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MAMMALIAN MASTICATORY APPARATUS

WILLIAM D. TURNBULL

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FIELDIANA: GEOLOGY

VOLUME 18, NUMBER 2

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FIELD MUSEUM OF NATURAL HISTORY

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WILLIAM D. TURNBULL

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Preface

HISTORIC PERSPECTIVE

It is common knowledge that the paleontologist, as compared with the neozoologist, is considerably handicapped by the nature of his materials. Usually, it is only the hard parts of an animal that are preserved as fossils, in the vertebrates teeth, cartilage, and bones. While these represent systems of fundamental importance, they nevertheless are only two of an array of inter-related functioning systems of the once-living organism. Since the soft parts that are so readily available to the neozoologist in the living animal are only rarely represented in fossil materials, the paleontologist must glean every bit of direct information about a fossil animal as a living whole from those portions of the skeletal and dental systems that are preserved, including any features of soft parts that may be reflected there.¹

Fortunately for the paleontologist, many soft structures do leave distinct, characteristic impressions on adjacent bone elements. The presence of already functioning soft parts at the time the skeletal elements are being laid down and their continued presence during the life of the individual often suffices to cause these same soft structures to be partially reflected in the details of the bone. The brain will illustrate this. With this outer surface in close proximity to the developing cranial wall, and because of the demands for foramina to serve vascular and nervous needs, the brain profoundly influences the form that the developing cranium will take. Other examples of soft-part control of the form of hard-parts are found in some of the otic and olfactory structures. Muscles, too, play a very important role in determining the definitive form, degree of development, and, especially, the surface texture of bones (see, for example, Dolgo-Saburoff, 1929)—and this is to be an area of concern in this paper. It is through their functioning, on the one hand, and their very physical presence, on the other, that muscles achieve this control. Crests, grooves,

¹ Indirectly, of course, much can be learned by inference from studies of the entombing sediments, and paleoecology, as well as from study of living relatives or forms with closely parallel specializations.

ridges, processes and rugosities are examples of the sorts of structures controlled by muscles. These features are often quite characteristic, usually marking muscular origin or insertion attachment areas, or the places to which tendons attach or over which they glide.

Many authors have given attention to the roll that the dorso-axial and locomotor musculature plays in determining the form of spine, limbs, and girdles, but surprisingly little attention has been given to those osteological features which are related to the jaw musculature. This is a shortcoming of considerable importance for the masticatory musculature is unique in that it is one soft-parts system that not only leaves its own mark directly upon the skeleton, but that can be related simultaneously through tooth wear and morphology to another hard-part system, the dental system. From this inter-relationship, it might be expected that proportionately greater importance should be attached to details of mammalian jaw musculature to give us a more thorough understanding of the masticatory apparatus. In this work detailed documentation of the masticatory apparatus (including relationship of musculature to skeleton) for a selected suite of mammals is presented.

ACKNOWLEDGEMENTS

I would thank many people for help and encouragement in this work. Translation assistance was given by Dr. Rainer Zangerl, the late Dr. D. Dwight Davis, and the late Mr. Shimon Angress. Technical advice on my own drawings was given by the following artists at the Field Museum: Mr. Douglas Tibbitts, Miss Phyllis Wade, Mrs. Maidi Wiebe Liebhardt, and Dr. Tibor Perenyi. Several sets of skull and muscle drawings and most of the other illustrations are the work of Dr. Perenyi. Other skull-muscle drawings were done by Mrs. Leibhardt and by my friend Charles Joslin, and Figures 34-37 and Figure 48 were drawn by Miss Marian Pahl. In each case credit is given in the appropriate section of the text as is credit for materials made available from sources outside of the Museum. Typing of the various drafts of the manuscript was done by Mrs. Evelyn Sharach, Mrs. Winifred Reinders, Mrs. Eleanor Pringle, Miss Jeannette Forster, and my wife.

Initially, interest in this subject was stimulated by Prof. Bryan Patterson and Dr. Davis. During the protracted period since beginning the work, Prof. Everett C. Olson (my senior professor) and Dr. Davis (until his death in 1965) have discussed, advised, encouraged,

and criticized all aspects of the paper. It is to these men, and to Dr. Zangerl and my wife Priscilla, that I am most indebted. Profitable and valuable discussions have been shared with each of them and with the following additional colleagues: Drs. Charles A. Reed, Nicholas Hotton III, Lloyd DuBrul, Henry Dybas, Phillip Hershkovitz, and Ernest Lundelius, Jr. I also thank Drs. David Wake, Karel Liem, Leigh Van Valen, and Ralph Johnson for critically reading the completed manuscript.

One final word of appreciation is due to the Museum's administrative staff, especially to Mr. E. Leland Webber, Director, who has given sympathetic support and encouragement.

I. Introduction

The bauplan of mammalian masticatory organization derives directly from the reptilian ancestry. Primitively and typically, reptiles do little food processing in the mouth. It is characteristic of the mammals (and presumably was for the mammal-like reptiles) that they not only procure their food with this apparatus at the entrance to the digestive tract, but that they perform the first of a series of food processing activities there. Hence, chemical and mechanical break-down is initiated in the mouth. Quite simply, the basic plan of the mammalian apparatus involves the development of a considerable salivary supply and a differentiated dentition. The latter is designed to perform a variety of separate and distinct, but at the same time closely related, functions. The most anterior teeth, the incisors and canines, are specialized first and foremost for the function of food procurement, whether or not this be their sole function. The cheek teeth, premolars and molars, are specialized to serve food processing functions, but on occasion other uses are made of them. In order for the dentition to operate, it must, of course, work in close co-ordination with the soft structures of the mouth, especially tongue, lips, and cheeks. In the broadest sense, even body locomotion and the particular use of the front limbs (digging, scratching, hitting, holding, or grasping) are directly concerned with the initial stages of food procurement.

Implementing the masticatory apparatus is the jaw musculature. In all mammals this comprises three distinct jaw-closing muscle groups: the masseter group, the temporalis group, and pterygoideus group; and a single jaw-opening muscle group: the digastric group.¹

¹ Several other muscles or groups of muscles which are related to the masticatory apparatus or which attach to the jaws of mammals should be mentioned. None of these is of any great importance in implementing jaw movements, although they may be important to other aspects of the masticatory activity. Of the latter, the hyoid group implements the tongue, and does much to floor the mouth cavity, and the buccinator and labial groups control the cheeks and lips, and in conjunction with the hyoid group, govern the size and shape of the oral cavity. A few other muscles related to the jaws occur commonly, the auriculo-mandibularis and the intermandibularis (probably a mylohyoid derivative). The mylohyoideus and platysma are always present, but need not concern us here.

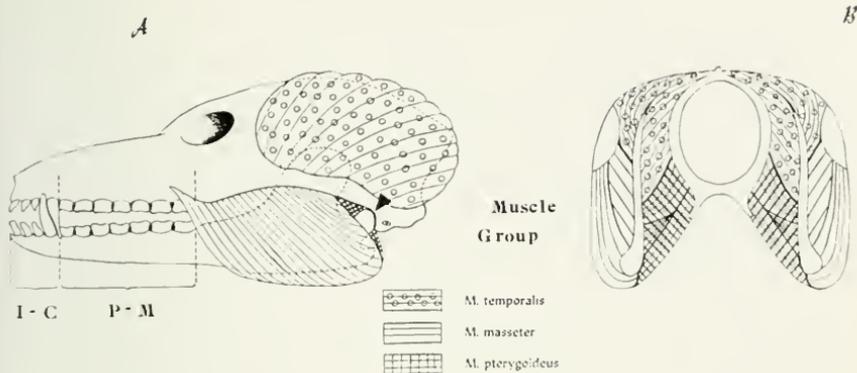


FIG. 1. Diagrammatic illustrations of the generalized basic plan of the masticatory apparatus in lateral (A) and cross-sectional (B) views showing the muscle groups which accomplish the jaw-closing movements. Also shown are the jaw-joint (fulcrum), and the incisor-canine (I-C) and premolar-molar (P-M) dental regions. The midpoints of these dental regions constitute the average working distances of the resistance lever arms in the lever mechanics systems of each region.

The basic plan of the masticatory musculature is shown in Figure 1 (modified after Becht, 1953, and others). Additional features important to jaw mechanics, the incisor-canine area, the premolar-molar area, and the glenoid-condyle joint (fulcrum) are also indicated. According to the ways in which these muscle groups (and, of course, the teeth and jaws as well) are modified in various mammals, several kinds of adaptively specialized groups have come to be recognized widely.

AIM OF THE WORK

The present work is an attempt to study, document, and interpret the anatomy of the masticatory apparatus of mammals. It is based upon dissections of nine representative Recent forms, and upon a wealth of osteological and paleontological comparative materials in the Field Museum collections. It draws broadly upon the literature, in order to bring together and relate all pertinent information. Throughout, the intention has been to gain a better understanding of the mechanics of jaw movements, and of the entire functioning of the masticatory apparatus.

GENERAL METHODS

With the dissections, careful attention was given to accurate mapping of muscle attachment areas in order that a reasonable estimate

of the mean direction of forces applied could be made. Individual muscles were weighed and their attachments noted (not just muscle groups), and, when feasible, separate subdivisions of muscles were weighed. Comparisons between muscle masses were made, incorporating all available data from the literature in addition to that from the dissections described here. A functional analysis which is broadly comparative is given. This involves development and use of a simple formula for estimating the comparative useful power of the various jaw-closing forces for the entire suite of mammals for which muscle weight (or mass or percentile) data are known. Specific methods are discussed, and materials studied are listed within the text where pertinent. The abbreviation "FMNH" stands for Field Museum of Natural History. It is used as a prefix to catalogue numbers of specimens in the zoology and paleontology collections.

PAST CLASSIFICATIONS

Most students have recognized either three or four groups within the mammals that conform to the major adaptive types of jaw apparatus.¹

Invariably, the three groups (or three of the four, where four have been designated) constitute well defined, adaptively specialized, highly successful masticatory types which cause few basic problems. The fourth group, a miscellaneous category, has received less consistent handling when it has not been ignored or left ill defined. Either it has been made into a composite group that includes some or all mammals not assigned to one of the three specialized groups or it has been made into a generalized group that may or may not have a miscellaneous residue of forms appended to it. Generally, the primitive fossil groups as well as the aberrant modern and fossil groups have been ignored.

From the broad comparative standpoint, this is an unsatisfactory situation. Indeed, there is validity to the past classifications, as far as they have gone, but I want a jaw-apparatus classification that encompasses all of the Mammalia, and I aim to 'order' the miscellaneous category. A composite, miscellaneous group including the generalized, the aberrantly specialized, the degenerate, and the poorly-known forms is too inclusive a category. I think the general-

¹ See for example, Teutleben, 1847; Lubosch, 1907; Worthmann, 1922; Bluntschli & Schreiber, 1929; Brodie, 1934a and 1939; Becht, 1953; Maynard Smith & Savage, 1959; and Schumacher, 1961a.

ized forms must be placed in a group by themselves, for this group more than any other captures the focus of attention in comparative work. Hence, I use a Generalized Group in addition to the three already well-defined specialized ones. That a modified residual miscellaneous category is still needed will become evident. As I use it, this includes *all* of the remainder of the mammals within the following sub-categories: 1) those forms that are poorly known or inadequately understood, such as some of the Mesozoic forms, and Tillodonta, Pantodonta, etc., which will in all probability remain in the miscellaneous category for a long time; 2) some aberrantly specialized groups (Edentata, Taeniodonta, Sirenia, Desmostylia, Proboscidea); and 3) various dentally degenerate forms (Pholidota, Tubulidentata, Cetacea). It is from these last two subdivisions that we may expect to see progress made within the foreseeable future by the designation and characterization of other distinctive groups.

CHARACTERIZATION OF CATEGORIES OF MAMMALIAN MASTICATORY CLASSIFICATION

GENERALIZED GROUP. In this group the masticatory apparatus is relatively unspecialized and is structurally intermediate between that of the three (following) specialized groups. In it, the three jaw-closing muscle groups exhibit the primitive relationship (inherited ultimately and with modification from the therapsid ancestry) wherein the temporal is the dominant muscle and masseter and pterygoid groups are only moderately developed and act as accessories to the temporal (Adams, 1919; Crompton, 1963a and b; Barghusen, 1968). The position and alignment of the temporal make it best serve the simple hinge (orthal) closing movements. The Generalized Group thus represents the basic, primitive condition of the metatherian-eutherian mammals. It probably represents that of the other infraclass of the Theria too (i.e. Pantotheria including Orders Symmetrodonta and Pantotheria). Quite possibly it may even represent that of many non-Therian mammals as well (Prototheria, Allotheria) and some orders of uncertain subclass (Triconodonta and Docodonta), particularly their stem line forms.

SPECIALIZED GROUPS. These are characterized by the striking ways in which they depart from the conditions pertaining in the Generalized Group. Different adaptive modifications of the masticatory apparatus are developed in each group, departures which differ in

degree as well as kind. In one group these changes involve mainly the teeth and jaws, with but slight modification of the musculature. In another, more marked changes occur, and in yet another, the changes are quite radical and include a considerable remodeling of the jaw muscles. These are as follows:

SPECIALIZED GROUP I, "carnivore-shear" or "scissors" type.

A group in which the closing of the jaws is by a straight, simple, hinge movement ("orthal" of Ryder, 1879; Cope, 1889 and others) that involves little, if any, appreciable movement forward, backward, or laterally, and which in its fullest expression has the opposing teeth shear past one another in scissors-like manner. Specialized Group I is typified by the placental carnivores.

SPECIALIZED GROUP II, "ungulate-grinding," or "mill" type.

A group in which a mill action, or grinding motion, predominates. In this group, masticatory movements are in three subequal opposing directions: in a fore-and-aft direction (the least developed movement), in a medial and lateral direction (the characteristic mill movement is from lateral to medial during the grinding stroke), and the usual vertical (orthal) direction. Specialized Group II is typified by the ungulates.

SPECIALIZED GROUP III, "rodent-gnawing," or "anterior shift" type.

A group in which the jaws operate in two distinct positions—the usual posterior one for the true mastication function, and another, more anterior one for the gnawing function. The dentition also is adapted to serve these two initially quite distinct functions. Gnawing is accomplished in several ways: by biting together the upper and lower incisors; by scraping with either the recurved upper, or the procumbent lower, incisors; or by a combination of these. In each case where the jaws are used, they are protruded for gnawing. Since the span from condylus to incisive occlusal surface is shorter for the lower jaw than is the corresponding span above (glenoid fossa to the incisive occlusal surface), the only way for the incisors to occlude is by a forward shifting of the lower jaws. Accordingly, the glenoid is modified into a trough. The grinding, and to some extent the crushing, functions of the cheek teeth are accomplished by vertical closing movements that are combined with horizontal and lateral movements in some (ectental of Ryder, 1879; Cope, 1889, and others), or by horizontal and anterior-posterior movements in others. These functions operate unilaterally at any given time be-

cause of the anisognathia¹ of the skull and jaws. The shifting for gnawing, and the gnawing movements themselves, all involve forward (palinal) and backward (proal) movements in conjunction with the closing and opening of the jaws. Specialized Group III is typified by rodents and lagomorphs.

MISCELLANEOUS.—This remnant category (mentioned above, p. 159), is necessary in order for the classification to encompass all of the diverse mammalia, living and extinct. Its three subcategories are not sharply defined, but can be recognized generally:

1) The poorly known or inadequately understood forms which may eventually prove to belong to one or the other subcategories (below), or to one or another of the major groups already designated (above);

2) the aberrantly (or otherwise) specialized forms which have specialized along lines differing from the three successful and long-recognized Specialized Groups,

3) the dentally degenerate forms with their own kinds of overall masticatory specialization. Thus, the miscellaneous category contains all mammals not clearly in one of the other major groups until we shall know more about them.

DISCUSSION OF THE LITERATURE

A review of the literature makes it apparent that there are two distinct levels of pertinent works. First, there are a vast number of studies that have some pertinence, but that skirt the fringes of the topic. Most often these discuss the myology of one species or deal with a particular muscle system. Others in this category have to do with mechanics as related to man, and a few are concerned with other peripheral areas. Only a small number, less than a dozen, can be considered as belonging in a second group of comparative works with a focus on the broad problems of mechanics and function. One of the more recent of these is a paper by G. Becht (1953) that offers much both in the imagination it shows and the methods and techniques it introduces. The works of Maynard Smith and Savage (1959) and Schumacher (1961) are different in scope and aims. The former is short and non-descriptive, an attempt to generalize and to offer a key to the analysis of mammalian jaw mechanics. The latter is largely descriptive, offers a wealth of data, and is adequately illustrated so

¹ This refers to unequal spacing between right and left cheek teeth rows of the palate and lower jaws.

that it constitutes the most extensive and best presentation of new data since Toldt.

