposteriorly and makes
extensive protrusive gliding movements possible.

Another conspicuous example of convergence in rodents and
lagomorphs is the hair covered infoldings of the lips with specialized
muscles for their movement. The infoldings are pulled inward by the
transverse palatine muscle, first described and related to Jacobson’s organ
by Broman, and the supramandibular muscles. The infoldings then divide
the oral cavity into the atrium, containing the incisors, and the oral cavity
proper, containing the cheek teeth. The antagonists of the transverse
palatine and supramandibular muscles remain to be studied. It is possible
that a muscle described by Eunice Greene as buccinator muscle is the
antagonist of the transverse palatine muscle.

A major difference between rabbits and squirrels is seen in
the symphysis or syndesmosis of the mandible. It is moveable in the
squirrel, rats, mice, and numerous other rodents. In the rabbit and some
rodents, e.g. the guinea pig, the symphysis does not allow a movement of
the two halves of the mandible. The mobility at the symphysis is corre-
lated with the development of the transverse mandibular muscle. This
Muscle is a derivative of the mylohyoid muscle which as a result is incomplete anteriorly. The anterior border of the mylohyoid muscle coincides with the posterior border of the transverse mandibular muscle. The apparent derivation of the transverse mandibular muscle from the mylohyoid muscle is further reinforced by the fact that it is the mylohyoid nerve that supplies the transverse mandibular muscle. The transverse mandibular muscle acts to invert the mandibles and abduct, spread, the lower incisors.

Where the symphyseal junction is moveable the two halves of the lower jaw are closely approximated in the superior portion of the symphysis but are separated inferiorly by a wide cleft. The cleft narrows when the two halves of the jaw are inverted. The axis of rotation of the everting-inverting movement of the mandible appears to pass through the superior portion of the symphysis and the condyle on each side. The lateral pterygoid muscle with its mediolateral direction acts in stabilizing the condyle during inversion and eversion of the mandible.

Part of the masseter muscle in the squirrel and rat wraps around the lower border of the mandible and inserts into the medial surface of the ramus. This bundle seems to function in everting the mandible and adducting, closing, the lower incisors, acting as an antagonist of the transverse mandibular muscle.

Examination of the morphology and wear facets of the cheek
teeth, and the morphology of the mandibular joint as well as observations on living animals during feeding reveal differences in chewing movements that cut through these orders rather than contrast them. In the rabbit the strong transverse ridges on the cheek teeth coupled with the near lack of contact of the upper and lower teeth when the mandible is centered mediolaterally and the limited anteroposterior movement of the lower jaw make it apparent that lateral excursions are used in chewing. In the squirrel chewing movements are also mediolateral in direction and the cranial articular surface of the mandibular joint is broad mediolaterally to allow for the lateral excursions of the mandible. However, in the guinea pig the chewing movement is primarily in an anterior-posterior direction and the cranial articular surface is restricted medially and laterally by strong, sagittally placed ridges (Fig. 49).

Another point of difference between rabbits and rodents is seen in the posterior extent of the hard palate. In all the rodents that have been observed the hard palate ends posterior to the last molar while in the rabbit it ends in line with the posterior surface of the first molar.

Though Gidley was right in proposing ordinal status for lago­morphs and their separate classification is now generally accepted, it is apparent that some of his data were incorrect. Regarding rodents he stated, "Palate progressively narrow, distance between upper tooth rows
less than lower". Though this is an accurate description for the guinea pig in which the upper tooth rows converge anteriorly so that the premolars nearly touch in the midline and the distance between the upper tooth rows is much less than between the lower tooth rows it is not true of the squirrel. In the squirrel the upper tooth rows are parallel and more widely separated than the lower.

In the rabbit Gidley describes the cranial articular surface of the mandibular joint as consisting of "an anterior ridge and a posterior pocket". Actually this "posterior pocket" lies above and behind the articular surface and takes no part in the articulation.

Again in describing lagomorphs Gidley states "Cheek tooth row in plane with ascending ramus of lower jaw". Actually the lower cheek teeth form two parallel rows and the plane of these rows lies inside the plane of the ramus as is also true for the rodents.
CHAPTER V I
SUMMARY AND CONCLUSIONS

It was the purpose of this investigation to make an integrated study of the structure and function of the masticatory apparatus, namely skeleton, teeth, mandibular articulation, and muscles, in a rodent and a lagomorph and to compare the two orders. The squirrel was selected as an example of a rodent and the rabbit as an example of a lagomorph. Detailed descriptions of their skulls, dentitions, mandibular joints, and masticatory muscles were presented along with observations on living animals during feeding. Data from unpublished studies on the guinea pig and rat was used to supplement the findings in the rodent.

