Chapter 17

The Mammalian Masticatory Apparatus: An Introductory Comparative Exercise

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Introduction

In order for undergraduate students to appreciate fully the aims, objectives, and methodology of comparative anatomy, exposure to well-circumscribed and tractable exercises is an important part of their training. The following procedure, which is an example of such an approach, has been utilized in our third year undergraduate course in vertebrate systematics and natural history for about ten years. Students undertaking this exercise will already have completed a one semester lecture and laboratory course in comparative vertebrate anatomy and will be asked to build upon the knowledge-base acquired in that course.

The jaw muscle dissection of the rabbit is not an isolated exercise, but sets the stage for three additional laboratories in which the range of dental and cranial structures, and then the range of skeletal anatomy in mammals is surveyed. These initial dissections and comparisons permit students to explore the range of functional morphological contrivances that suit mammals to particular sorts of diets. Students then explore the ways in which dentition and cranial anatomy have been integrated into, and form a large part of our fundamental understanding of, the systematics of mammals.

This exercise further illustrates the importance to students of the dissection of fresh, rather than fixed and preserved material. The latter forms the basis of much of the study that occurs in traditional comparative anatomy classes. While much detail is preserved in such material, there is little movement available and much of the contrast between different types of soft tissue is obscured as the muscles assume an ashen hue.

The choice of the rabbit as a model has been for pragmatic reasons. I wished to find a plentiful supply of material that could be used to demonstrate the basic components of the mammalian masticatory apparatus and that could be easy to procure and not expensive. The solution that I arrived at was to salvage the heads of rabbits that have been used for terminal experiments in teaching of animal physiology, and for various experimental purposes in our Faculty of Medicine. These heads can be gathered at any time during the school year and kept in the freezer until needed. There is always a plentiful enough supply that each student can be provided with his/her own specimen, although I prefer students to work in pairs and to discuss their dissection as they go. This means that each pair can be provided with another specimen for further investigation or review purposes. To assist in the study and visualization of the pterygoid muscles several partially-prepared rabbit heads are sagitally sectioned on a band saw to allow a relatively unimpeded approach from the medial side. Following the exercise students can also prepare the skull for future reference and thus obtain a study specimen from the course.

During the exercise, students attempt to understand the complexities and intricacies of muscle architecture as they relate to function and skeletal form. Questions are inserted into the text of the exercise so that students are prompted to think about the architecture of the masticatory apparatus as they reveal it. The rabbit is a good choice here as all three jaw-closing muscle groups (masseter, temporalis and pterygoid) have complex and intricate architecture and the jaw joint permits great degrees of freedom and two functional positions of operation.

Both qualitative and quantitative comparisons can be made during this exercise. The former is achieved on the basis of appearances, and prosections of other mammal masticatory systems permit this. Quantitative comparisons can be made by excising muscle groups and determining their volume as a proportion of the entire masticatory muscle mass. These results can then be compared to those provided by Turnbull (1970) in his survey of the mammalian masticatory apparatus. The data on the proportions, architecture and disposition of the jaw closing muscles of various groups can then be considered in light of the examination of the temporomandibular joint structure of various groups and the degrees of freedom that these various jaw joint configurations allow. After such considerations various topics such as gape, power, velocity and force can be discussed as they relate to the different modes of food procurement and oral breakdown in mammals.

Thus, the basic objectives of this laboratory exercise are as follows:

1. To refresh the student's knowledge of mammalian skull structure in a new animal.
2. To provide a framework for the understanding of the mechanics of oral food processing in mammals. This is to provide a bridge for the later investigation of mammalian dental diversity.
3. To provide the means of examining a muscle complex to reinforce the concepts of synergistic and antagonistic muscles.
4. To examine a muscle complex to gain some appreciation of muscle architecture, muscle complexity and muscle mechanics.
5. To examine the relationship between temporomandibular joint form, jaw design, and muscle architecture.
6. To provide a framework for the examination of the functional groupings of mammalian masticatory mechanisms as outlined by Turnbull (1970).
7. To examine the relationships between muscle mass, architecture and function in these groupings.
8. To provide an introduction to cranial form and dental morphology as they are applied to mammalian systematics.

Materials

One rabbit head for each pair of students
Dissecting trays or pans
Fine scissors
Scalpel handle and #10 blade
Fine forceps
Probe
Prepared rabbit skulls for skeletal reference
Plastic bags
Surgical gloves
Bisected rabbit heads (These are best bisected when the head is frozen. A band saw is needed for this procedure.)

Notes for the Instructor

This exercise is quite straightforward, but needs to be practiced before allowing students to participate. The rabbit heads can be kept frozen until needed. Sufficient thawing time is necessary before the laboratory exercise begins. Skinning the head can be a time-consuming process for the inexperienced, so it would be wise for the instructor to go through this part of the procedure several times and learn how to speed it up, so that these tips can be passed on to the students. Once the skin has been removed the muscles should be quite evident, although they will require considerable cleaning in order to reveal the intricacies of their architecture. The preparation should be kept moist at all times. Remember, the muscles in question are bilaterally symmetrical, so examining superficial structures on one side and deeper structures on the other is possible.

Student Outline

Dissection of the Jaw Closing
Musculature of the Laboratory Rabbit

"Two rather different sets of problems are addressed in studies of mastication. First, the chewing apparatus is a particularly intriguing piece of machinery, with its tight occlusion and variable hinges - how does it work on a purely mechanical basis? (For this a comparative approach is not required.) The second set of problems centers around the interpretation of morphological change during evolution. The diversity of dental apparatus and jaw muscles in extant mammals seems to be an obvious consequence of adaptive evolution. Studies here are obligated to be comparative and typically involve "classical" functional morphology, defined as combining information on anatomy, mechanics and behavior in order to understand selective influences on the animals." (Herring, 1993: 289-290)

Your objective in this laboratory is to refresh your knowledge of mammalian skull structure and to become familiar with the major patterns of food processing in mammals. You will accomplish the latter by a careful dissection and manipulation of the jaw closing muscles of the rabbit and a comparison of this with demonstrations of the other major structural types of trophic apparatus of mammals. Overall you should concentrate on the form and variability of the mammalian skull and the way in which this is related to methods of food processing. The functional groups you will consider are the shear and scissors; grinding mill; anterior shift and generalized groups. Note that members of each functional group come from a variety of taxa (orders) and that a single order may be represented in more than one functional group. This indicates that similar solutions to dealing with various food types have been achieved on multiple occasions in the history of mammals. You will use the information gained in this laboratory exercise to aid your understanding of mammalian dental diversity and of mammalian ordinal radiation. This will be used to help you understand the foundations of mammalian systematics. This exercise allows you to employ your deductive abilities when confronted with a mammalian skeleton that you have not seen before.