Several other recent works worthy of mention are more peripheral to a comparative mechanical treatment. Gregory (1951) gives some basic information that is applicable though it is incidental to his main thesis. In Fiedler (1952, 1953) are to be found discussions of the history of the comparative study of mammalian masticatory apparatus and an extensive comparative investigation of generalized mammals. This includes insectivores (even including some specialized ones), generalized carnivores, and primates. The 1953 work is a well illustrated and detailed study of innervation and its bearing upon relationships and muscle homologies, but it gives no muscle proportions. Yoshikawa and Suzuki et. al. (1961) and Yoshikawa and Suzuki (1965), in works that deal exclusively with the masseter complex of the jaw musculature, provide information on a broad taxonomic base, but they do not give muscle weights or attachment maps.

In 1935, Edgeworth published his extensive and voluminous *Cranial Muscles of Vertebrates* which is profusely illustrated. It is comparative and developmental in its treatment, but the text is usually brief. I find it most useful for its illustrations, though inadequate for the mammals. Klott (1928) provides much jaw muscle proportion data, especially for the Carnivora. Worthmann (1922) and Adams (1919) both offer interesting ideas and give evidence of considerable insight. Unfortunately, Worthmann's mechanical analyses are quite primitive and somewhat oversimplified, and are only superficially comparative, the focus being on man. Adams' work is helpful in that his approach is phylogenetic, although by trying to trace the development and homologies of structures throughout all the vertebrates, he omitted many details in treating the mammals. His attempts to reconstruct the musculature of fossil forms are of direct interest. In this regard, Simpson (1926, 1933b), too, has done some interesting work—especially that on the Mesozoic mammals. This brings us to what is undoubtedly the most detailed comparative work and thus the most important study of all: Toldt (1905). It has but one major weakness: too few illustrations. A work of this sort should be abundantly illustrated so that the serial removal of layers of muscles from the superficial to the deep may be clearly demonstrated. In view of the paucity of illustrations, it is indeed fortunate that Toldt, when he describes something, really describes fully! His work, old as it is, is by far the best comparative study to date. No more extensive or detailed original comparative anatomical data on jaw muscles is

available from any other single source. Before Toldt, there was very little interest in this field. Lubosch (1907), Cope (1889 and later), and Ryder (1879) are the most outstanding for that period.

The bibliography includes cited references and a lengthy listing of works not cited—in all about 450 papers. Most entries are annotated by keyed symbols that provide information as to subject matter contained. This seemed worthwhile because of the peculiar and scattered nature of this literature. Many of the works cited are veterinary papers, but no concerted attempt to search that extensive literature was made. It therefore is not a complete bibliography, but taken together with the listing of Schumacher (1961) it provides a breadth sufficient for the current study.

II Description

This section contains extensively illustrated descriptions of the jaw musculature of nine selected mammals based upon detailed unilateral dissections of one adult individual of each species.¹ No attempt to account for individual variation is made, except where other studies provide a means of its assessment. The nine species were selected to include at least one member of each major adaptive type, and according to the need, to provide material for exploration of subdivisions within these types. Thus it was possible to evaluate the methods and procedures of other workers and to select and utilize those found to be best suited for this comparative study. Hence, corroboration, elaboration or modification of earlier work, as well as presentation of new material, is involved. Uniform and comparable data are presented in the illustrations and weight tables in every case.

Dissection of the greater part of the digastric and masseter muscle groups, the superficial part of the temporalis group, and the insertion end of the *M. pterygoideus internus* (pterygoideus group) was managed layer by layer from the surface inward. Access to the more deeply-lying portions required: 1) removal of the zygomatic arch (cut free at its buttresses); 2) separation of the jaws at the symphysis whenever the nature of symphysis permitted this, or cut through the ramus somewhere in front of the jaw-muscle attachment area (usually in a diastemal region); and 3) a cut through the joint capsule in order to remove the jaw ramus. Effort was made to prevent desiccation of the specimens, and all muscle weights were made on a glass-enclosed beam balance, except for the larger specimens. Fat and fascia were removed from the surface of each muscle, but the tendons were left intact. A prepared skull of a second individual of the same, or closely allied, species was used to map the muscle attachment areas.

GENERALIZED GROUP

Current morphological and paleontological knowledge provides a structural history of the metatherian-eutherian grade mammals which

¹ Except in the case of *Odocoileus* and *Equus* where sub-adults were used.

permits us to appreciate the generalized condition of the stem line (Simpson, 1945; Romer, 1945, 1966; Gregory, 1951; *Traité de Paléontologie*, 1958, 1961 (Piveteau, ed.); Winge, 1924; Weber, 1927-8, etc.). Living today are a number of forms which are morphologically close to the ancestral line in that they continue to utilize the primitive structural condition much as did their Late Mesozoic ancestors. *Didelphis* and *Echinosorex* are two such animals. This and their availability led to their selection as the forms to represent the generalized group.

Didelphis marsupialis

Figures 2.A,B; 3.A,B; 4.A,B; 5.A,B.

A prepared skull and jaws, FMNH 41088, served as the basis for the osteological illustrations, and for mapping the limits of the muscle attachment areas on the bone surface. Two preserved specimens were dissected, FMNH 0-1432 and 57542. The former served as the basis for the muscle drawings. The latter was fresh-killed, embalmed, and then quickly dissected for the weighing of the individual muscles. In both cases, the dermis and all of the superficial musculature associated with it (Mm. panniculus carnosus, platysma myoideus, and occipito-frontalis), as well as the buccinator and auricular and orbicular muscle groups were removed to expose the masticatory musculature. Of the numerous published studies of the opossum, Coues' 1872 paper, "The Osteology and Myology of *Didelphys virginiana*" is the only one that deals with the masticatory musculature in any detail, and because it is inadequate for this work, I have prepared new, detailed descriptions with accompanying illustrative material.

The corner of the mouth (angle of opening) lies back nearly at the level of the last molars, $M \frac{3}{3-4}$.

The masseter is a bulging, roughly triangular muscle mass, even when the mouth is agape at a 30° angle (fig. 2.A). Its upper border follows a ridge that marks the upper limit of the lateroventral facet of the zygomatic arch. In back of the orbit the border of the muscle runs nearly straight back to the jaw joint. Beneath the orbit, the anterior border of the muscle curves inward and downward and exhibits a rounded concavity of its upper third as a result of the nearly straight backward pull of the superficial tendon fibers in this region. The lower two-thirds of the anterior border of the muscle is a bit irregular. It extends downward and a little backward from the level of the occlusal plane to the lower edge of the mandible. The anterior border of the masseter lies behind the last molars for its entire length.

The postero-ventral border of the muscle follows along the gently rounded posterior third of the jaw bone. The muscle is thick, many layered, and is basically divided into two components: an external one, pars superficialis, and a deep one, pars profunda. The latter is nearly completely covered by the pars superficialis. Two small areas of the deep masseter protrude from beneath the body of the superficial portion, one a very tiny area in front near the insertion, and one that is fusiform in shape and that lies immediately beneath the zygoma along the dorsal border of the muscle. This last portion has a tendinous surface that is fused anteriorly with the more or less continuous aponeurosis that covers both the masseter and the temporalis superficially.

The superficial masseter takes origin by a tendinous sheath from the small osseous protuberance above M^4 , on the maxillary and jugal bones, and from the front edge of the ridge on the jugal that leads onto this prominence (fig. 2,A,B). Thus the origin is directly beneath the orbit and beneath the origin of *M. zygomaticus*. The muscle fibers fan somewhat as they run backward and downward to their insertion. The insertion of the superficial masseter is mostly fleshy and is onto the broad, flat ventral surface of the ramus on the triangular area formed by the incurving, inflected angular process. The superficial portion is tendinous over the greater part of its surface. It receives innervation from a trunk of the N. massetericus that leaves the main nerve and passes laterally through a split in the mass of the deep masseter, near the insertion. The split is located in the anterior half of the muscle.

The deep masseter (fig. 2,B) has a relatively small tendinous area that corresponds roughly to the fusiform portion of the muscle not covered by the superficial masseter. The origin, which is mostly fleshy, though tendinous superficially, is from the entire length of the ventro-lateral facet of the lower edge of the zygomatic arch. The muscle fibers fan a bit more than in the superficial portion, and many more run downward. The insertion is almost entirely fleshy and is on the antero-dorso-lateral area of the ascending ramus in a region extending from immediately in front of the condyle to almost as far forward as the last molar tooth. Innervation is by a trunk of the masseteric nerve that passes out of the *M. zygomaticomandibularis* near its middle.

The *M. zygomaticomandibularis* (fig. 3,A) takes origin from the greater part of the medial surface of the zygomatic arch from about

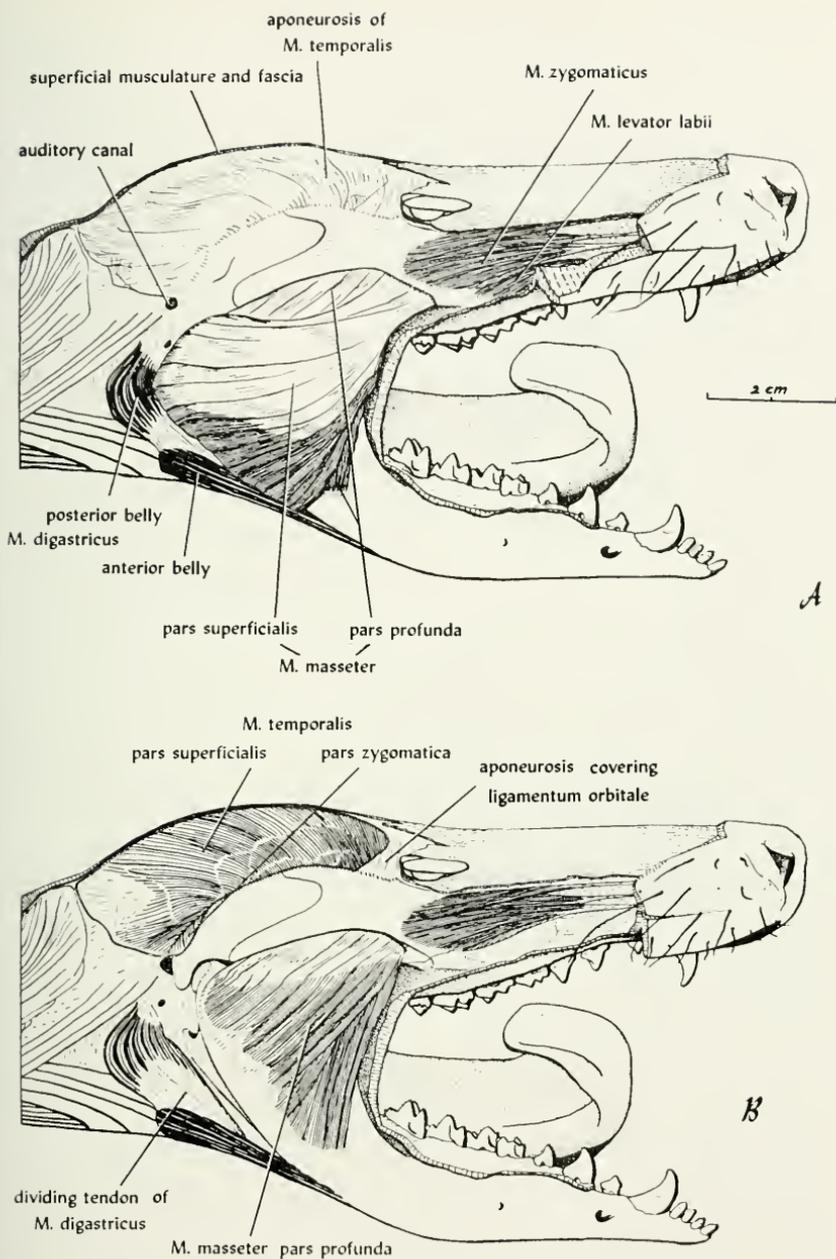


FIG. 2. Masticatory musculature of *Didelphis* seen in lateral view. A, Superficial dissection showing nasal (*M. zygomaticus*) and labial levator muscles and the aponeurosis of *M. temporalis*. *M. digastricus* and *M. masseter* are fully exposed. B, The same, with the temporal aponeurosis and *M. masseter*, pars superficialis removed to expose *M. temporalis* and *M. masseter*, pars profunda to view.

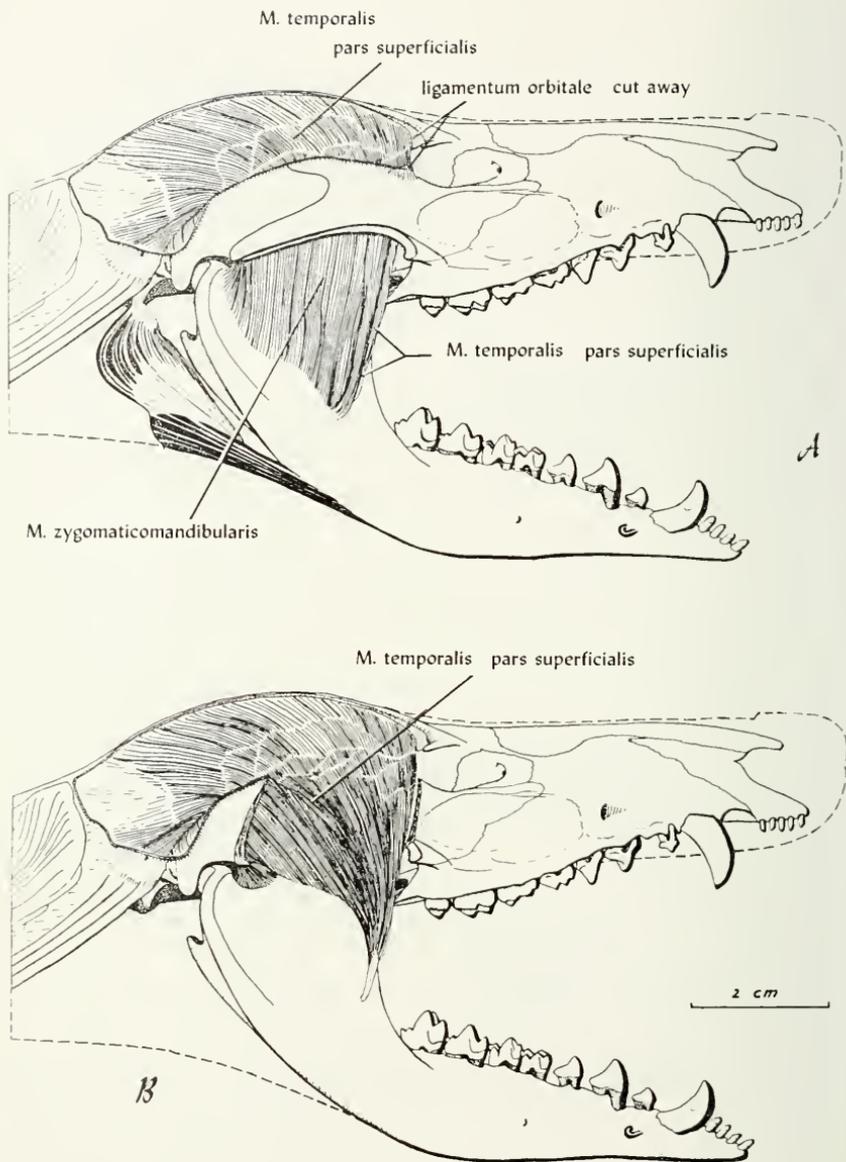


FIG. 3. Masticatory musculature of *Didelphis* seen in lateral view. A, Dissection at sufficient depth to expose *M. zygomaticomandibularis* to full view. B, Deep dissection showing *M. temporalis* exposed to full view with most of zygomatic arch cut away.

the level of the back edge of the orbit back to the posterior root of the arch. To a certain extent the temporal aponeurosis also serves as the origin attachment. The muscle is not clearly distinct superficially from the deepest layers of the masseter. The direction of the fiber-bundles is, in general, more nearly straight down in the zygomaticomandibularis than it is in the deep masseter, but a similar degree of shifting of fiber direction is encountered as one moves from superficial to deeper layers within the deep masseter. The medial surface of the muscle is intimately united with the temporal muscle posteriorly but is more readily separated anteriorly. The area of insertion flares a bit posteriorly. It lies above that of the deep masseter on most of the lower portion of the ascending ramus.

The *M. temporalis* (figs. 3,B; 4,A) is massive. It completely fills the temporal area to a level flush with the top of the sagittal and occipital crests, and the zygomatic arch. Superficially, the temporalis is covered by a heavy, whitish aponeurosis. Most of the more superficial fibers of the muscle take their origin from this aponeurosis, from over most of its extent. The fascia, which is superficial to, but intimately associated with, the aponeurosis, forms a continuous sheet that covers the arch and runs down over the masseter. It also fuses with the postorbital ligament. Superficially, the muscle fiber-bundles converge above the coronoid process: those fiber-bundles that originate the farthest posteriorly at the lateral edge of the occipital crest run nearly straight forward, while at the other extreme, those that originate immediately behind the postorbital ligament run in a direction nearly perpendicular to the sagittal crest. Only those fiber-bundles that originate laterally from the aponeurosis in the vicinity of the zygomatic arch descend more directly to insert onto the lateral surface of the coronoid process. The insertion field is curved, and lies above and in front of that of the zygomaticomandibularis, but beneath the rugose, striated tip of the process. The temporalis is divided into two unequal portions by the *planum tendineum temporalis*, an extensive insertion sheet buried within the muscle, which attaches to the tip of the coronoid process. Its superficial surface serves for the insertion of some of the fleshy fibers of the deepest parts of the superficial temporalis, and its medial (deep) surface does the same for the more superficial fibers of the deep temporalis. The deeper layers of the superficial temporalis are fleshy. They originate from the sagittal and occipital crests.