Similarities, apparently the result of convergence, were noted in the two orders. The most conspicuous similarities were continuously growing, chisel-shaped incisors and hair covered infoldings of the lips with specialized muscles for their movement.

Numerous differences in the masticatory apparatus of the two orders were seen. These included:

<table>
<thead>
<tr>
<th>Lagomorpha</th>
<th>Rodentia</th>
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<tbody>
<tr>
<td>1. Four upper incisors.</td>
<td>1. Two upper incisors.</td>
</tr>
</tbody>
</table>
2. Vertical groove on the anterior surface of the large upper anterior incisor.

3. Enamel of the incisors not pigmented.

4. Basal end of the upper incisors in the premaxilla.

5. Basal end of the lower incisor in the body of the mandible medial to the third premolar.

6. Incisors thicker mediolaterally than anteroposteriorly.

7. Posterior end of the hard palate in the plane of the first molars.

8. Cranial surface of the mandibular joint convex anteroposteriorly and concave mediolaterally.


10. Masseter muscle arises from zygomatic arch.

11. Zygomatic bone projects backward posterior to posterior root of zygomatic arch.

12. Coronoid process poorly developed.

13. Digastric muscle not attached to hyoid bone.

2. Incisors not grooved.

3. Enamel of the incisors pigmented.

4. Basal end of the upper incisors in the maxilla.

5. Basal end of the lower incisor posterior to the premolars.

6. Incisors thicker anteroposteriorly than mediolaterally.

7. Posterior end of the hard palate posterior to the last molar.

8. Cranial surface of the mandibular joint sagittally disposed, semicylindrical trough.

9. Cranial surface of mandibular joint long anteroposteriorly.

10. Masseter muscle arises from zygomatic arch and lateral surface of maxilla and premaxilla.

11. Zygomatic bone ends posteriorly at the posterior root of the zygomatic arch.

12. Coronoid process well developed.

13. Digastric muscle firmly attached to hyoid bone.
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Figure 1. Lateral view of rabbit skull

Figure 2. Front view of rabbit skull
Figure 3. Superior view of rabbit skull

Figure 4. Inferior view of rabbit cranium
Figure 5. Lateral view of rabbit cranium

Figure 6. Superior view of rabbit mandible
Figure 7. Lateral view of rabbit mandible

Figure 8. Medial view of rabbit mandible
Figure 9. Articular surface of the rabbit cranium

Figure 10. Articular surface of the rabbit mandible
Figure 11. Lateral roentgenogram of sagittally cut rabbit head with mandible in occlusal position. Note the relations of the articular surfaces of the mandibular joint.

Figure 12. Lateral roentgenogram of sagittally cut rabbit head with mandible in protrusive position. Note the relations of the articular surfaces of the mandibular joint.
Figure 13. Lateral view of rabbit head dissected to show masseter and temporal muscles.
A. Temporal muscle
B. Anterior superficial head of masseter muscle
C. Posterior head of masseter muscle

Figure 14. Same as Figure 11 with anterior superficial head of masseter muscle cut.
A. Temporal muscle
B. Anterior superficial head of masseter muscle
C. Anterior deep head of masseter muscle
D. Posterior head of masseter muscle
Figure 15. Medial view of sagittally cut rabbit head dissected to show the medial pterygoid and digastric muscles. Also note bundle of masseter muscle wrapped around the inferior border of the mandible.
A. Digastric muscle
B. Medial pterygoid muscle
C. Masseter muscle

Figure 16. Same as Figure 13 except the digastric muscle was removed, and the medial portion of the medial pterygoid muscle was cut.
A. Medial portion of medial pterygoid muscle
B. Lateral portion of medial pterygoid muscle
C. Masseter muscle
Figure 17. Inferior view of sagittally cut rabbit head dissected to show the lateral pterygoid muscle, and portions of the masseter and temporal muscles. Note oblique direction of the lateral pterygoid muscle.
A. Lateral pterygoid muscle
B. Temporal muscle
C. Masseter muscle

Figure 18. Superior view of sagittally cut rabbit head dissected to show the temporal muscle, and a portion of the masseter muscle. Note especially the origin of a portion of the temporal muscle from the orbit.
A. Temporal muscle arising on the neurocranium
B. Temporal muscle arising in the orbit
C. Masseter muscle
Figure 19. Sagittally cut rabbit head dissected to show temporal muscle. The other muscles and the zygomatic arch have been removed.
A. Temporal muscle arising in the orbit  
B. Temporal muscle arising from the neurocranium  
C. Cut ends of zygomatic arch