While examining the jaw closing muscles of the rabbit, pay attention to the proportions of the temporalis, masseter and pterygoid muscles and compare these with those of other functional groups. Note also the orientation and direction of the fibers of the major bellies of these muscles. Where possible, freshly dissected examples of the heads of mammals belonging to other functional groups will be made available. It is important that all material examined be fresh and not preserved so that you may gain some appreciation of the real feel of "soft anatomy" and the mobility of joints.

For this exercise the functional masticatory groupings of mammals as outlined by Turnbull (1970) and the myological and osteological terminology of Weijs and Dantuma (1981) have been adopted. Additional details of the masticatory mechanisms of rabbits can be gleaned from Craigie (1948), Ardran et al. (1958) and Barone et al. (1973). An excellent and up-to-date overview of the functional morphology of mammalian mastication is given by Herring (1993).

Skinning the Head

Examine the rabbit skulls provided (Fig. 17.1 and Appendix A) to become familiar with general topography, especially of those areas directly associated with the origin and insertion of the jaw closing muscles.

Before beginning the dissection, wet the head thoroughly in order to control loose hair. Make a mid-ventral incision in the skin and, working from the neck forward, remove the skin and superficial facial musculature by snipping through the connective tissue with scissors or separating it with a scalpel handle or the blunt side of a scalpel blade. While doing this keep the scalpel handle or scissors away from the deeper structures to avoid damaging the masticatory muscles. The large fat deposits situated at the base of the ear cartilages should be removed with the skin. The ear cartilages themselves should be severed close to their bases to permit examination of the temporal muscles.

When the skin has been freed as far as the posterior and ventral edges of the orbits, the connective tissue holding the eyes in place should be cut through and a pair of closed forceps run between the eye and the orbit wall to free the former. The eyes should be removed after removal of the skin by severing the optic nerve and extrinsic eye muscles. The skin may then be quite easily removed from the rest of the head and the orbits cleaned of connective tissue and glands to expose the origins of the deep temporal complex (Figs 17.6, 17.7).

Cleaning the Head

Carefully clean away all connective tissue, fat deposits and glands to expose the masseter muscle clearly. This is the large muscle covering the lateral jaw surface (Fig. 17.2). The superficial temporalis muscle should also be exposed in the same manner (Fig. 17.2). In doing this pay special attention to the fatty deposits surrounding the auditory region and clear them away with care.

Turn the head ventral side up, with the posterior end toward you and, holding onto the fat and connective tissue of the mid-ventral region, carefully separate the hyoid musculature (those muscles associated with the root of the tongue and the larynx) from the medial pterygoids. This may be achieved by passing forceps or a scalpel handle between the muscles covering the medial surface of the angle of the lower jaw and the muscle masses medial to them. The digastric muscles may be removed at this point. These appear as thick muscle bands running parallel to the mandibles from the level of the symphysis posteriorly. They may be freed by severing their insertions at, and close to, the symphysis. These muscles serve to open the mouth by lowering the lower jaw.

Turning the head on its side, remove the cheek pouch of the side facing you. These line the oral cavity lateral to the teeth and their attachments may be released by carefully cutting with scissors or a scalpel. Repeat the operation for the other side. The tongue and its associated muscles should then be freed and removed, if it was not already removed with the hyoid apparatus. This may be accomplished by severing all connections of these structures with the head skeleton and removing the entire mass by pulling it posteriorly through the floor of the mouth between the mandibles. Finally, clear away all extraneous material around the masticatory muscles and rinse the cleaned head under running tap water. Keep the head moist during the dissection by laying it on moistened paper towels.

Dissection of the Masticatory Muscles

Before dissecting any further, manipulate the lower jaw while holding the skull firmly by the orbits. Note that the transverse tooth ridges (examine a prepared skull to see these more clearly) meet transverse grooves of the opposing teeth. These ridges and grooves serve as grinding guides and cutting devices at the same time. Grinding takes place from lateral to medial and generally occurs on one side only for several chewing cycles, before being switched to the opposite side. Note that the upper dental arcade is spaced more widely than the lower, necessitating effective chewing to be restricted to one side of the mouth at a time. Also examine the skull, with attached muscles, in the "resting" position and note that the cheek teeth are in occlusion and the incisors meet or almost meet at the same time (compare this with your own teeth and with the teeth of a rodent).

The superficial temporalis is a bipinnate muscle that originates from the dorso-lateral surface of the skull just posterior to the position of articulation of the lower jaw (Fig. 17.1), along the border of the parietal and squamosal bones. The fibers converge to a tendon as the muscle curves through the canal at the posterior edge of the orbit (Fig. 17.1). A pulley is thus created around which the superficial temporalis pulls, so that the horizontal alignment of the muscle belly is translated into a vertical jaw closing and joint stabilizing component. The tendon of this muscle inserts along the length of the lateral crest of the ascending ramus of the mandible (the anterior aspect of the coronoid process) (Fig. 17.1). Observing the skull from the front, open the jaws and pull on the central tendon of the superficial temporalis where it passes ventrally into the orbit. Repeat for each side and then "contract" each muscle simultaneously to determine the direction of jaw movement produced in each case. Reconsider this muscle later; especially consider this muscle's stabilizing effect upon the jaw joint when examining the masseter and pterygoideus muscles.

Table 17.1. Synopsis of the Jaw-Closing Muscles of the Rabbit.