The deep portion of the temporalis is larger than the superficial part. Its origin is fleshy, and is from the greater part of the cranial

roof, beneath that of the superficial portion, and from the base of the sagittal crest. Insertion is onto the medial side of the coronoid process. Anteriorly, along the front edge of the coronoid process, where the superficial and deep portions meet, they are fused into an enveloping tendon sheet. This enveloping fold extends beyond the coronoid process in the anterior part of the muscle in an upward and inward curve that approaches the aponeurosis and more medial origin areas. A small fleshy pars zygomatica (really a division of the superficialis portion of the muscle) takes origin from the anterior, upward and inward facing surface of the rear buttress of the zygomatic arch above the joint capsule. Its insertion is for the most part onto the postero-medial edge of the coronoid process, but a few bundles insert on the postero-lateral edge.

M. pterygoideus internus (fig. 4,B) is smaller than temporal or masseter. Its origin, mostly fleshy but with a light tendinous envelopment, is broad. It draws off from the lateral edge of the pterygoid bone, and also to some extent from the neighboring contiguous part of the palatal bone and the sphenoidal pterapophysis and forms into a thick, compact fleshy mass. The muscle fibers converge on a smaller area of insertion which is located on the medial edge of the inflected angular process, beneath the inferior dental foramen and the insertion area of the deep portion of the temporal. The insertion area does not extend forward nearly as far as that of the ventrally adjacent superficial masseter, which is longer by half again. There is a suggestion of a subdivision of this muscle on its external side, but it is not expressed on the medial side. A distinct cleavage runs no more than half way into the muscle. The innervation was not traced. Immediately adjacent to the internal pterygoid on its medial side is M. tensor tympani, which takes a tendinous origin from the pterygoid bone medially adjacent to the origin area of the internal pterygoid, chiefly from the hammular process.

The M. pterygoideus externus (fig. 4,B) is a slight, short, rather cylindrical muscle, which takes fleshy origin from the ventro-lateral surface of the cranium (from the alisphenoid), just lateral to and behind the foramen ovale. Its fibers run directly to their short tendinous insertion onto the very limited medial edge of the wide condyle. The innervation was not traced.

The digastric (figs. 2,A,B; 3,A) is clearly divided into two bellies; a dividing tendon serves for the insertion of the posterior belly and for the origin of the anterior. The posterior belly originates from the small postero-externally directed facet on the tip of the paroccipital

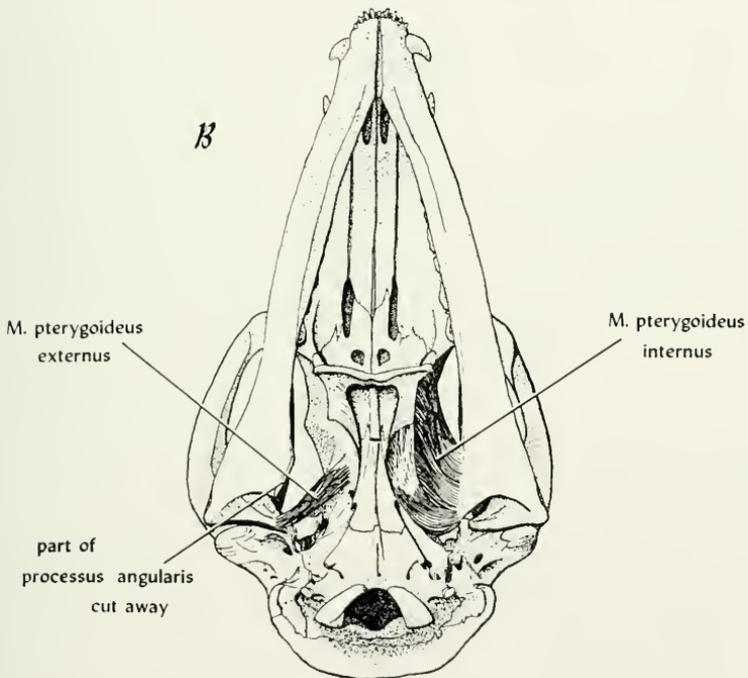
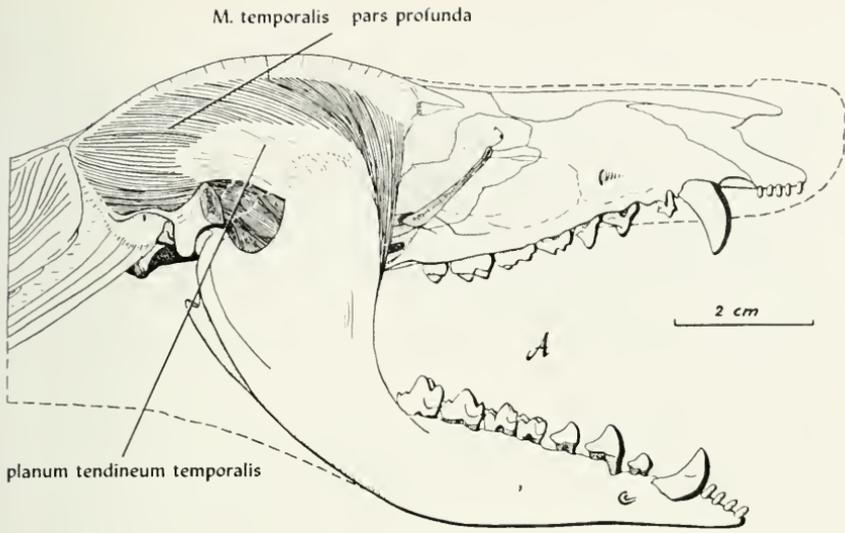


FIG. 4. Masticatory musculature of *Didelphis*. A, Deep dissection in lateral aspect showing M. temporalis, pars profunda exposed to view. B, Ventral view showing Mm. pterygoideus internus and pterygoideus externus.

process. The fiber direction within this mass is oblique to the axis of the muscle in an antero-medial, postero-lateral direction. That of the anterior belly is in the antero-posterior alignment. The insertion of the anterior belly is in a superficial position, is both fleshy and tendinous, and is onto a long narrow area about half the length of the jaw on the ventral border of the jaw ramus. The insertion begins near that of the masseter, and extends forward almost to the symphysis. Both of the anterior bellies, through their associated fascia and their own mass, are situated so as to contribute significantly to the flooring of the mouth.

The *M. mandibulo-auricularis* which is present in some marsupials and rodents but is not present in most mammals, is not strictly a muscle of mastication. It is mentioned here because of its close proximity to the muscles of mastication. It originates from the jaw close beneath the articulation capsule, adjacent to the deep masseter, and beneath the edge of the superficial masseter. Its insertion presumably onto the anterior ear cartilage was not traced.

TABLE I.—Weights and percentages of masticatory muscles: *Didelphys*

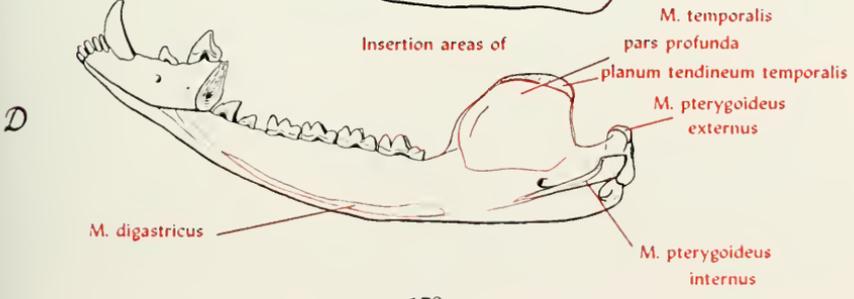
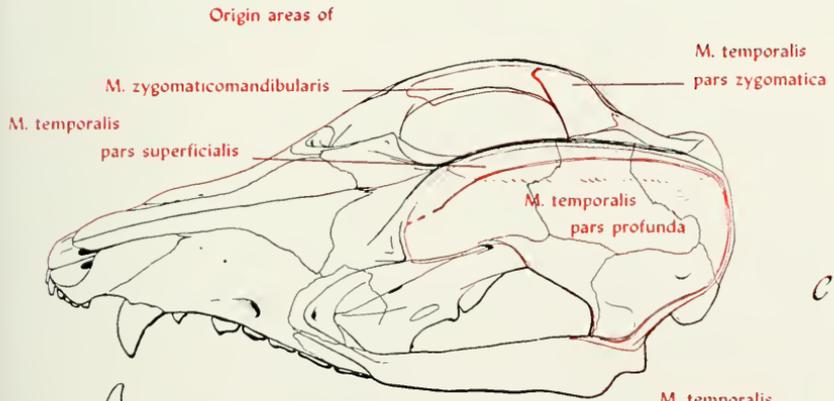
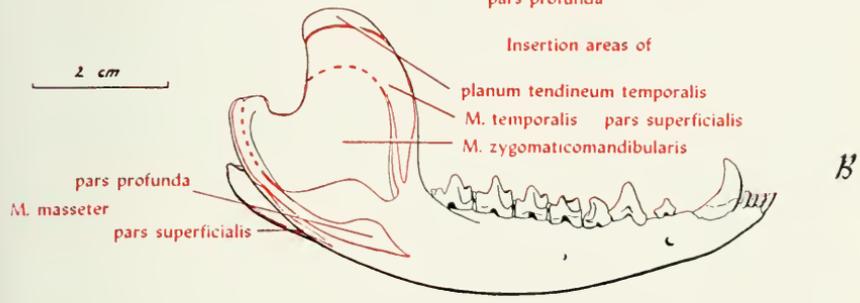
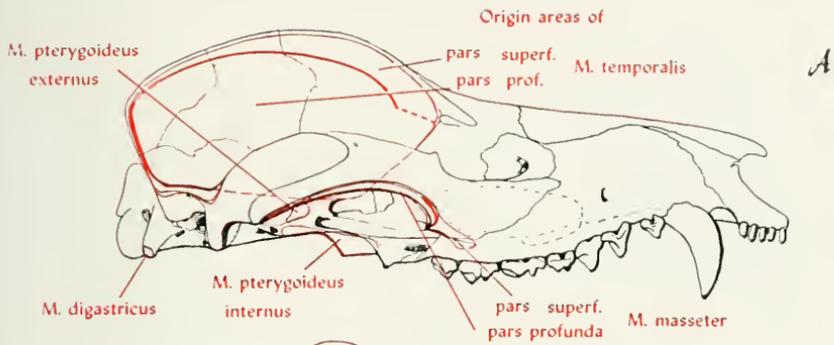
Muscle	Weight (in grams)	%	% without digastric
<i>M. masseter</i>	6.1	23.6	24.8
<i>pars superficialis</i>	3.7	14.3	15.0
<i>pars profunda</i>	2.4	9.3	9.8
<i>M. zygomaticomandibularis</i>	2.3	9.0	9.4
<i>M. temporalis</i>	14.0	54.2	57.0
<i>pars superficialis</i>	5.1	19.7	20.8
<i>pars profunda</i>	8.9	34.5	36.2
<i>M. digastricus</i>	1.2	4.7	—
<i>M. pterygoideus externus</i>	0.4	1.6	1.6
<i>M. pterygoideus internus</i>	1.8	7.0	7.3
Totals	25.8g	100.1%	100.1%

Echinosorex gymnurus

Figures 6,A-C; 7,A-C; 8,A-D; 9,A-E; 10.

During his joint expedition to Borneo with R. F. Inger, D. D. Davis collected several heads of these animals, one of which he kindly provided for this dissection: FMNH 68732, a female, from the Sandakan region, North Borneo, collected July 14, 1950. A prepared

FIG. 5. Skull and jaws of *Didelphys* showing the origin and insertion attachment areas of the jaw muscles (mapped in red). A, Skull in lateral aspect. B, Lower jaw in lateral aspect. C, Skull in dorso-lateral aspect. D, Lower jaws with most of one ramus cut away, seen in ventro-lateral aspect.



skull and jaws, FMNH 32673, also female, from the same region was collected by F. C. Wonder on July 7, 1929. It was used to map the muscle attachment areas. The illustrations are the work of Dr. Tibor Perenyi, and are based on my sketches and photographs.

Beneath the skin there is a well-developed temporal aponeurosis (fig. 6,A). It gives rise to the more superficial fiber-bundles of *M. temporalis*, including its *pars profunda*, over most of its extent. This aponeurosis covers the zygomatic portion of the *temporalis* also, and is connected to that part of the *planum tendineum temporalis* where it reaches to the superficial surface of the muscle, above and medial to the *pars zygomatica*. Anteriorly, immediately behind the orbit, the aponeurosis joins other less tendinous connective tissue. The latter, together with the adjacent anterior edge of *M. temporalis*, serves to form a posterior wall to the orbit. The *Mm. levator labii* and *levator nasi* arise from the flared surface of the anterior third of the zygomatic arch, from just behind its anterior buttress, in a region situated beneath the posterior half of the orbit.

M. masseter (figs. 6,A-C; 7,A) is composed of the usual two portions, *pars superficialis* and *pars profunda*, of about equal mass. The *pars superficialis* (figs. 6,C; 9,D) takes origin tendinously from the entire ventro-lateral edge of the arch. There is a heavy concentration of tendon fibers anteriorly. They fold upon the ventral flange of bone that comes directly off from the anterior buttress of the arch. The muscle is entirely tendinous superficially in its dorsal third, but becomes a very considerable fleshy mass ventrally. Its fibers run nearly horizontally backward, especially in the tendinous region. They descend more rapidly in the rear of the muscle, both in the tendinous and in the fleshy regions, except along the ventral limits of the fleshy area where they converge, and thus some run quite horizontally. There are virtually no tendinous bands within the fleshy portion of the muscle, and it inserts almost entirely into a common raphe with the *M. pterygoideus internus*. There is a very restricted area of insertion onto the lateral face of the tip of the attenuated angular process (fig. 9,A).

M. masseter, pars profunda has much the same outline as the overlying *pars superficialis* (fig. 7,A). It originates mostly tendinously from the ventral edge of the zygomatic arch, for the greater part of its length (fig. 9,D). It immediately becomes fleshy, so that at first glance it appears entirely so. Actually, some fleshy fibers of the deep masseter draw off from the medial side of the origin tendon

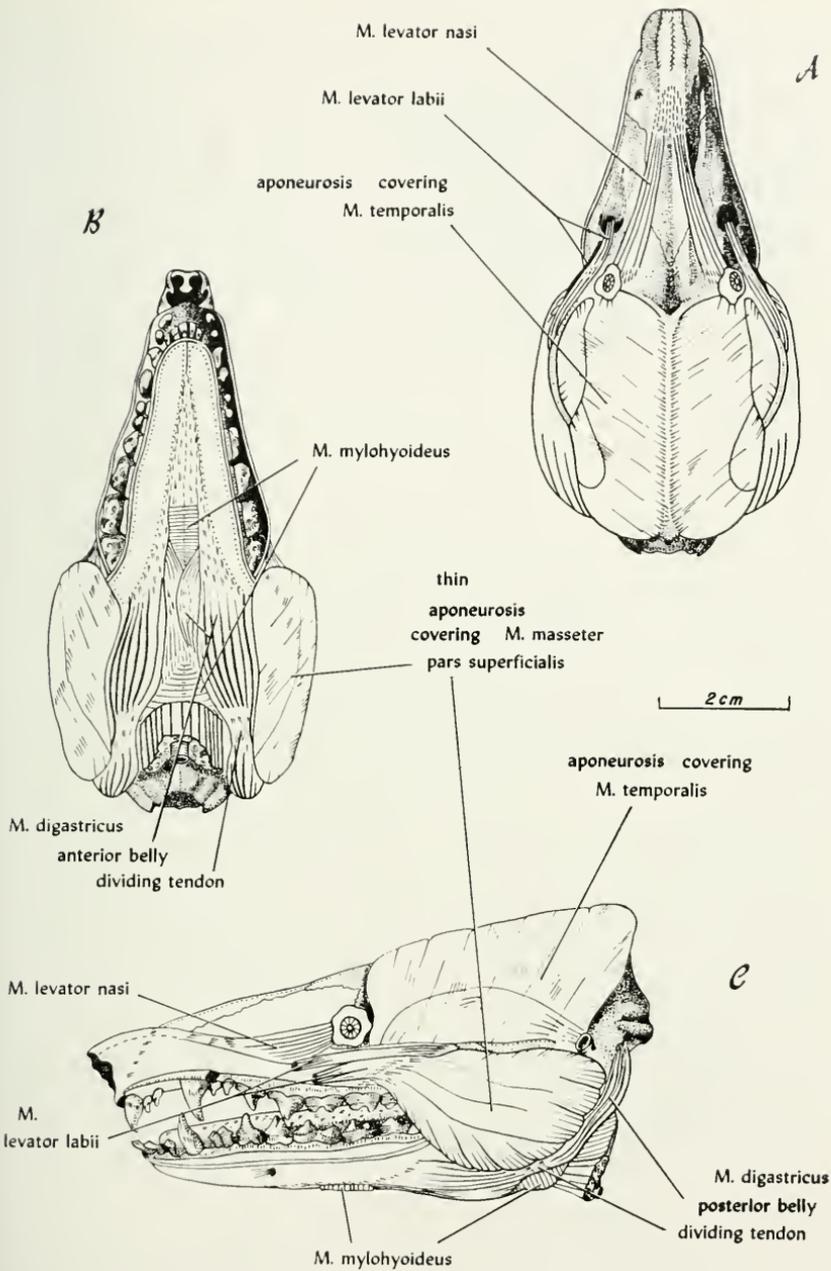


FIG. 6. Masticatory musculature of *Echinorex* in superficial dissection seen in (A) dorsal, (B) ventral, and (C) lateral aspects.