Figure 20. Rabbit head dissected to show transverse palatine muscle.
A. Transverse palatine muscle
Figure 21. Rabbit head dissected to show supramandibular muscle.
A. Supramandibular muscle

Figure 22. Medial view of sagittally cut rabbit head showing fur covered infoldings of the lips (arrow).
Figure 23. Inferior view of rabbit head showing mylohyoid muscle.
A. Mylohyoid muscle
B. Digastric muscles divided and spread
C. Masseter muscle
D. Hyoid bone, greater horn
Figure 24. Lateral view of squirrel skull

Figure 25. Front view of squirrel skull
Figure 26. Superior view of squirrel skull

Figure 27. Inferior view of squirrel cranium
Figure 28. Lateral view of squirrel cranium

Figure 29. Superior view of the squirrel mandible
Figure 30. Lateral view of squirrel mandible

Figure 31. Medial view of squirrel mandible
Figure 32. Articular surface of the squirrel cranium

Figure 33. Articular surface of the squirrel mandible
Figure 34. Lateral roentgenogram of sagittally cut squirrel head with mandible in occlusal position.

Figure 35. Lateral roentgenogram of sagittally cut squirrel head with mandible in protrusive position.
Figure 36. Lateral view of a squirrel head showing the masseter and temporal muscles.
A. Temporal muscle
B. Masseter muscle

Figure 37. Same as Figure 36 with a probe under the anterior superficial head of the masseter muscle.
Figure 38. Medial view of a sagittally cut squirrel head dissected to show the medial pterygoid and masseter muscles. Note a bundle of the masseter muscle wrapping around inferior border of the mandible and inserting into the medial surface of the ramus.
A. Medial pterygoid muscle
B. Masseter muscle

Figure 39. Inferior view of sagittally cut squirrel head dissected to show the cut insertions of the medial pterygoid and transverse mandibular muscles, and the whole extent of the lateral pterygoid muscle. The mandible is rotated laterally to show the lateral pterygoid muscle clearly. Note the nearly lateral direction of lateral pterygoid muscle.
A. Lateral pterygoid muscle
B. Temporal muscle
C. Masseter muscle
D. Medial pterygoid muscle (cut)
Figure 40. Superior view of a sagittally cut squirrel head dissected to show the temporal and masseter muscles. Note especially the origin of a portion of the temporal muscle in the orbit and the development of the deep portion of the masseter muscle, arising from the medial surface of the zygomatic arch.
A. Temporal muscle arising from neurocranium
B. Temporal muscle arising in the orbit
C. Posterior deep head of masseter muscle
D. Anterior deep head of masseter muscle

Figure 41. Sagittally cut squirrel head dissected to show the orbital origin of the temporal muscle. Masseter muscle and zygomatic arch cut away.
A. Temporal muscle arising in the orbit
B. Temporal muscle arising from the neurocranium
C. Masseter muscle
Figure 42. Squirrel head dissected to show the transverse palatine muscle.
A. Transverse palatine muscle

Figure 43. Squirrel head dissected to show the supramandibular muscle.
A. Supramandibular muscle
Figure 44. Medial view of sagittally cut squirrel head showing the fur covered infoldings of the lips (arrow).

Figure 45. Inferior view of squirrel head dissected to show the digastric muscle.
A. Anterior belly of the digastric muscle
B. Posterior belly of the digastric muscle
C. Masseter muscle
Figure 46. Inferior view of squirrel head showing transverse mandibular muscle just posterior to the mandibular symphysis. Note the mylohyoid nerve (arrow) running forward on the inferior surface of the mylohyoid muscle to reach the transverse mandibularis muscle.

A. Transverse mandibular muscle
B. Mylohyoid muscle
C. Masseter muscle

Figure 47. Inferior view of squirrel head showing divided transverse mandibular muscle and probe under mylohyoid muscle. Note that the posterior border of the transverse mandibular muscle and the anterior border of the mylohyoid muscle lie in the same plane.
Figure 48. Inferior view of squirrel head showing the geniohyoid muscle.

Figure 49. Inferior view of guinea pig cranium. Note medial and lateral restriction of the mandibular joint.
A. Cranial surface of mandibular joint
The thesis submitted by Dr. Robert J. Pollock, Jr. has been read and approved by four members of the Departments of Anatomy and Oral Biology.

The final copies have been examined by the Director of the thesis and the signature which appears below verifies the fact that any necessary changes have been incorporated, and that the thesis is now given final approval with reference to content, form, and mechanical accuracy.

The thesis is therefore accepted in partial fulfillment of the requirements for the Degree of Master of Science.

May 18, 1962
Date

Signature of Adviser