Muscle Mass	Major Components	Subdivisions
Temporalis	Superficial	
	Deep	Lateral
		Medial
Masseter	Superficial	Reflected Portion
		Part 1A
		Part 1B
		Part 2
	Deep (Zygomaticomandibularis)	Anterior
		Posterior
Pterygoideus	Medial	
	Lateral	Superior
		Inferior

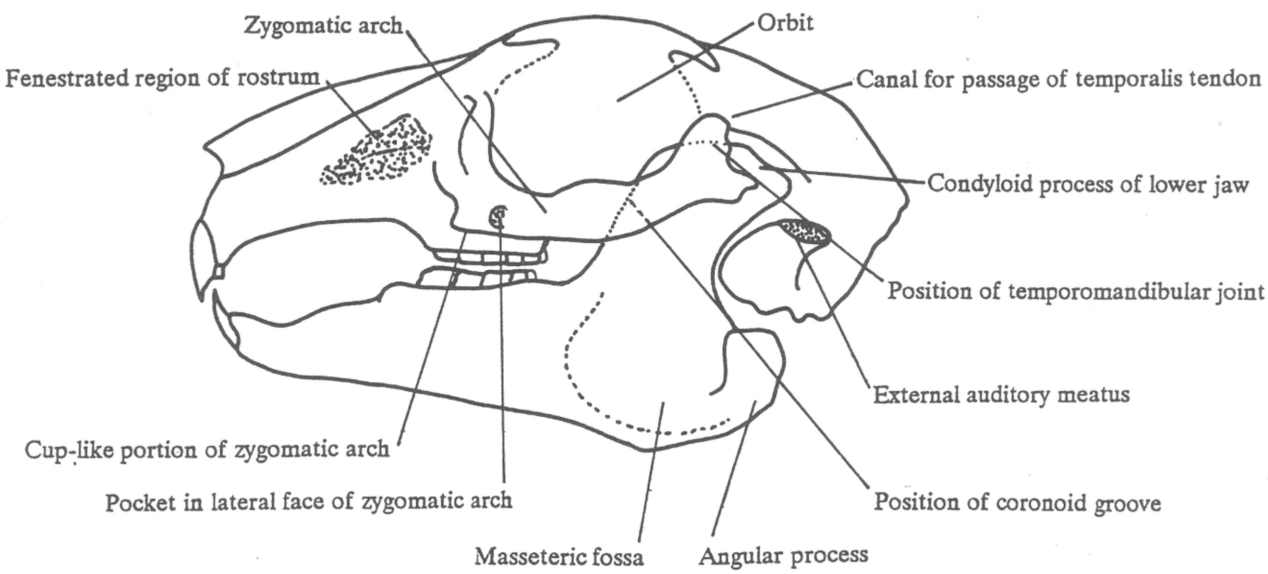

Figure 17.1. Lateral view of the skull and lower jaw of the rabbit (see also Appendix A).

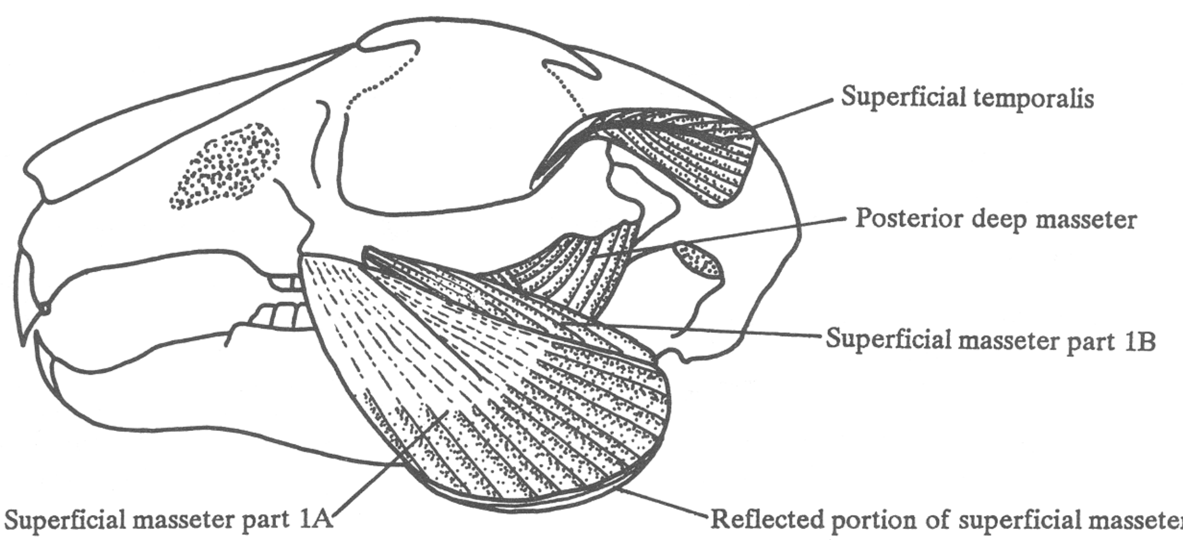

Figure 17.2. Lateral muscles with skin removed.

Proceed now to a dissection of the masseter muscle mass before returning to consider the deep temporalis that lies within the orbit.

The masseter is the largest and most complex of the masticatory muscles of the rabbit and may be divided into two main components and a number of subdivisions of these (see Table 17.1). The superficial and deep components are clearly separable posteriorly, but are tightly integrated anteriorly and can only be separated with difficulty.

The lateral-most head of the superficial masseter is a complexly subdivided unit that originates from the anterior end of the zygomatic arch. The most anterior point of origin is from a flattened, plate-like flange on the ventral border of the anterior end of the zygomatic arch. The reflected portion of the superficial masseter is a small band of muscle originating from a small tendon at the anterior-most end of the zygomatic arch. It passes almost vertically downwards and then curves posteriorly around the ventral edge of the mandibular angle (Figs. 17.2, 17.9). The fibers lie almost horizontally along the length of the ventromedial edge of the angular process and insert all along this region. Grasping the tendon of origin with forceps pull upward on the muscle with the mouth open and again note the direction of jaw movement.

The superficial masseter part 1A can be seen as the most massive portion of the masseter muscle (Fig. 17.2). It originates from the ventral and lateral surfaces of the anterior plate-like portion of the zygomatic arch (Fig. 17.1) just posterior to the origin of the reflected portion. The fibers of the superficial masseter part 1A fan out towards their insertion along the length of the posterolateral edge of the angular process. A thick sheet of fascia invests the proximal portion of this muscle (Fig. 17.2). Attempt to determine the jaw movements produced by contraction of the superficial masseter part 1A.