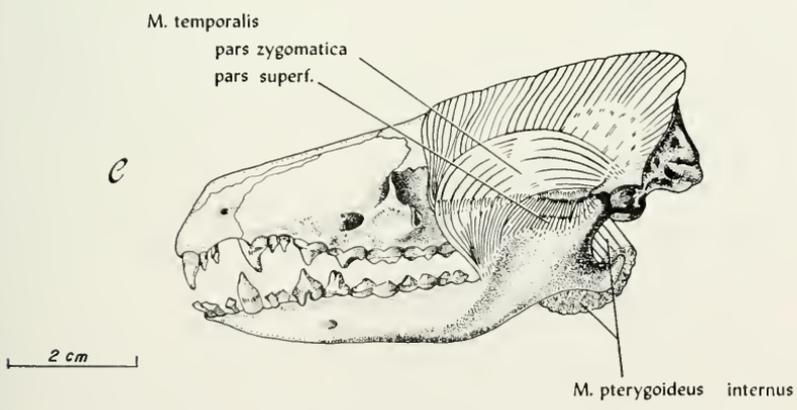
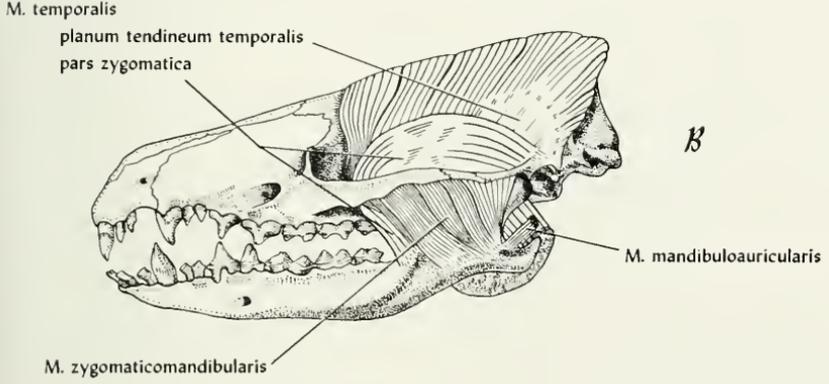
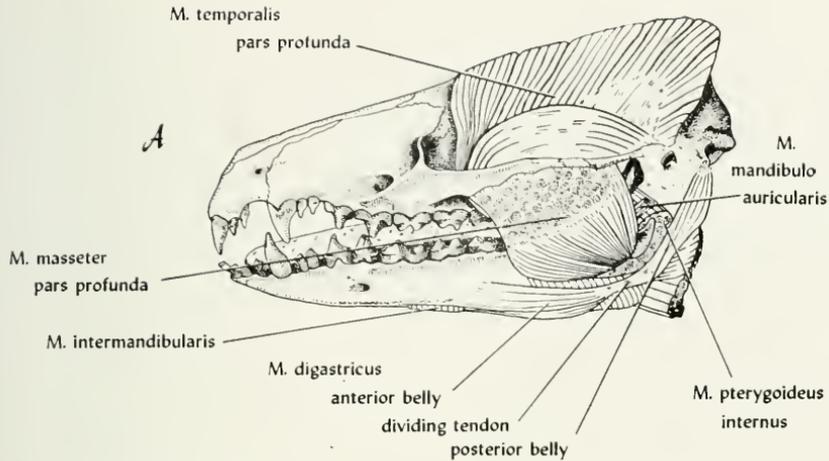
of the superficial masseter, while others come from their own tendon sheet that is continuous with the medial surface of the muscle. Thus, immediately beneath the zygomatic arch, the muscle is already a thick, fleshy mass. Insertion is primarily fleshy, but with a few tendinous bands throughout the mass, and is onto the lower part of the lateral surface of the angle of the jaw. The average fiber-bundle direction runs at about 45° to the horizontal in the postero-ventral half of the muscle and is somewhat less in the anterior half.

Removal of the deep masseter exposes the *M. zygomaticomandibularis* (figs. 7,B; 9,A,D). It is entirely fleshy, quite small relative to the divisions of the masseter, and originates from the ventro-medial surface of the zygomatic arch. Its fiber-bundles descend nearly straight downward, with only a slight backward inclination, and a slight tendency to converge at the ventral edge of the muscle.

Beneath the zygomaticomandibularis, at greater depth, lie two distinct portions of the *M. temporalis*, pars superficialis complex: pars zygomatica and the very small pars superficialis (figs. 7,C; 8,A; 9,A,C). The pars zygomatica which arises from the top and lateral surfaces of the posterior buttress of the arch, courses upward and forward, then straight forward, and then steeply downward, so as to pass medial to the anterior portion of the arch; it inserts at the base of the anterior edge of the ascending ramus. It is largely fleshy with a slight tendinous covering, especially in its attachment regions. Beneath the posterior half of the arch lies the most lateral portion, the superficial temporalis proper. It takes a fleshy origin from the antero-dorsal edge of the posterior third (to half) of the arch. It is relatively short-fibered immediately beneath the arch where the fiber direction slopes slightly anteriorly and medially from the vertical. It inserts on the upper part of the ascending ramus. It is entirely fleshy at the surface.

M. temporalis, pars profunda (figs. 8,B; 9,A,C) takes origin from the temporal aponeurosis, from the entire dorso-lateral cranial wall, and from the continuous surfaces that run from this wall onto the prominent sagittal and occipital crests. The origin is tendinous at

FIG. 7. Masticatory musculature of *Echinorex* in lateral view. A, After removal of all aponeuroses and *M. masseter*, pars superficialis, *M. temporalis* and *masseter*, pars profunda are exposed to view. B, A deeper dissection exposing *M. zygomaticomandibularis* to full view. C, A deep dissection with *M. zygomaticomandibularis* removed and the zygomatic arch cut away to expose *M. temporalis* to full view.



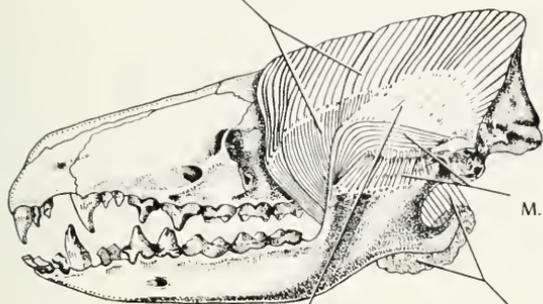
the surface, especially in that part arising from the sagittal crest. The muscle and a large mass of connective tissue form the posterior wall of the orbit. It is by far the largest portion of the temporal muscle, and, in fact, of all of the masticatory musculature. Its fiber bundles and those of the associated planum tendineum temporalis converge laterally to insert upon the medial surface of the coronoid process. The insertion is both fleshy and tendinous; the tendinous portions are mainly in front and along the lower border of the muscle, and are very extensive at the top of the coronoid process where the planum tendineum temporalis inserts.

M. digastricus is composed of the usual two bellies, separated by a raphe-like dividing tendon (figs. 6,B,C; 7,A; 9,A,B,D; 10). They are both small compared with masseter and temporalis, though relatively large in proportion to the total masticatory complex and to those of other mammals. The posterior digastric is shaped rather like a bent cigar, with rounded cross-section. It originates tendinously from the tip and front of the tiny paroccipital process and is fleshy throughout to its insertion in the dividing tendon which runs quite oblique to the axis of the muscle. The anterior digastric has a more complex relationship to its adjacent structures. Immediately in front of the dividing tendon, the anterior digastric has an oval cross-sectional outline that becomes rapidly flattened anteriorly. The main mass of the muscle runs directly to its thin, obliquely-situated insertion area on the ventro-lateral margin of the mandible, beneath the molar teeth. The more medially situated portion of the muscle forms a flat sheet which is in intimate contact with the mylohyoideus throughout. In this midline area, the muscle is limited posteriorly by a thin, arched tendinous band that runs diagonally toward the midline where it is continuous with its counterpart from the opposite side. The fibers of the median part of the anterior digastric take origin from this tendon, and run nearly straight forward. As these fibers approach the insertion area they turn laterally to insert as a sheet that is continuous with the anterior part of the main mass of the muscle. In the immediate area of the midline, instead of joining its opposite in a simple raphic union as might be expected, the thin median sheet of the anterior digastric

FIG. 8. Masticatory musculature of *Echinosorex*, all deep dissections. A, Lateral aspect showing M. temporalis with pars zygomatica removed. B, Lateral aspect showing M. temporalis, with pars superficialis (proper) removed. C, Ventral aspect showing Mm. pterygoideus internus and pterygoideus externus. D, Lateral aspect showing Mm. pterygoideus internus and pterygoideus externus.

M. temporalis pars profunda

A



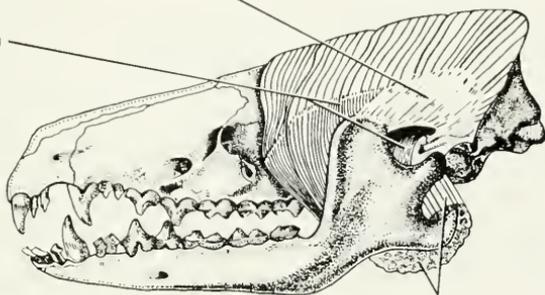
M. temporalis
pars superficialis

planum tendineum temporale

M. pterygoideus internus

M. temporalis
pars profunda

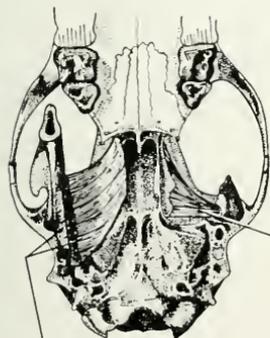
2 cm



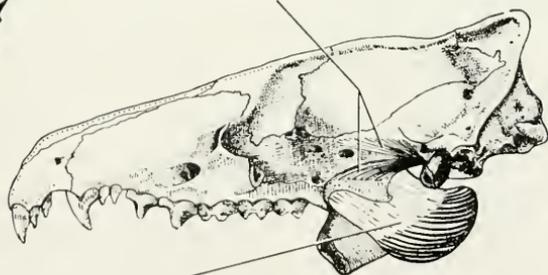
B

M. pterygoideus internus
cut at common raphe with
M. masseter pars superficialis

C



M. pterygoideus
externus



M. pterygoideus internus

D

overlaps its opposite by an intertonguing of two layers from each side (fig. 10). At the anterior-most limits of the muscle there is a raphic union with a thin layer of the anterior mylohyoid¹ (?intermandibularis).

In dissecting the pterygoid muscles, it is best to remove the mandible on the side being dissected. This is accomplished by first breaking the union of the two rami at the symphysis, then dissecting both pterygoids and the M. mandibuloauricularis free from their insertions. M. pterygoideus internus (figs. 8,C,D; 9,B,D,E) takes origin from the ventro-lateral face of the pterygoid bone, from the open groove and pit that is formed by the descending process and the lateral wing of the bone. It has a tendinous covering over most of its medial surface, and a more massive tendon sheet midway through it, especially toward its distal end. This tendinous layer inserts upon the inner face of the angular process to a distinct dorsal crest of the process. The rest of the insertion onto the angular process is mainly fleshy. Those fibers that join the superficial masseter by raphic union are oriented at about 45° to the horizontal, while those that lie more superficially and that are more intimately associated with the insertion tendon take a somewhat more vertical course in the anterior region of the muscle, although the posterior fibers lie at approximately the same angle as those that join the raphe.

M. pterygoideus externus (figs. 8,C,D; 9,B,D,E) takes origin by two heads. It is almost entirely fleshy. The ventral head comes off from the dorsal surface of the pterygoid wing, while the dorsal head arises from an oblique, oval-shaped area immediately above the alisphenoid canal and the associated foramina. The bellies of these two divisions converge backward, and where they touch, the fibers insert into a common tendon that, along with the remaining

¹ This is a little sheet of muscle that runs transversely between the mandibles. It should probably be considered as a layer or division of the anterior mylohyoid rather than a true intermandibularis as its attachment is contiguous with that of the rest of the anterior mylohyoid. In general, I found conditions of the musculature that floors the mouth to be about equivalent to that of *Podogymnura truei*, as illustrated by Fiedler (1953, fig. 3A, p. 111). However, I did not find the anterior digastric to be crossed in the region of the dividing tendon by the stylohyoideus, as in *Podogymnura*. Rather, I found the main mass of mylohyoid to appear more as Fiedler (fig. 3B, p. 111) shows it in *Erinaceus*.

FIG. 9. Skull and jaws of *Echinosorex* with the various masticatory muscle attachment areas shown (mapped in red). A, Lateral view of skull and jaws. B, Medial aspect of a lower jaw. C, Dorsal aspect of skull. D, Ventral aspect of skull. E, Ventro-lateral aspect of a portion of skull.

Origin areas of

Insertion areas of

M. temporalis pars profunda

M. temporalis
planum tendineum temporalis
pars zygomatica
pars superf.
pars prof.

M. levator
nasi

M. zygomaticomandibularis
M. mandibuloauricularis

M.
levator labii

M. masseter
pars superf.
pars prof.

M. zygomatico -
mandibularis

M. digastricus

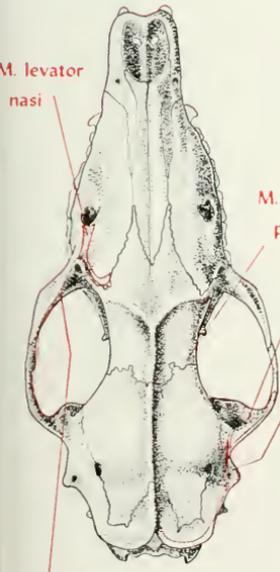
M. digastricus

B

M. pterygoideus
internus

M. pterygoideus ext.

C



Origin areas of

D

M. levator
nasi

M. masseter
pars superficialis
pars profunda

M. zygomatico -
mandibularis

M. temporalis
pars profunda
pars zygomatica
pars superficialis

M. pterygoideus int.
M. pterygoideus
ext.

M. zygomaticomandibularis

3 cm

E



M. digastricus

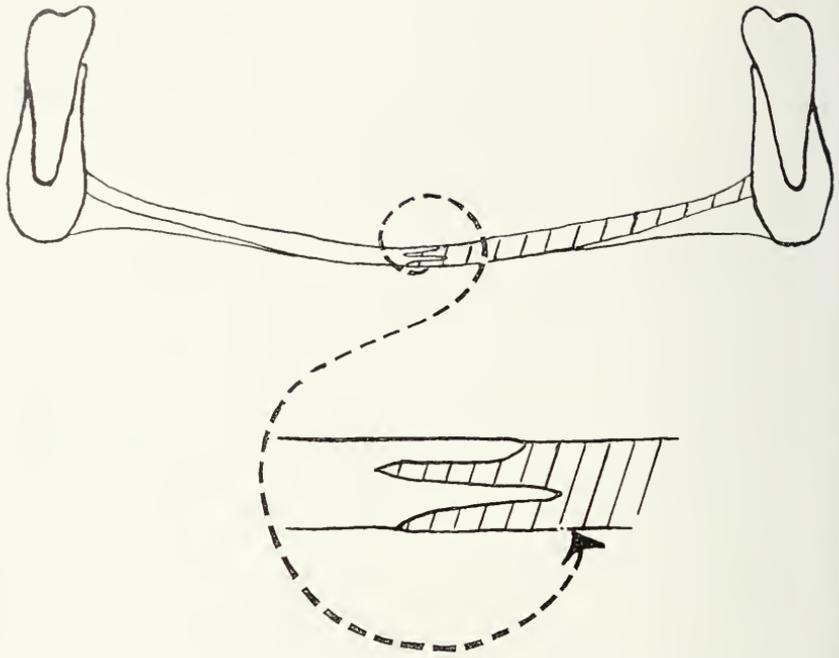


FIG. 10. Detail of inter-tonguing of layers of *M. digastricus*, anterior belly in the midline area, in *Echinorex*.

fiber bundles, runs back and inserts onto the medial side of the joint capsule, to the inner edge of the condyle, and to the neck of the condyle.

TABLE II.—Weights and percentages of masticatory muscles: *Echinorex*

Muscle	Weight (in grams)	%	% without digastric
<i>M. masseter</i>	2.18	21.5—	23.2
<i>pars superficialis</i>	1.12	11.0	11.9
<i>pars profunda</i>	1.06	10.4	11.3
<i>M. zygomaticomandibularis</i>	0.35	3.4	3.7
<i>M. temporalis</i>	5.74	56.5	61.2
<i>pars zygomaticus</i>	0.51	5.0	5.4
<i>pars superficialis</i>			
<i>proper</i>	0.15	1.5—	1.6
<i>pars profunda</i>	5.08	50.0	54.2
<i>M. digastricus</i>	0.78	7.7	—
<i>anterior</i>	0.43	4.2	
<i>posterior</i>	0.35	3.4	
<i>M. pterygoideus externus</i>	0.16	1.6—	1.7
<i>M. pterygoideus internus</i>	0.95	9.4—	10.1
Totals	10.16 g	100.1%	99.9%

SPECIALIZED GROUP I, "carnivore-shear" or "scissors" type.

This group has received more attention than the others both with regard to the variety of taxa and the number of workers involved. One form only was dissected to form a basis for a judgement of the other works, and to make certain that a comparable and uniform suite of comparative features was treated.

Felis domestica

Figures 11,A,B; 12,A-C; 13,A,B.

This genus was selected for two reasons: it exhibits as fully as any the extreme of the shear-type of masticatory apparatus, and it is readily available. None of the numerous guides to the dissection and anatomies of the cat delves deeply into the details of the jaw musculature. The works of Reighard and Jennings (1935), and Adams (1919) are not complete. Huber's work (1918) is detailed, but deals primarily with the superficial musculature, and only incidently treats the masticatory musculature. His later work (1925a) is an extensive and comparative study of a very minor muscle, *M. mandibuloauricularis*. It touches on, and provides some illustration of the masticatory muscles. Toldt's work is the most detailed and useful (Toldt, 1905). Inasmuch as I find only a very few, quite minor differences, and because his descriptions are so detailed, I have included a partial translation of the pertinent portion (1905, pp. 345-351). This is followed by my comments and additions. By this approach (i.e., translating Toldt rather than giving redescriptions of my own), it is possible to illustrate adequately his excellent descriptions and to make his work more readily available and usable. Skull drawings (fig. 13,A,B) are based on FMNH 0-1416. The muscle dissection was made on a specimen (FMNH 57537) donated by the General Biological Supply House through the courtesy of Mr. Arnold Blaufus (fig. 11,A-C). Toldt's description (translated) is as follows:

The *M. masseter* (fig. 1)¹ is powerfully developed, strongly arched laterally, and covered on its superficial surface by a widely extended aponeurosis. Its outline is not approximately rectangular as in man and the higher apes, but retort-shaped, rounded ventrally and posteriorly; its line of origin is also convex dorsally, while its anterior border is slightly concave; the strongest arching is directed posteriorly. The muscle covers the whole posterior border of the mandible, and is also rolled around the lower border of the ramus, while anteriorly it leaves all the molar teeth exposed as its anterior border

¹ Figure references within the translated sections refer to figures in the original works.

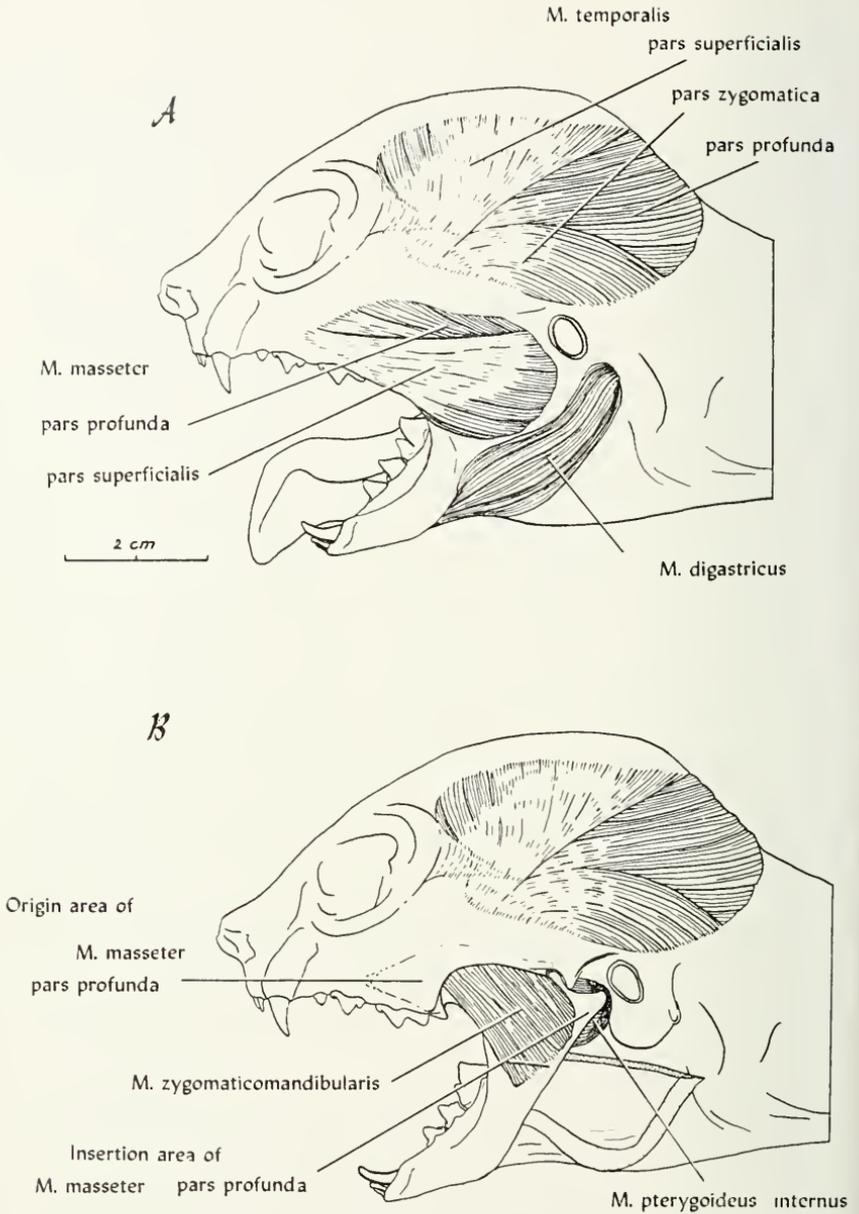


FIG. 11. Masticatory musculature of *Felis*. A, Lateral view showing the most superficial aspect of Mm. masseter, temporalis and digastricus. B, Lateral view after removal of M. masseter and M. digastricus, showing M. zygomaticomandibularis and M. pterygoideus internus.

descends behind the last molar. It shows a strong, posteriorly inclined fiber direction, the most superficial tendon and muscle fibers running at an angle of about 45° to the lower edge of the mandible. Only the most anterior fibers take a more vertical direction at first, until they reach the border of the mandible. Closer study of the muscle shows that its structure is rather complex. It originates as a compact fleshy mass from the lower part of the lateral surface, and from the ventral surface, of the zygomatic arch, as well as from a tendon sheet that forms an extension of a continuous covering of the arch. As it descends, the muscle divides into four fleshy lobes situated one behind the other, but partially overlapping one another. A common aponeurosis extends over the whole. Each of the four lobes consists of superficial and deep divisions.

The most anterior fleshy lobe arises chiefly from the thickened, most anterior part of the tendon of origin, which is attached to the zygomatic process of the maxilla immediately above the last molar. The most anterior of its deep fleshy layers inserts onto a rough line that runs above the ventral border of the ramus of the mandible to the angular process (*crista masseterica*), while the more posterior ones run more and more obliquely to the ventral border of the ramus, and the most posterior ones pass to the medial surface of the angular process. Consequently, the line of insertion of these deep fleshy layers runs from the lateral surface of the ramus, around its lower border, to the medial surface of the angular process. The superficial fibers of the most anterior lobe embrace the lower border of the ramus far forward; they have no attachment to the bone, however, but go over into a tendinous raphe that unites the *M. masseter* very closely with the *M. pterygoideus internus*. The second fleshy lobe is very wide. Its approximately vertical, deep fibers insert tendinously above the first lobe on the masseteric crest and the lateral surface of the angular process, while its superficial fibers embrace the lower border of the ramus and the angular process, and go over into the raphe in such a way as to overlie the posteriorly directed fibers of the anterior-most lobe. The third lobe is narrow and consists predominantly of superficial fibers which, in order to reach the raphe, curve around the posterior end of the angular process and thereby cover the posterior portion of the second lobe. Finally, the fourth lobe embraces the posterior border of the mandible, and its deep fibers insert tendinously onto the upper side of the angular process, while its superficial fibers run to the posterior end of the raphe.

The raphe (fig. 2) into which the superficial fiber-layers of all four fleshy lobes of the *M. masseter* pass, is, as stated above, a form of tendinous intersection that unites this muscle with the superficial portion of the *M. pterygoideus internus*. It continues posteriorly from these muscles in the form of a flat, tight band which, on the one hand, is attached to the upper border of the tympanic bulla and the lower border of the bony external auditory canal, and, on the other, goes over into a tight membrane that connects the cartilage of the external auditory canal to the duct. This tendinous intersection has a connection with the mandible only insofar as it is joined by a somewhat looser connective tissue to the insertion tendon of the deep layers of the *M. masseter* which attach to the angular process. Out from the raphe, backward toward its origin, it is clearly attached to the temporal bone by a small ligament. Thus, fiber-bundles of both muscles are united through the raphe, find no insertion on the bone, and maintain their determined direction

—a very peculiar and extremely interesting arrangement that no doubt is correlated with the very strong development of the masseter relative to the dimensions of the mandibular rami, and which make unnecessary a greater expansion of the surface of the angular process.

As the deeper portion of the *M. masseter* is considered to be a relatively thin layer of fibers that arises fleshily from the lower border of the zygomatic arch, its parallel, slightly posteriorly directed fleshy bundles go over into several very delicate tendinous sheets, stratified upon one another. By this means, it inserts on the lateral surface of the mandibular ramus, on the anteriorly extended lower border of the triangular muscle fossa.

After removal of the *M. masseter*, a muscle mass completely covered by it becomes visible. It corresponds in man to the so-called deep layer of *M. masseter* together with the zygomatic portion of the *M. temporalis*. Accordingly, it consists of two divisions, an anterior and a posterior, the demarcation of which, it is true, is indicated here only by a small gap for the passage of the *N. massetericus*. Both divisions show the most intimate relationship to the *M. temporalis*, and will be discussed together in more detail below as the *M. zygomaticomandibularis* (*profundus*). Here it will only be observed that the posterior division of this muscle mass arises in direct connection with *M. temporalis*, partly fleshily and partly tendinously, from the lower surface of the posterior part of the zygomatic arch. It is situated in the triangular fossa on the lateral surface of the mandibular ramus into which it also inserts. Its fiber-bundles maintain an oblique, forward and downward direction. The anterior division arises from the anterior half of the medial surface of the zygomatic arch, and sends its somewhat converging fiber-bundles partly into the tendon of the *M. temporalis* and partly onto the anterior border of the coronoid process and the *linea obliqua* which continues downward from it.

The *M. pterygoideus internus* consists of two parts. The superficial is by far the larger. It arises from the lower border of the infratemporal fossa and it forms, together with the deep portion, a large part of the ventral wall of the orbit. The posterior-most part arises in the true pterygoid fossa near the tendinous part of the superficial portion, descends in a somewhat posteriorly and laterally inclined direction toward the lower edge of the ascending ramus, to unite in large part by the aforementioned tendinous raphe with the medially recurved fiber-bundles of the *M. masseter*. Only a few of these fiber-bundles find insertion on bone. Further forward, the more anterior part of the superficial portion coming from the palatine bone has a very strongly backward, but mostly somewhat laterally sloping, fiber-direction. It inserts, in large part tendinously, onto the posterior half of the lower edge of the ascending ramus, up to the posterior edge of the angular process. The deep portion is well separated from the superficial: only in front are they bound together by a common tendon plate. It is much smaller than the superficial portion, and completely covered by it. While it arises from above the superficial portion, yet its field of origin does not extend beyond the latter, neither forward nor backward. Its approximately parallel, strongly backward and laterally sloping, tendinously infiltrated fiber-bundles insert above the insertion line of the superficial portion, from the *crista pterygoidea* to the angular process. On its outer side, its fleshy bundles attach to those of the *M. masseter*.

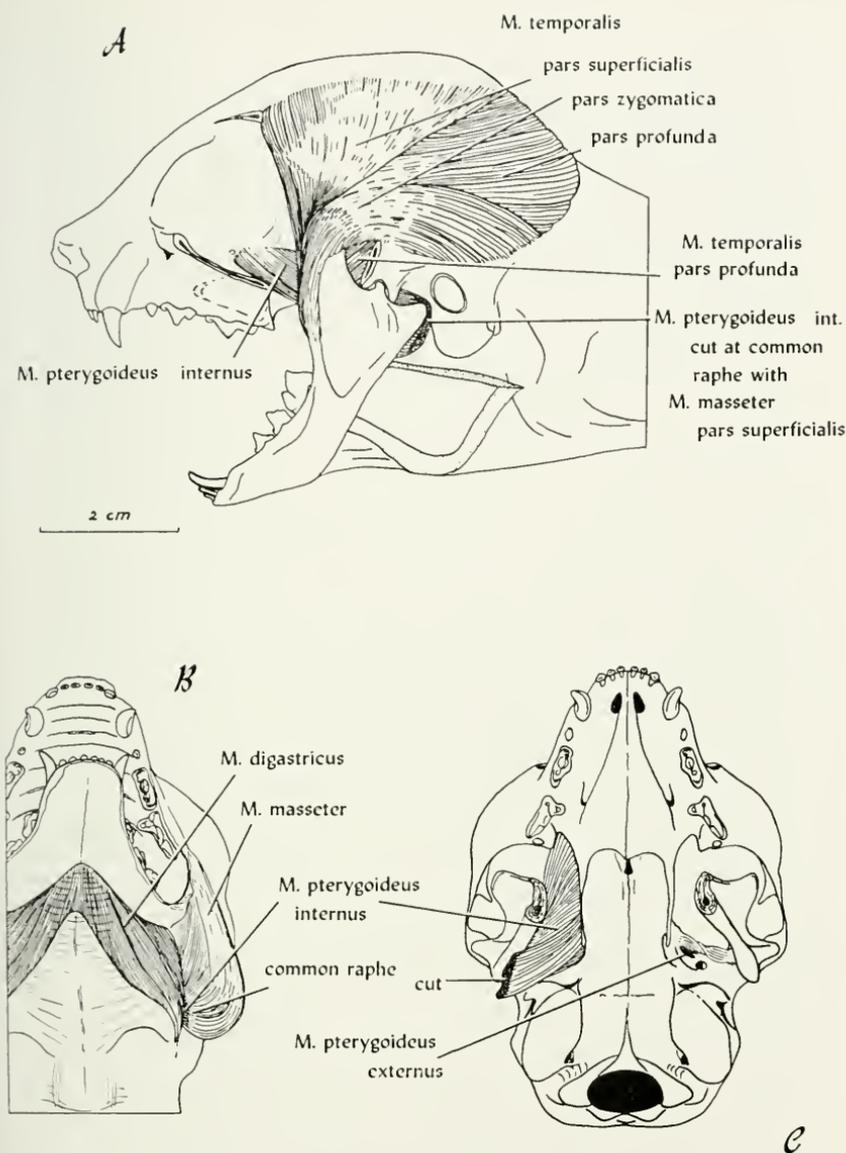


FIG. 12. Masticatory musculature of *Felis*. A, Lateral view with zygomatic arch and *M. zygomaticomandibularis* removed exposing *M. temporalis* to full view. *M. pterygoideus internus* can be seen at greater depth, beneath the angular process and the ascending ramus of the jaw. B, Ventral view showing the superficial musculature: *Mm. digastricus*, *masseter* and *pterygoideus internus*. C, Ventral view, deep dissection with most of the lower jaws removed to expose *Mm. pterygoideus internus* and *pterygoideus externus*.

Both muscles, the *M. masseter* and *M. pterygoideus internus*, differ from their counterparts in man and the majority of the apes in not only the ability to close the jaws against the upper jaws with greater strength, but in the possession of a very strong forward-pushing component, and in unilateral action, for the sideward movement of the lower jaws. As the superficial fleshy layers of both muscles join together completely, immediately below and behind the lower and hinder edge of the ascending ramus, they there form a powerful sling whose pulling action is directed forward and upward. An analogous condition exists in the deep portion of the *M. pterygoideus internus*.