Lying deep to part 1A of the superficial masseter, and originating from a pocket in the lateral face of the zygomatic arch lying immediately posterior to the plate-like flange, is part 1B of this muscle mass. The insertion of part 1B is overlain by the posterior-most region of insertion of part 1A. Part 1B inserts at the rim of the angular process by means of an aponeurosis, and has a mean fiber direction similar to that of part 1A. Leaving the muscles of one side intact, carefully segregate part 1A from the underlying part 1B of the other side by severing the connective tissue between them, beginning at the point of origin. Part 1A can be separated at its point of origin and flapped ventrally to reveal the extent of part 1B and to reveal deeper parts of the masseter complex. When it is exposed, pull on superficial masseter part 1B parallel to its fiber direction. What would be the result of contraction of this muscle mass on one side only, and with equal force on both sides simultaneously?

The superficial masseter part 2 (Fig. 17.4) is vertically oriented, originating from the ventral margin of the zygomatic arch and inserting onto the masseteric fossa and mandibular angle, partially fleshily and partially by means of an aponeurosis. Anteriorly the demarcation between this portion of the medial masseter, the more lateral superficial masseter part 1 and the more medial anterior deep masseter is not clear. Expose this portion of the masseter by severing the attachment of superficial masseter part 1B from its site of origin and reflecting it. On the basis of its fiber direction and extent of origin and insertion, try to determine the actions resulting from contraction of part 2 on one side alone and on both sides simultaneously.

Reflect the superficial masseter part 2, again by separating the muscle from its origin, and carefully peel it from the muscles below. Again leave the insertion intact. The anterior deep masseter should now be visible although much of it may have been destroyed in the reflection of the superficial masseter part 2. The fibers of the anterior deep masseter are oriented more vertically than those of the other heads of the masseter so far mentioned. The fibers of this head originate on the ventral and medial surfaces of the zygomatic arch (Fig. 17.4). The area of origin may be easily seen on the medial surface by looking down into the orbit. What are the consequences of contracting the anterior deep masseter?

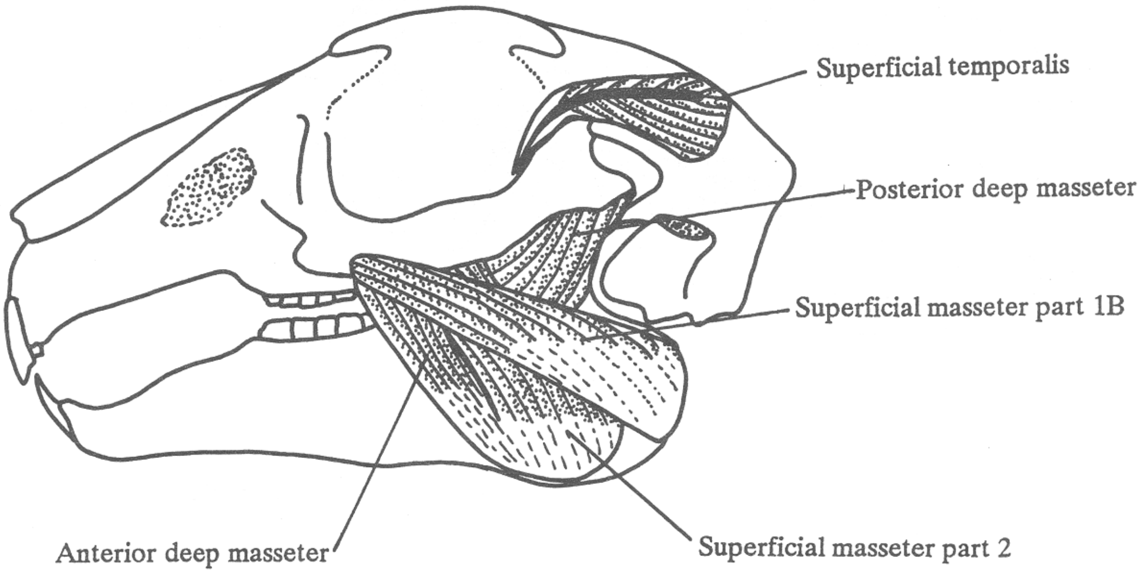

Figure 17.3. Superficial masseter part 1A and reflected portion removed.

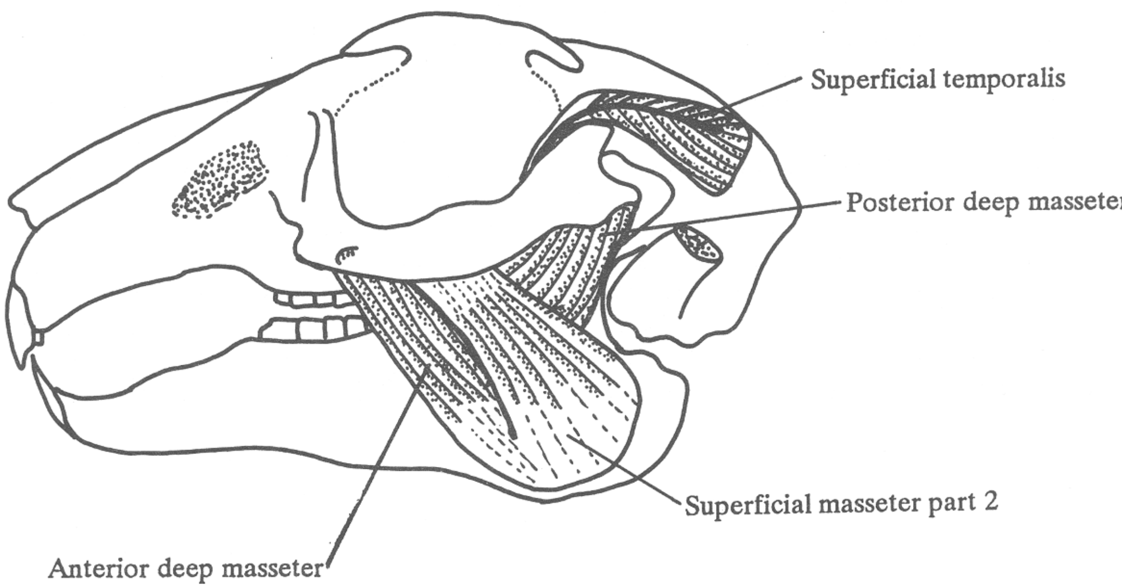

Figure 17.4. Superficial masseter part 1B removed.