In this connection, we turn to the *M. pterygoideus externus* whose function is chiefly the forward and sideward movement of the lower jaws in man, and which here is limited to a slender bundle, scarcely three mm. in diameter. It arises from beneath the foramen rotundum, from a low bony ridge corresponding to the lamina lateralis of the pterygoid process, and runs in a nearly horizontal, only slightly backward sloping direction, going horizontally to the medial corner of the articular head of the jaw, and inserting just beneath this. A second division of this muscle does not exist. In acting to move the lower jaws forward, this muscle can only function in a very small way.

As antagonists in the complete working action of each muscle which is arranged in a position for the forward movement of the mandible, there appears a strongly backward inclined component of the very powerfully formed *M. temporalis* and the posterior portion of the *M. zygomaticomandibularis*. In addition to these, the *M. digastricus* runs a nearly straight course, from back to front. This powerful muscle, in the cat, forms no connection with the hyoid bone. Its insertion line runs along the under-edge of the *M. masseter*. The bellies are separated, not by a dividing tendon, but by a thin, though distinct inscription tendon. They are joined in close connection to the *M. masseter* just under the edge of the ascending ramus, as a parallel-fibered, straight backward directed muscle, extending in this way nearly as far backward as its origin where it spans the bulla formed by the temporal bone, somewhat behind the angle. There it reaches an especially favorable condition for the opening of the lower jaws, since it is but indirectly connected with the upper jaws. In closing the jaws it must function by exerting force to retract them.

Considering this peculiar arrangement of the masticatory musculature, it is to be emphasized that in the Carnivora, as a result of the structure of the mandibular joint and because of the interlocking occlusion of the upper and lower teeth when the mouth is closed, neither forward shifting nor lateral movement of the mandible is possible. The nearly exactly horizontally situated articular condyle is implanted in a relatively deep, identically shaped glenoid cavity that is approximately congruent with the condyle, with a very thin articular disc intervening. Thus, both jaw articulations have a common axis of rotation and appear, as Langer¹ and Henke² have already emphasized, to be a purely hinge joint. The mandible pressed straight against the upper

¹ C. Langer, Das Kiefergelenk des Menschen, Sitz. Ber. d. Akad. d. Wiss., math.-naturw. Kl., 39 Bd. (1860).

² W. Henke, Der Mechanismus der Doppelgelenke mit Zwischen knorpeln, Henle u. Pfeufer's Zeitschr., 4 R., 8 Bd., S. 47.

jaw from below. The movement itself is neither grinding nor gnawing, but snapping (ortale). However, the position of the axis of articulation is not an entirely fixed one, for in opening the mouth, the articular condyle, together with the separating disc, slides against the forward wall of the glenoid, so that the axis of rotation becomes shifted somewhat forward. Consequently, in the partly opened mouth there is a forward and a lateral movement though only to the slightest extent possible. Under these conditions the very considerable components for the forward movement of the jaws which the MM. masseter and pterygoideus internus possess cannot actually perform these movements to any great degree. Their greater significance is to be found in the cooperation of these muscles with the M. temporalis. Thereby, all three, with their similarly directed components united, aim the powerful closure of the mandible against the upper jaw, working with their opposing components somewhat fixed by the ascending ramus; they assist in the positioning of the axis of rotation and give unity to the snapping action of the jaw, exhibiting this precise behavior. The greater the opening of the lower jaw, so much more does a single direction become necessary, and the stronger the posteriorly directed component of the M. temporalis is, the more the oppositely directed components of the MM. masseter and pterygoideus internus must come into play. From the form of the M. masseter, it appears that its components for closure of the mandible cannot function independently since all of its divisions contain more or less vertically directed fiber-bundles as well as diagonally inclined ones. All of these conditions make possible the greatest use of the molars in cutting bone into small pieces as they move with the lower jaws in an oscillatory way, back and forth. That the M. pterygoideus externus becomes completely insignificant under these conditions requires no supporting discussion; that it is completely missing in the cat as C. Langer reports is found to be untrue.

There is essential agreement between these muscles and those of other animals having a tapered angular process, and very powerful dentitions associated with proportionately small ascending rami; thus particularly the Carnivora.

In three areas I find differences in the jaw musculature of *Felis* from the description presented by Toldt.¹ First, M. masseter does not exhibit nearly as clear-cut a division into four lobes, each with its superficial and deep portions. The subdivision is strongly suggested in the ventral part of the muscle, at its insertion, but becomes increasingly difficult to trace toward the origin. Toldt's description of conditions of the union of M. masseter, pars superficialis with M. pterygoideus internus is correct in nearly every detail. The only exception was a very minor part of M. masseter pars superficialis which was found to insert directly on bone at the postero-lateral edge of the angular process and not in the raphe as reported by Toldt. The more deep-lying M. masseter pars profunda, which is

¹The first two of these probably represent only relatively minor individual variations.

distinct in this area, inserts on the lower edge of the mandible and its angular process.

Second, *M. zygomaticomandibularis* is quite completely fused with the deepest bundles of *M. masseter pars profunda*, contrary to Toldt's implication that the two may be readily separated. However, the intimate fusion of the deepest fiber-bundles of *M. zygomaticomandibularis* with the most superficial fibers of *M. temporalis* agrees with Toldt's description. Separation of *Mm. masseter, pars profunda* and *zygomaticomandibularis* from one another was forced by proceeding from their distinct origin areas toward their insertions. Similarly, it was necessary to force a separation of *M. zygomaticomandibularis* from *M. temporalis*. In this case again, the areas of origin provide a clear-cut separation, though once in contact, the muscles merge into one by a mixing of fiber bundles. All fibers of *M. zygomaticomandibularis* originate from the medial surface of the zygomatic arch (and to a very minor extent from the medial surface of the temporal aponeurosis) and insert in the distinct fossa of the mandible.

Third, perhaps the most significant disagreement with Toldt's description concerns *M. pterygoideus externus*. This muscle is as small and slender as Toldt reports, but it has a most peculiar structure. It is twisted upon itself in such a way that the fiber-bundles can be traced through parallel spiral paths from their area of origin, rotating about 180° before inserting onto the medial surface of the condylar head. DuBrul (personal communication) has suggested that in order for a muscle with this degree of twisting to function, i.e., to contract, without wringing out its fluids, it must actually be organized in divisions so that a muscular belly lies adjacent to a tendinous band. This is exactly the condition which I found (fig. 12,C). The muscle is subequally divided into two portions. One of these, on origin, is fleshy, and partially surrounds the other antero-ventrally. The latter originates as a fine tendinous cord. By following these two divisions of the external pterygoid twisting about one another to their insertions, one can see that the portion which has a fleshy origin grows more tendinous until it inserts as a fine tendinous cord, and the one that began as a tendon inserts by a fleshy belly.

Toldt did not describe *M. temporalis*; therefore I include a description here (figs. 11; 12,A; 13,A-C). It is a very massive muscle, about equal in bulk to all of the rest of the masticatory musculature, and is formed of two major divisions, *pars superficialis* and *pars*

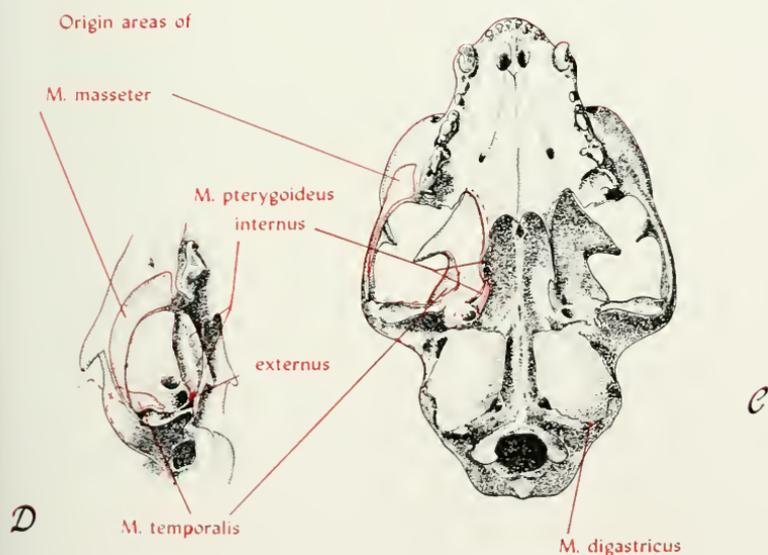
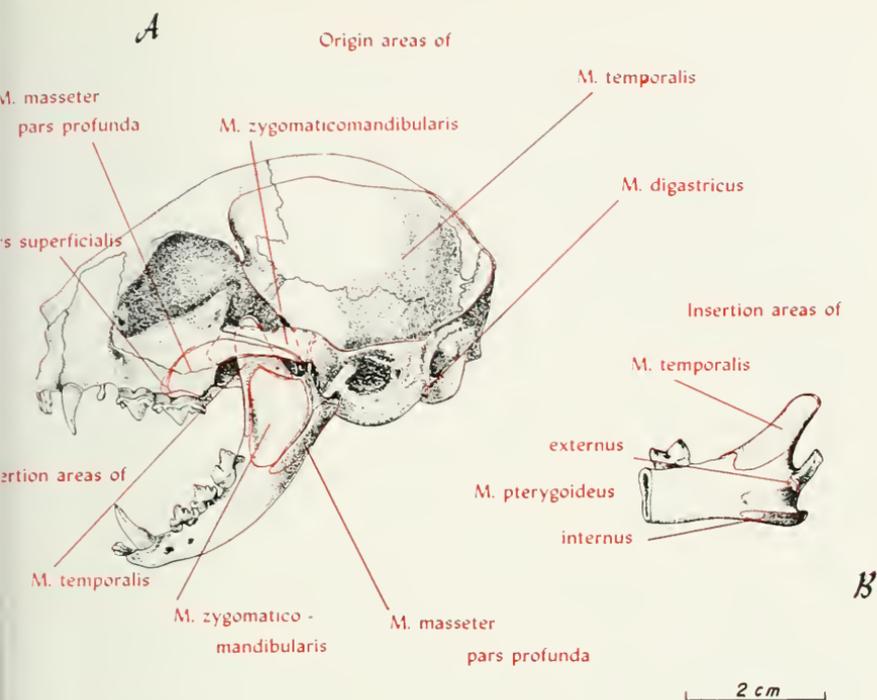


FIG. 13. Skull and jaws of *Felis* showing the origin and insertion attachment (in red) of the masticatory muscles. A, Lateral view. B, Medial view of the rear half of a lower jaw. C, Ventral view of skull. D, Ventral-lateral oblique view of a portion of a skull.

profunda. These subdivisions are shown on the muscle drawings, but are not recorded on the muscle attachment maps. The pars superficialis is further divided by the presence of a distinct pars zygomatica. The whole is covered by a temporal aponeurosis that has a wide circle of attachment, from the zygomatic process of the frontal in front, along the frontal and parietal bones, then onto the sagittal and lambdoidal crests and finally out onto the top edge of the zygomatic arch—especially in its posterior portion, and to close the ring, from the postorbital ligamentous bar. A few of the more superficial fibers of the pars superficialis (including its pars zygomatica) occasionally arise from the inner surface of this aponeurosis. Most of its fibers, however, arise from the frontal and temporal bones. The trace of the outline of the muscle's origin extends from the tip of the zygomatic process of the frontal, and from the ridge leading in a backward arch toward the midline and onto the parietal where it follows a line that diverges slightly from the midline at first, then curves in to join the midline at the sagittal crest. In other words, the origin is superficial, and for the most part anteriorly situated within the temporal fossa. The pars zygomatica originates from the dorsal surface of the posterior buttress of the zygomatic arch, from the crest above the bulla that connects the arch with the lambdoidal crest, and from the posterior end of the inner surface of the arch itself, where separation from the zygomaticomandibularis is indistinct. All of these fibers converge upon the coronoid process of the jaw where they insert either largely tendinously near the tip of the process and along its anterior edge, or mostly fleshily to its lateral surface. The pars zygomatica contributes most of the insertion onto the lateral surface of the coronoid process, above the insertion of the *M. zygomaticomandibularis*, while the rest of the insertion of the superficial temporalis occupies the forward-facing edge of the process. A *planum tendineum temporalis* attaches to the very tip of the coronoid process, enveloping it, and fanning upwards so that it covers the deep portion of the *M. temporalis*. Many of the deepest fibers of the pars superficialis insert onto the lateral surface of this tendon sheet. *M. temporalis pars profunda* in its anterior portion originates from the wall of the temporal bone, and in its posterior part from virtually all of the cranial wall beginning at the base of the sagittal and lambdoidal crests. It runs forward steeply inclined and inserts onto the inner surface of the *planum tendineum temporalis* and onto the whole inner face of the coronoid process and even extends down onto the top of the horizontal ramus

in front of the condyle just above the inferior dental foramen. It is largely fleshy throughout.

Muscle weights are given in Table III as wet weights. No efforts were made to trace the detailed innervation, as this would require a delicate dissection and would be of little use in this project.

TABLE III.—Weights and percentages of masticatory muscles: *Felis*

Muscle	Weight (in grams)	%	% without digastric
M. masseter	1.79	24.0	26.2+
M. zygomaticomandibularis	0.61	8.2	9.0—
M. temporalis	3.70	49.7	54.3—
M. digastricus	0.63	8.5	—
M. pterygoideus externus	0.03	0.4	0.4+
M. pterygoideus internus	0.69	9.2	10.1—
Totals	7.45 g.	100.1%	100.0%

SPECIALIZED GROUP II—The “ungulate-grinding” or “mill” type.

Prior to the appearance of Schumacher's work (1961a), there were few published reports that gave jaw muscle weights for this group. Previously the group had been given attention by illustrative descriptions of a few forms. Becht (1953) listed zebu, European bison, and horse in his weight tables and Zey (1940) had reported muscle weight data for *Ovis*. My coverage of the group originally was selected both to check and supplement the data for *Equus* and *Ovis*, and to broaden the taxonomic spread by adding *Odocoileus*. Schumacher (1961a) added *Sus*, *Camelus*, and *Capreolus*, genera unrepresented earlier, and provided a further check on *Ovis*. As a result, Specialized Group II is much better represented today than it was only a decade ago.

Equus caballus

Figures 14,A,B; 15,A-D; 16,A,B; 17,A,B.

Through Mr. Stearn of the Judge Packing Co., Spring Grove, Illinois, I was able to obtain the head of a freshly killed horse for this study. To him go my thanks for providing me with a specimen for dissection. The animal from which the head was taken was an adult individual; the head is preserved in the Museum's alcohol collection, FMNH 57541. The bone and muscle attachment drawings which were based on the skull of a young adult male specimen, FMNH 41095, and on photos of my dissection, were made by Dr. Tibor Perenyi and by me.

Of the many works on the anatomy of the horse, none that I am aware of illustrated the masticatory musculature adequately for the present purpose. Toldt (1905) gives the best description, but again there is the deficiency of illustrative material. Ellenburger and Baum (1943 ed.) give only a short description, but their work includes a few excellent but limited illustrations. The Sisson and Grossman (1938) translation of Ellenburger and Baum gives an expanded text on the jaw musculature, but eliminates one of the figures given in the original. As in the case of the cat, the procedure followed is to present a translation of Toldt. Minor emendations in brackets and a series of accompanying figures are given. Translation of Toldt's (1905, pp. 411-416) description follows:

Masseter. The extensive, but only slightly bulging, masseter is bounded anteriorly by an almost vertical border which is slightly backwardly inclined. It descends behind the fourth upper molar [i.e., 4th cheek tooth or M¹]. The lower edge of the muscle runs backward along the corresponding edge of the mandible and passes gradually onto the posterior edge at the rounded angle of the mandible. The posterior edge extends nearly to the jaw articulation. The upper border of the muscle makes approximately a straight line. Its structure is characterized by regular relations of the fiber groups to the origin and insertion tendons which make it possible to differentiate four separate layers, each of which is not always distinct. The fiber direction and the insertion areas on the lower jaw give clear indication of the individual layers. The superficial layer of the muscle arises from the bony edge that separates the lateral and ventral surfaces of the zygomatic arch from one another by means of a powerful tendinous aponeurosis which is heavily thickened in front and which extends back onto the posterior third of the arch. It forms the lateral surface of the muscle, binds it together, and extends nearly to the posterior and ventral edge of the muscle as a shiny tendon all the way. On the anterior edge of the muscle, the origin tendon strikes out for itself, runs around toward the medial side, and attaches in part to the under-surface of the zygomatic arch. Further back, however, it originates on the lateral surface of the body of the upper jaw, and it, too, goes over into a powerful shiny tendon. Thus, the whole front third of the muscle, even on its medial side, remains free of the upper jaw and the superficial tendon facing the M. buccinator remains independent from it. On the lateral surface of the muscle, the direction of the tendon and muscle fiber-bundles is uniformly divergent, so that the foremost suitably approach the origin line [i.e., are nearly perpendicular to it], while the hindmost form a very sharp angle to it. The fleshy bundles of this superficial muscle layer come off from the origin tendon and the aponeurosis from very different levels and are of unequal length. They gather together near to the lower and posterior edge of the jaw, in a thick, continually fleshy layer that follows along the mentioned edge of the jaw, fleshy throughout.

Further preparation of the muscle shows that throughout its breadth it is penetrated by three tough tendon layers to which as many fleshy layers correspond. After removal of the superficial muscle layer [i.e., M¹—see

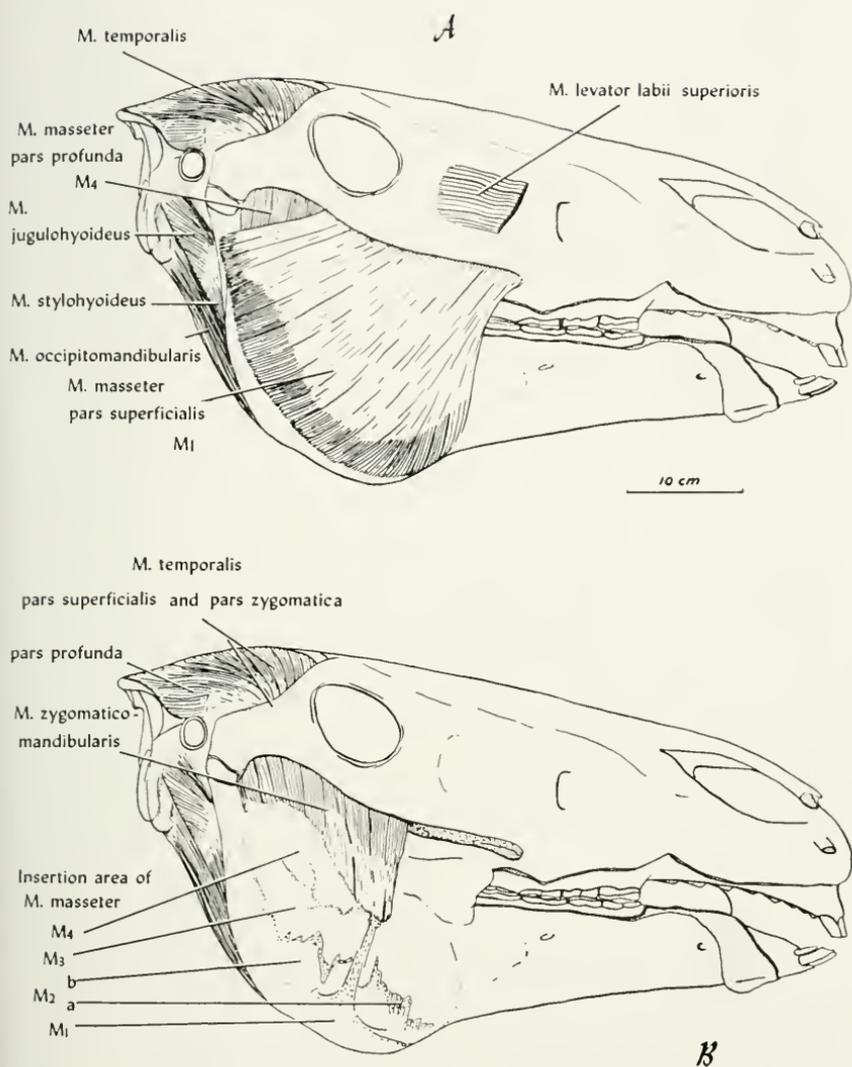
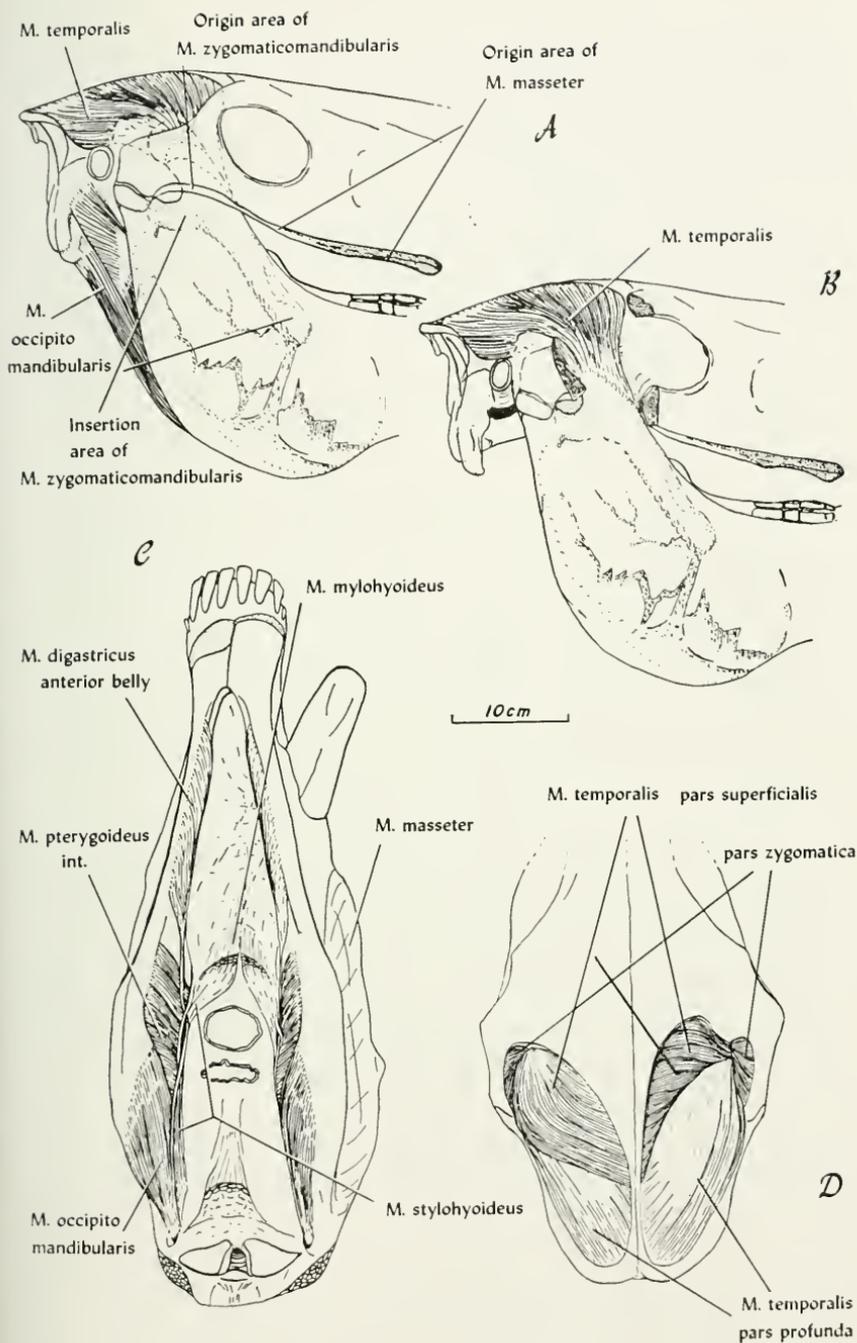


FIG. 14. Masticatory musculature of *Equus*. A, Superficial dissection showing Mm. temporalis, masseter, jugulothyoideus, stylohyoideus, occipitomandibularis and levator labii superioris in lateral view. B, The same view, but with Mm. masseter and levator labii superioris removed, and with M. zygomaticomandibularis exposed to view.

Figs. 14 and 17] the first of these tendinous sheets appears; it begins in the upper quarter of the muscle, at first quite slender, thickens more and more as it descends, however, and inserts covered by the superficial fleshy layer onto the jaw near its lower and posterior edges. It gathers itself into a fleshy mass, which arises partly fleshy from the under-surface of the zygomatic arch, partly from the overlying superficial aponeurosis and the next deeper tendinous plate, and thus describes the second layer of the entire muscle [M2a and b of Fig. 14B]. Within the anterior third of the muscle, extending from the first intramuscular tendinous sheet is a thick tendinous wall that slopes backward in depth, and fastens to the jaw by a bony crest which runs from the bend of the angle, inclined forward, to the linea obliqua; it [the tendon] serves as the insertion for a considerable portion of the muscle mass that originates from the tendinous sheet of the medial surface of the muscle.

Here Toldt is ambiguous. While he clearly states that this considerable (but smaller—see next sentence of his text) portion of the second layer of the masseter (M2) inserts on the dividing tendinous wall which he says penetrates this and all deeper layers of the muscle, he does not tell us the exact position of the insertion field—whether it is onto the front, back or both the front and back sides of that tendon wall. The ambiguity continues in the following sentence where first he describes the insertion of the other larger portion of the second layer of the masseter as being divided completely by the tendon wall, but then proceeds to the further statement that it inserts on the lateral surface of the ascending ramus in front of the tendon wall. In my specimen the dividing tendon wall penetrated only the second layer of the masseter (M2), separating a very large anterior portion (M2a) from a less extensive posterior portion (M2b), and it marked the anterior limits of the remaining two deepest layers of the masseter (M3 and M4). The large anterior portion (M2a) originates in the anterior third of the entire muscle, from the deep side of the covering aponeurosis and the continuous inflected and recurved portion of this tendon sheet, as well as from the part of the maxillary crest which is surrounded by this tendon envelopment. Insertion is in front of the dividing wall of tendon onto a large subtriangular area in the front part of the angle of the jaw. The smaller posterior por-

FIG. 15. Masticatory musculature of *Equus*. A, Deep dissection showing attachment scars of the various portions of the masseter complex after its removal. B, The same except most of zygomatic arch has been removed to expose *M. temporalis* to full view. C, Superficial dissection, ventral view showing *Mm. digastricus* and *pterygoideus internus*. D, Superficial dissection in dorsal view: normal aspect of *M. temporalis* is seen on left, and a deeper level is exposed on right by reflecting *M. temporalis, pars superficialis*.



tion (M2b) inserts behind the tendon wall, from low down on the angle and up along the side of the jaw adjacent its posterior edge, up nearly to the condyle in an irregularly shaped curved area above the posterior portion of the insertion field of the superficial masseter.

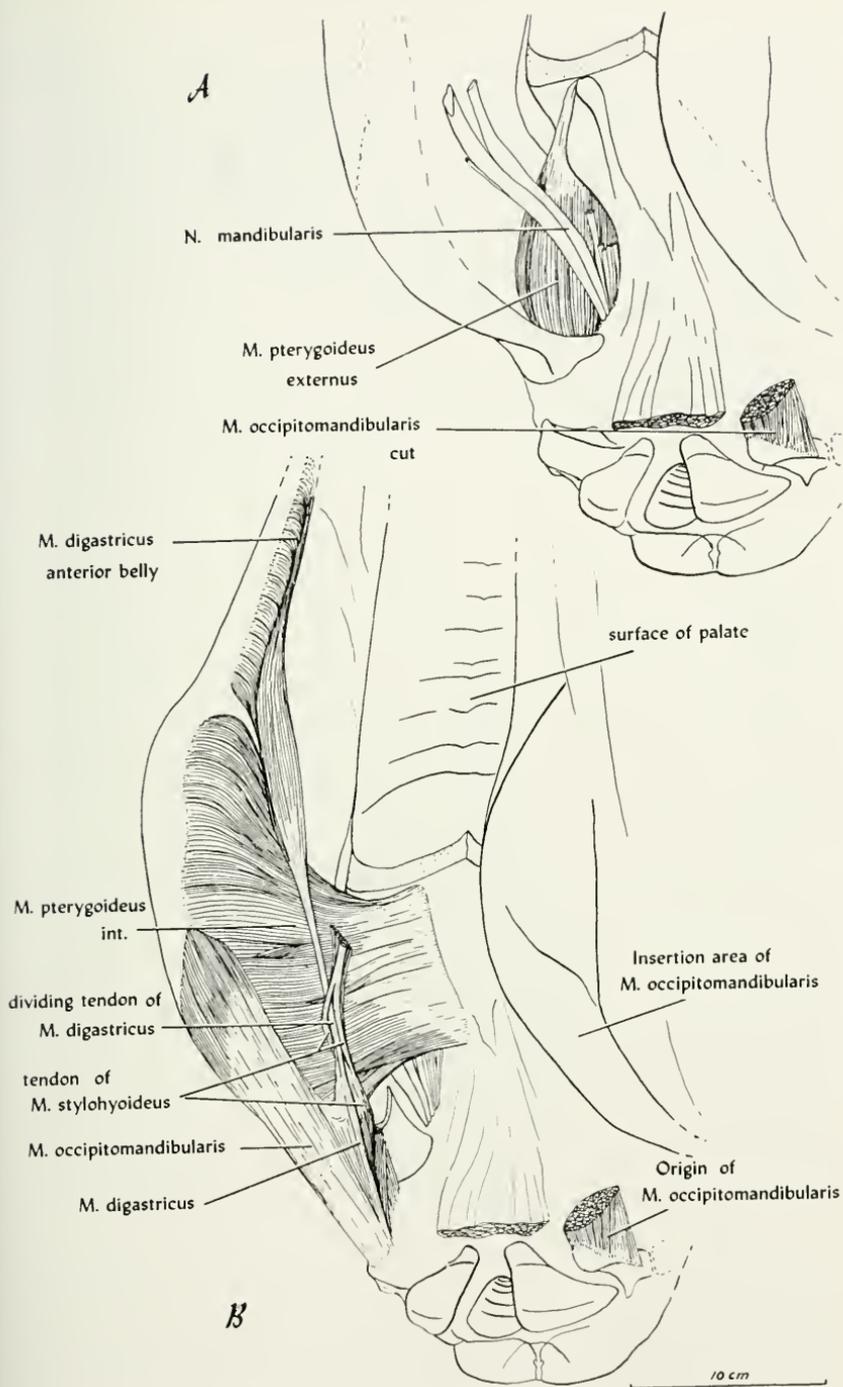
. . . The remaining, larger portion, which comes off from the folded-over portion [i.e., the anterior inflected part] of the superficial origin tendon [aponeurosis] and from the deeper tendinous sheet, is completely divided by the above-mentioned separating wall; it inserts on the lateral surface of the ascending ramus in front of the insertion line of the tendinous partition onto a triangular bony field which is limited in front by a line that begins on the lower edge of the jaw exactly at the boundary between the body [horizontal ramus] and ascending ramus, proceeds diagonally backward and upward and unites with the insertion line of the sloping partition beneath the linea obliqua. The direction of this deep-lying fleshy mass is inclined sharply backward.

After removal of the first intramuscular tendinous plate and fleshy layers belonging to it, a second tendinous sheet appears which arises thick from the under-surface of the zygomatic arch, thins downward gradually however, and sends its fleshy mass downward and backward. This forms the third muscle layer [M3, Fig. 14,B] and attaches fleshy in a narrow zone on the lateral face of the ascending ramus, which is situated in front of and above the insertion line of the first tendinous sheet along the curve of the angle of the jaw-bone. The second tendinous plate reaches forward only as far as the much referred to tendinous diaphragm, into which it also sinks some of its associated fleshy bundles. It originates from the zygomatic arch from behind the origin of the superficial tendon. The direction of both tendinous and fleshy fiber-bundles in this layer is somewhat divergent and is inclined a little more backward than in the first or second.

A fourth, shortest, and deepest-lying layer of the masseter [M4] arises largely fleshy from the posterior half of the zygomatic arch. Its uppermost and hind-most part is not covered by the layers just mentioned. The larger, lower forward section of this layer is thick and grows larger as it descends and goes over into a strong tendinous plate separated from the third layer. Its fiber direction may be described as descending obliquely forward. Its insertion extends forward up to the insertion line of the above described tendinous diaphragm, and runs back from this above the insertion zone of the third muscle layer over a considerable portion of the lateral face of the ascending ramus, nearly to its back edge.

M. zygomaticomandibularis [figs. 14,B; 15,A; 17] is proportionately slender and is completely covered by the fourth layer of the masseter. Its posterior portion appears as a parallel-fibered muscle strip about 2 cm. broad, which takes fleshy origin from immediately in front of the articular eminence

FIG. 16. Masticatory musculature of *Equus*. A, Deep dissection, ventral oblique view showing M. pterygoideus externus. B, Superficial dissection, same view as A, showing Mm. digastricus, occipitomandibularis and pterygoideus internus in detail.



on the under-surface of the posterior root of the zygomatic arch, and from the fibrous jaw articulation capsule. It runs downward in a somewhat forwardly inclined direction, and attaches largely tendinously below the incisura mandibulae, and onto the base of the coronoid process. Along its insertion, a broad vein runs in a horizontal direction against the back edge of the jaw. The proportionately broader anterior portion of the muscle terminates without any boundary on the *M. temporalis*. It arises in part tendinous, in part fleshy, from the median surface of the zygomatic arch, and runs with parallel fiber-bundles approximately perpendicularly downward. Its posterior-most fibers, which are the shortest, insert on the lateral surface of the coronoid process, where they radiate directly upon the tendon of the *M. temporalis*, while the most anterior and longest fibers attach on the *linea obliqua* down to the upper end of the insertion line of the slanting tendinous portion of the *M. masseter*. The *N. massetericus* passes between the two parts of the muscle through a narrow slit.