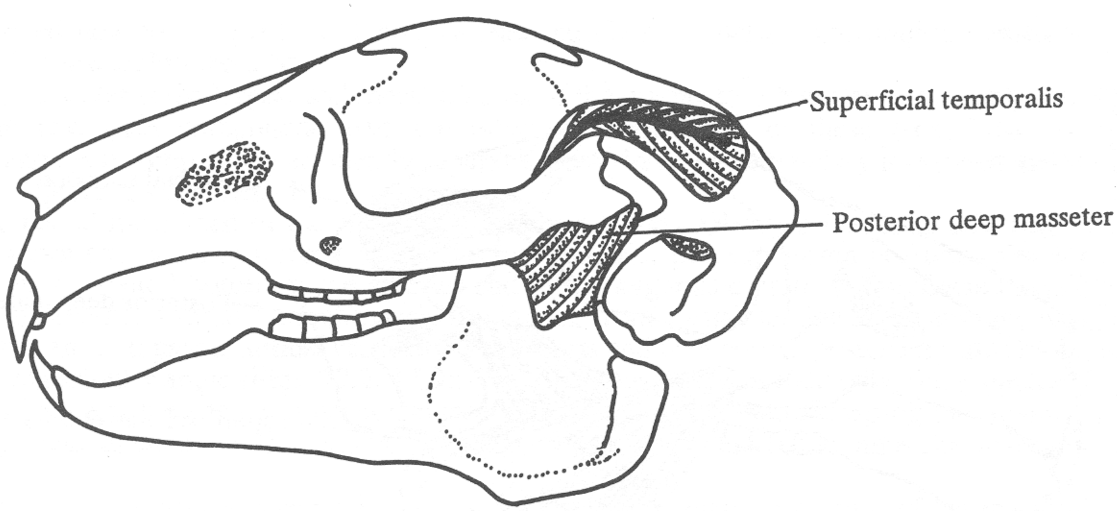

Figure 17.5. Superficial masseter part 2 and anterior deep masseter removed.

The posterior deep masseter may be seen lying posterior and medial to the anterior deep masseter (Figs. 17.4, 17. 5). The fibers of this belly are oriented in an anteroventral direction from their origin on the ventral and medial surfaces of the posterior extremity of the zygomatic arch. The fibers converge upon the lateral surface of the condyloid process of the mandible, where they insert. The insertion is more easily seen if the anterior deep masseter is reflected from its origin. This head appears to be a joint stabilizer.

Grasping the skull firmly by the orbits, manipulate the lower jaw and note the conditions under which the various muscles begin to be stretched. Considering that muscles develop peak tension at or near their resting lengths (neither stretched nor contracted but in tonus), try to deduce how the temporal and superficial masseter muscles differ in their actions. How does the width of gape affect the usefulness of these muscles and which muscles produce the power for grinding? Check your conclusions by examining a dynamic system (yourself). Open your mouth and place your fingertips just above your temples. Close your mouth slowly until your cheek teeth occlude. Your fingertips are placed over part of the mass of your temporalis muscles. Note when you begin to feel the muscles bulge. With your teeth in occlusion clamp your jaws firmly together and again note the amount of muscular expansion that takes place. Now move your fingertips to a position about 3 cm above and 3 cm anterior to your jaw angle. Repeat the movements indicated above. Your fingers now lie over the mass of your masseter muscle. How do the relative expansions of the temporal and masseter muscle masses compare at the positions mentioned? Muscles of great length and small leverage permit an extensive range of motion but lack power, while short muscles of greater leverage are more powerful but limit the range of movement.

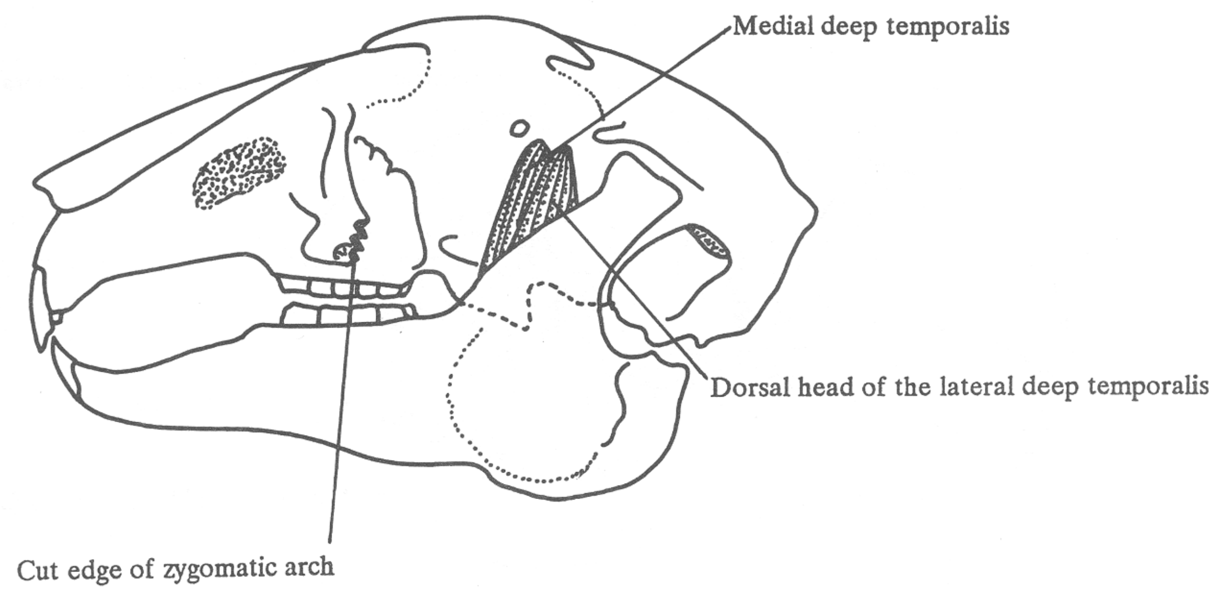

Figure 17.6. Deep temporalis with zygomatic arch cut away and superficial temporalis removed.

The deep temporal mass is composed of two parts which originate on the posterior wall of the orbit. The lateral deep temporalis (Figs. 17.6, 17.7), visible as a large mass lying just medial to the descending portion of the superficial temporalis, passes ventrolaterally forward to insert in the coronoid groove (Fig. 17.1). A relatively large ventral head of the lateral deep temporalis (Fig. 17.7) originates on a bony ridge just ventral to that of the dorsal head of the lateral deep temporalis (Fig. 17.6) and fans out ventrally toward its insertion in a depression on the medial surface of the neck of the coronoid process (Fig. 17.7). Its insertion may be observed by slightly lifting the medial pterygoid complex (the muscle mass covering the medial surface of the angular process - see below) and carefully pulling it medially at its anterior end. A large nerve (the mandibular branch of the trigeminal) passes between the medial pterygoid and the insertion of the ventral head of the lateral deep temporal.

The medial deep temporalis originates from a small depression anterior to the origin of the lateral deep temporalis. The fibers of the medial deep temporalis converge to a small tendon which inserts on a small bony protuberance of the anteromedial surface of the neck of the coronoid process (Fig. 17.6). With the jaw open "contract" the deep temporal mass by pulling on its origins and note the resulting jaw movement.

The medial pterygoid complex, which covers most of the medial surface of the mandibular angle, may be observed by turning the head ventral surface upwards. It is composed of two layers, differing in fiber orientation, that are virtually impossible to separate. These various portions originate from the pterygoid process of the alisphenoid (Fig. 17.8) and from within the pterygoid fossa (Fig. 17.8). They form a thick, fan-shaped muscle mass that inserts over the entire medial face of the angular process (Figs. 17.9,17.10). What effect would contraction of the medial pterygoid on one side only have; on both sides simultaneously; on one side only with the masseter of the same side; and on one side only with the masseter of the opposite side? Consider the three-dimensional nature of the skull and jaw and the directionality of the muscle fibers in the vertical plane (Fig. 17.10).

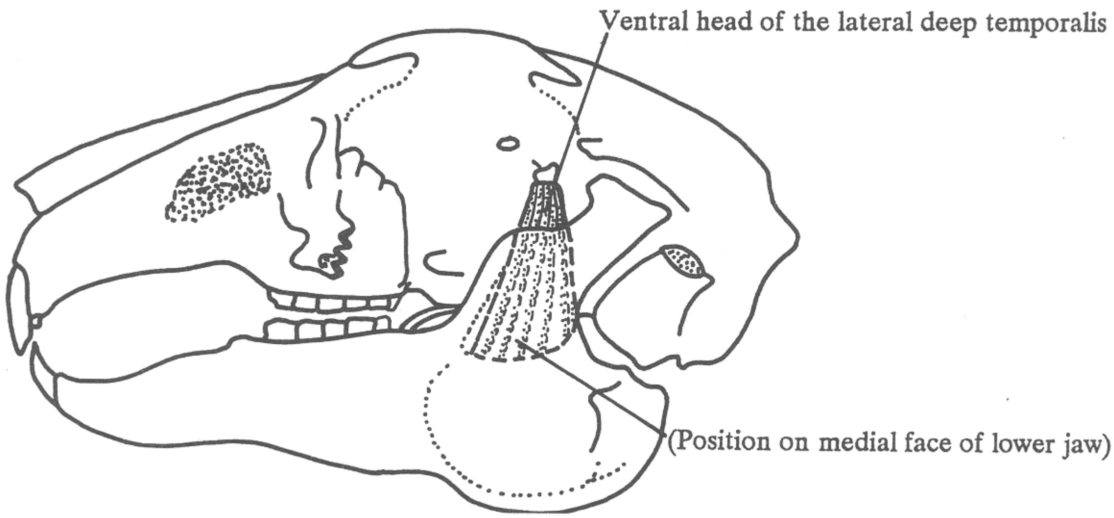

Figure 17.7. Ventral head of lateral deep temporalis.

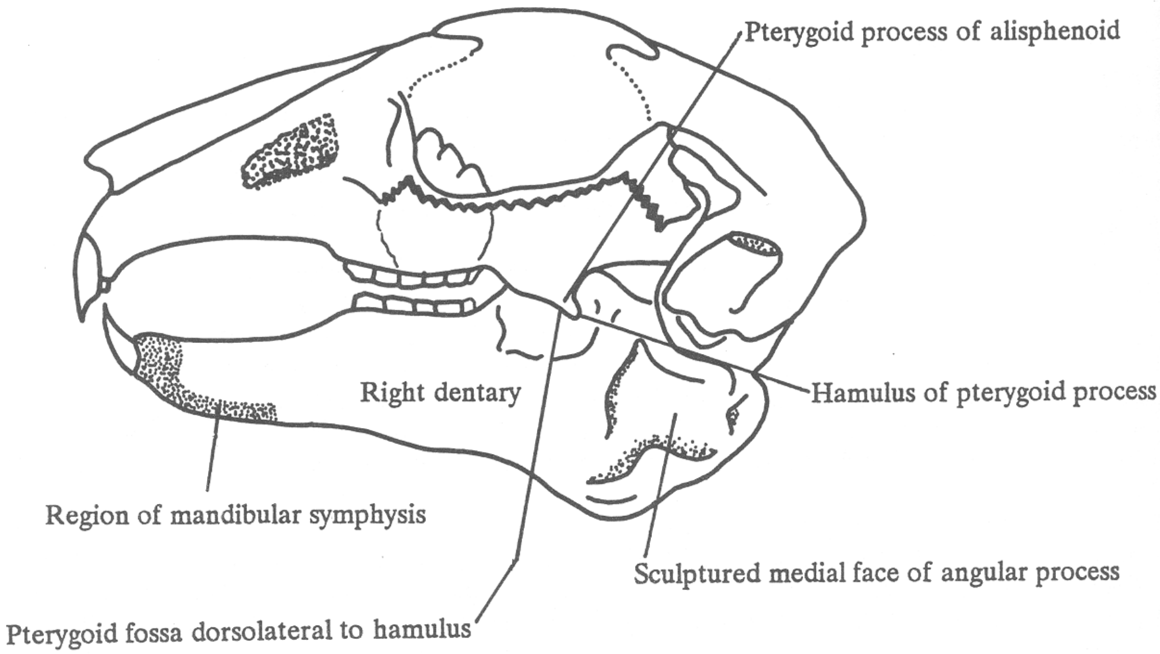

Figure 17.8. Lateral view of the skull and lower jaw of the rabbit with left zygomatic arch and left side of lower jaw removed (see also Appendix A).

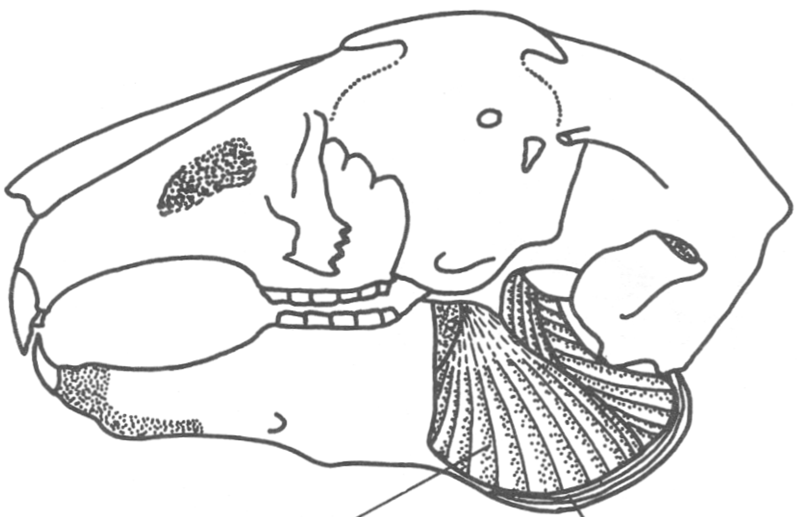

Figure 17.9. Insertion of medial pterygoid complex.

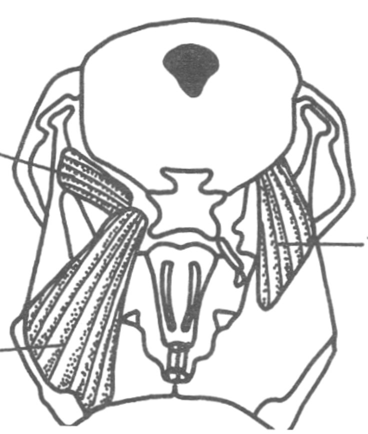

Figure 17.10. Posterior view of skull to show orientation
of the muscles inserting on the medial face of the lower jaw.

The lateral pterygoid is composed of two heads, the origins of which may be seen on the ventral wall of the orbit after the anterior temporal mass has been removed and the skull has been bisected (such bisected heads may be provided separately from the head you are dissecting). The superior head is very small and originates on the dorsal surface of the junction between the alisphenoid, palatine and pterygoid bones, and passes postero-dorsally medial to the deep temporal mass to insert in a small depression just below the condyle on the medial surface of the condyloid process (Fig. 17.11).

The larger inferior head arises from the dorsal surface and posterolateral edge of the pterygoid bone and follows the path of the superior head to insert in a larger depression surrounding the insertion tendon of the medial pterygoid (Fig. 17.12). Observing the head from the front, manipulate the jaw noting the positions in which the components of the lateral pterygoid complex become taut.

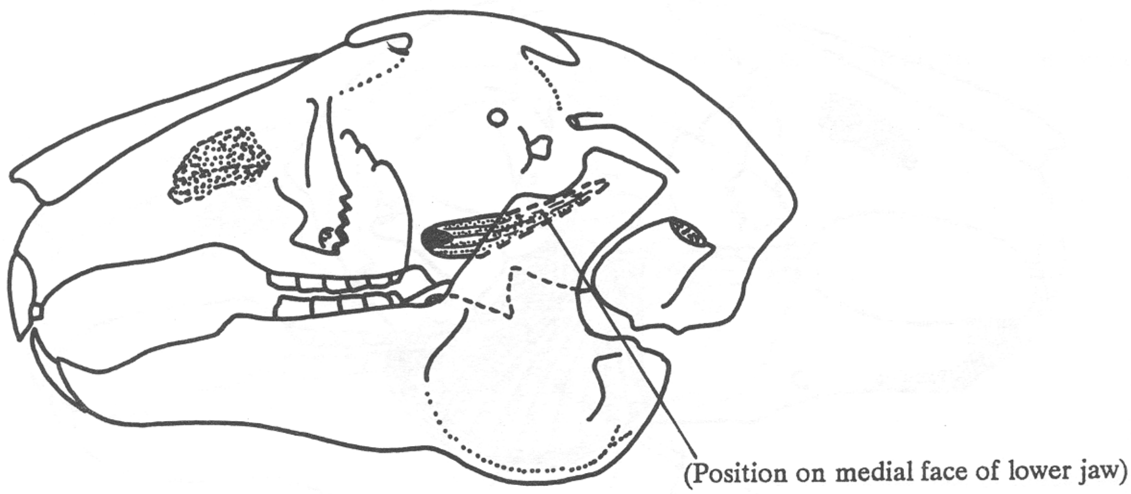

Figure 17.11. Lateral pterygoid, superior head.

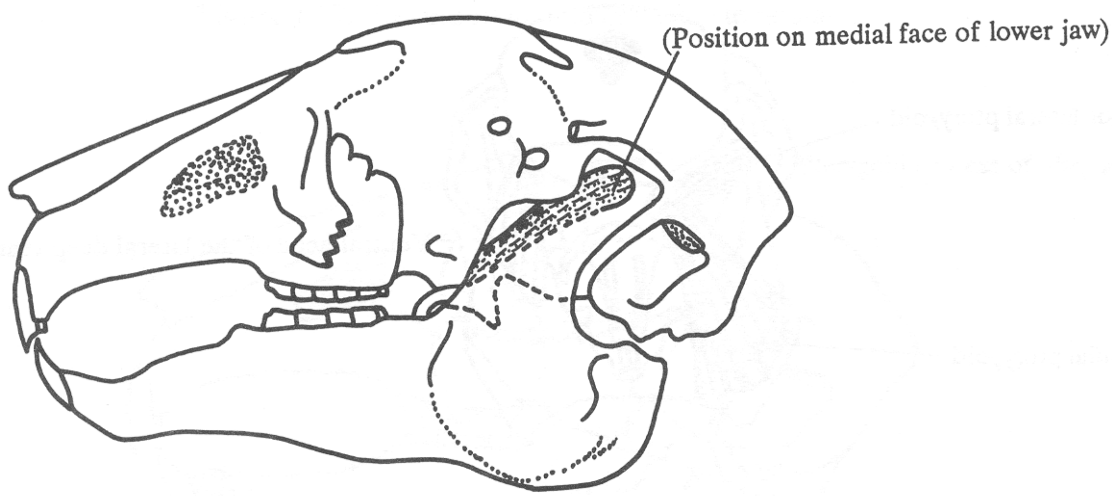

Figure 17.12. Lateral pterygoid, inferior head.

From the foregoing you should realize that the jaw closing muscles of the rabbit (and of all other mammals also) are complex structures which are capable (by being able to be utilized individually and in various combinations) of bringing about a wide range of jaw movements rather than merely straight, symmetrical jaw closure. Bear in mind the activities of the living animal and realize that whilst cropping is occurring the lower jaw must be centered in order for the incisors to occlude correctly, whilst in grinding only one upper and lower jaw quadrant may be used at any one time. Thus the same muscles can bring about this entire range of movements. This is only an approximation of the dynamics of the living system but it should serve to give you some appreciation of the latter. The rabbit is a herbivore and its jaw articulation mechanism permits the wide range of movements. Examine the jaw joint of a carnivore and determine the movement available. Try, then, to correlate the differences with differences in diet and habits.

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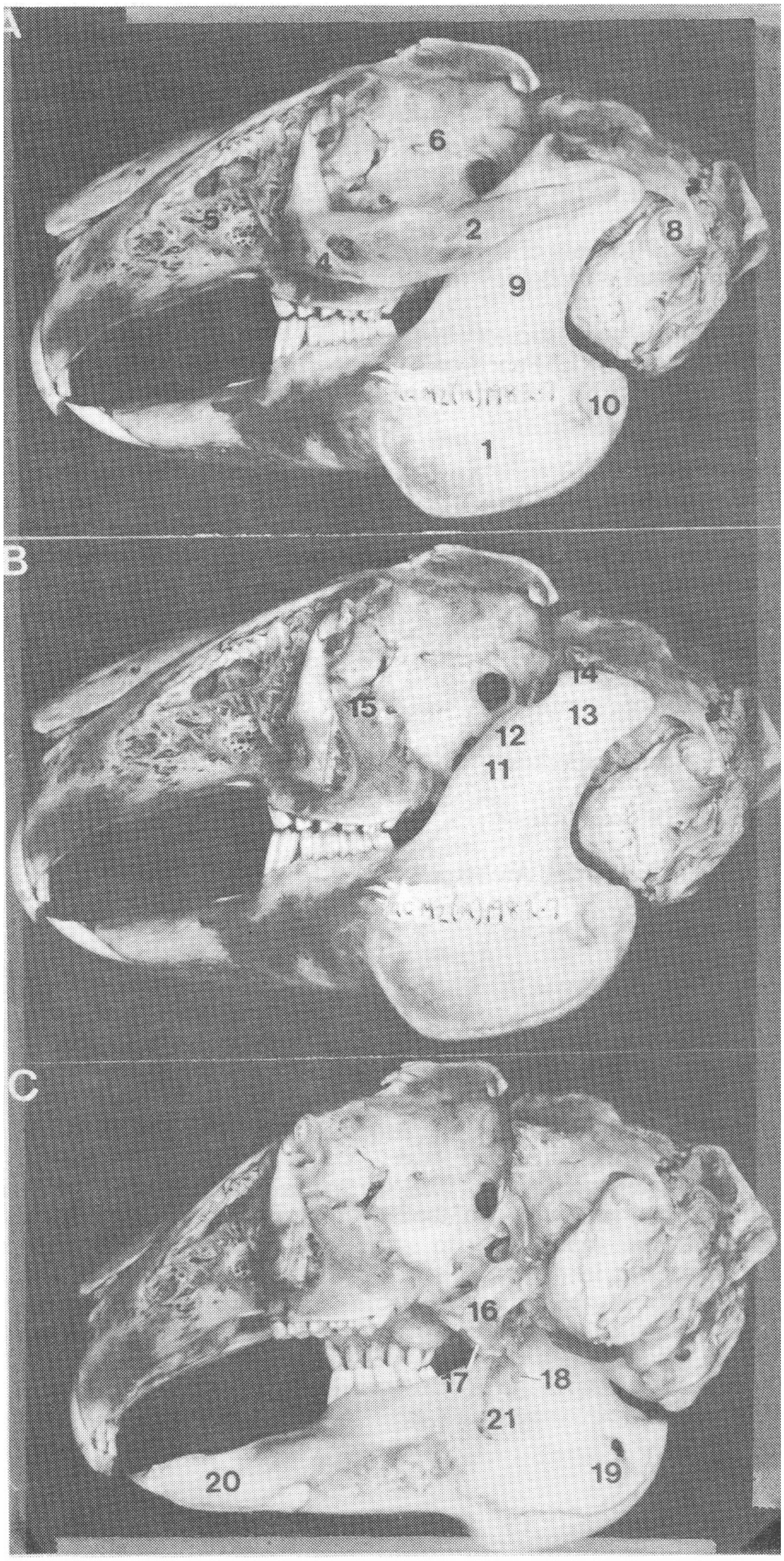
Appendix A
Photographic Atlas of the Rabbit Skull

A. Lateral View of Skull
1. Masseteric fossa
2. Zygomatic arch
3. Pocket in lateral face of zygomatic arch
4. Cup-like portion of zygomatic arch
5. Fenestrated region of rostrum
6. Orbit
7. Fossa for superficial temporalis
8. External auditory meatus
9. Ascending ramus of mandible
10. Angular process

B. Lateral View of Skull with Zygomatic Arch Removed
11. Coronoid process
12. Lateral crest of ascending ramus
13. Condyloid process
14. Temporomandibular joint
15. Alveoli of cheek teeth

C. Lateral View of Skull with Zygomatic Arch and Left Side of Lower Jaw Removed
16. Pterygoid process of alisphenoid
17. Pterygoid fossa
18. Hamulus of pterygoid process
19. Sculptured medial face of angular process
20. Region of mandibular symphysis
21. Fossa for insertion of ventral head of the lateral deep temporalis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