M. pterygoideus internus [figs. 15, C; 16, B; 17] runs from its origin toward its insertion in a very considerable width, and divides into two very poorly separated portions. Of these, the superficial reaches further forward in its insertion end, while the deeper with its considerable posterior portion is prominent. The superficial portion reaches downward, in general, with its slight divergences, in numerous compact tendinous layers and cords that penetrate fleshy masses, to the lower edge of the ascending ramus, inserting on this and the bend of the angle. The fiber direction of the deeper portion takes a strongly divergent course, so that the posterior fibrous portion not covered by the overlying portion approaches the posterior edge of the jaw in a nearly horizontal direction. The insertion area of the deeper portion reaches back so as to be situated below the foramen mandibulare and the sulcus mylohyoideus on the flat, deepest part of the median face of the ascending ramus, all the way to the posterior edge of the latter.

The *M. pterygoideus externus* [figs. 16, A; 17, B] arises in two heads, one below on the lateral faces of the wing-shaped processes (pterygoid wing), and one above that runs backward and upward along a bony crest situated lateral to the foramen rotundum on the temporal surface of the large sphenoid wings. Both heads soon unite into a strong fleshy body, somewhat flattened laterally, which in large part is prominent behind and above the internal pterygoid and is inclined at an angle of about 22° to the sagittal plane, and runs approximately horizontally backward to the articular process of the lower jaw. It inserts on this immediately below and in front of the medially projecting part of the articular process. The muscle fiber-bundles become increasingly shortened from bottom to top, because of their backward inclination and because of the upward sloping direction of the line of their origin. Thus, the topmost have only about one-third the length of the lowermost. The *N. buccinatorius* runs between the two heads of the muscle.

M. digastricus [figs. 16, B; 17]. All authorities have noted the peculiar behavior of this muscle in the horse, though it has not been described in exactly similar ways. It is comprised essentially of the very strong posterior belly that arises from the point of the processus jugularis (paroccipital process) and that fastens, with by far the greatest part of its flesh, along the curve of the angle of the jaw in intimate junction with the overlying internal ptery-

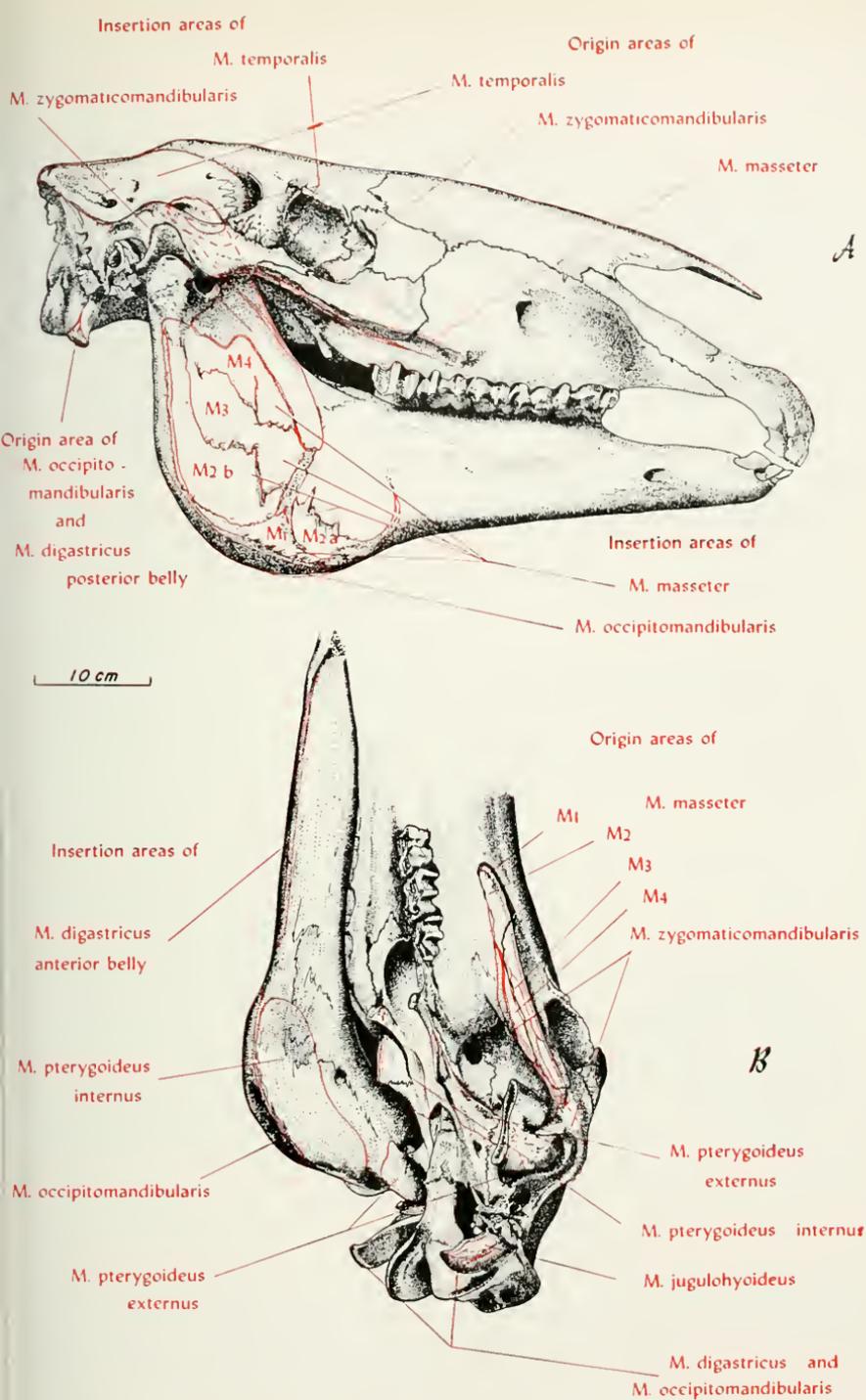


FIG. 17. Skull and jaws of *Equus* showing the origin and insertion attachment areas (mapped in red) of the masticatory muscles. A, Lateral view. B, Ventrolateral view with one jaw ramus removed except for its condyle, neck and coronoid process.

goid (*M. jugulomandibularis*, Martin [= *M. occipitomandibularis*]. It gives off also, from the upper side of the muscle belly a little before its insertion, a thin fiber group (ventro posterior *M. digastricus*, Martin), which in turn soon goes over into a slender forward running tendon bound together with the stylohyoideus. From this the anterior belly of the digastric proceeds. It is thin, spindle-shaped, and inserts anteriorly by a long band-shaped tendon that passes forward on the medial surface of the body of the mandible in close contact with the mylohyoideus, and finally adheres tightly to the anterior segment of the lower edge of the jaw. The *M. jugulohyoideus*, which, according to Martin,¹ was referred to the digastricus group in the horses, seems to me not to belong there even though it is united with the posterior belly of the digastric in the horse. I do not consider this to be true for the reason that the proper origin of the jugulohyoideus as can be seen in other ruminants where it arises separately (Hirsch, Reh), is not from the tip of the processus jugularis [fig. 10] but, on the contrary, is from its anterior edge. Beyond this, there is a direct relationship of the posterior belly to the stylohyoid which is in no way characteristic of the digastricus.

I have no points of disagreement with Toldt's description (for I found conditions in my animal to be essentially as he has described them). I have used the terms paroccipital process and occipitomandibularis respectively in place of Toldt's use of the terms processus jugularis and jugulomandibularis.

TABLE IV.—Weights and percentages of masticatory muscles: *Equus*

Muscle	Weight (in grams)	%	% (omitting digastric)
<i>M. masseter</i>	1032.0	42.6	45.6
<i>M. zygomaticomandibularis</i>	202.0	8.3	8.9
<i>M. temporalis</i>	330.0	13.6	14.5
<i>M. digastricus</i> (incl. occip. mandib.=jugulo-mandib.)	158.5	6.5	—
<i>M. pterygoideus internus</i>	606.0	25.0	26.7
<i>M. pterygoideus externus</i>	95.0	4.0	4.2
Totals	2423.5 g.	100.0%	99.0%

Odocoileus virginianus

Figures 18,A,B; 19,A,B; 20,A,B; 21,A,B; 22,A-C.

The specimen available to me for dissection had been recently received from the Chicago Zoological Society, FMNH 57536. Supposedly a young adult male, it proved to be subadult; the horns were just budding and the tooth replacement just beginning at the time of its demise. The teeth in place were $Dp \frac{2-1}{2-4}$, $M \frac{1}{1}$. The most

¹P. Martin. Lehrbuch d. Anatomie d. Haustiere. Stuttgart 1904. II, Bd. S. 317.

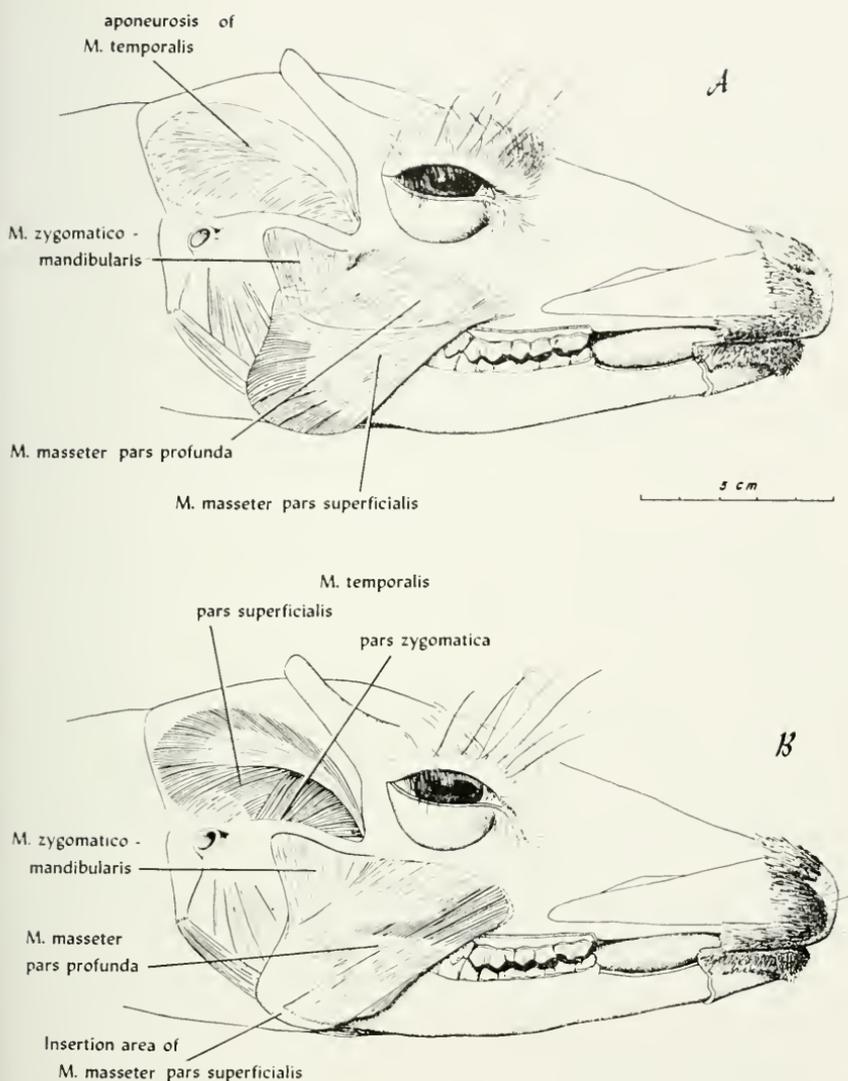


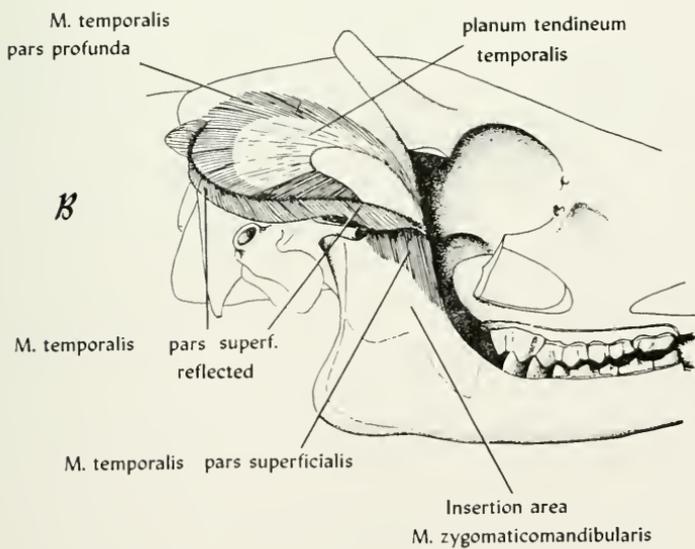
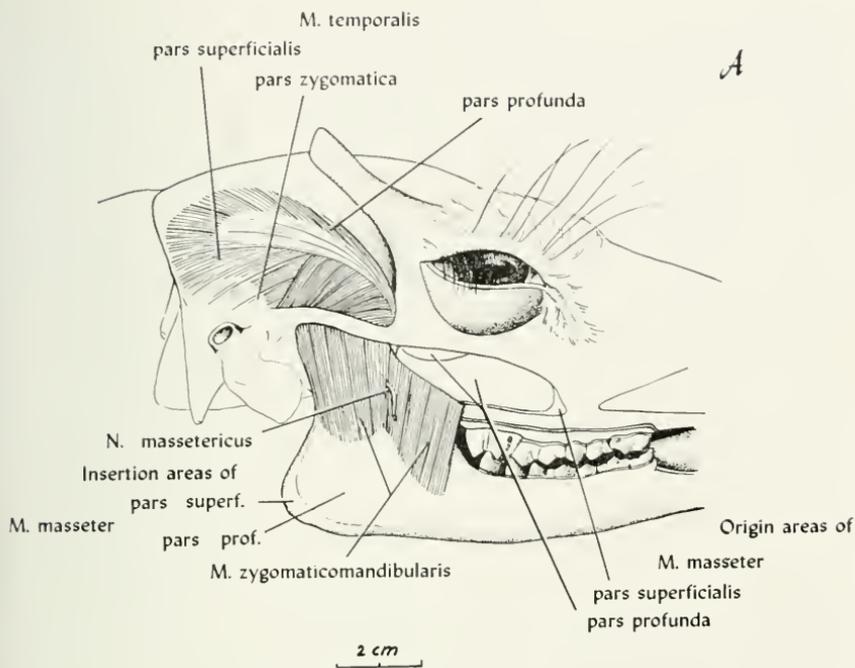
FIG. 18. Masticatory musculature of *Odocoileus*. A, Superficial dissection showing the aponeurosis covering M. temporalis, and the exposed portions of Mm. zygomaticomandibularis, masseter, posterior digastric and stylohyoideus. B, Same aspect showing M. temporalis with its aponeurosis removed and M. masseter with its pars superficialis removed.

adequate description of the masticatory musculature of a deer has been made by Toldt (1905) for the European reh, *Capreolus capreolus*. In general, I find Toldt's descriptions of his animal also apply to *Odocoileus virginianus*. His illustrations for the reh are more numerous than for most other forms, although I find them inadequate for the pterygoid and digastric musculature. I here present my own description, and illustrations made for me from my sketches by Mrs. Maidi Wiebe Liebhardt. Important differences between *O. virginianus* and *C. capreolus* are noted. An adult female, FMNH 44829, was used to map the origin and insertion areas, and served as the basis for the osteological and attachment area illustrations.

After removal of the skin and its associated tissues (musculature, fat, connective tissue, and fascia), the superficial layers of the Mm. masseter and temporalis come into prominent view laterally (fig. 18,A). Both bellies of the digastric can be seen (provided the parotid gland is removed), although, of course, M. digastricus is best seen from the ventral side. A considerable portion of the deep masseter may be noted immediately beneath the zygomatic arch, where it is not overlain by the superficial masseter. Behind this a bit of the zygomaticomandibularis may be seen below the posterior part of the zygoma.

M. masseter superficialis has a glistening tendinous covering over more than two thirds of its surface (fig. 18,A). All except its postero-ventral region is so covered. Along the dorsal edge, there is a slight mixing of some of the tendon fibers with those belonging to the deep portion of the muscle there exposed. The fiber direction of the superficial masseter radiates fan-shaped, postero-ventrally, from its origin. The primary, crescentic area of origin is located in front of, and beneath the orbit from a region on the maxillary bone above the last premolar and first molar. Along the anterior border of the superficial masseter, the sterno-mandibularis fuses with it tendinously. This fusion is illustrated by Toldt's (1905) Figure 10, pl. II, and appears to be similar to its counterpart in the ox (Sisson and Grossman, 1938, p. 349). The superficial masseter has a tendinous flange anteriorly that extends in an arch around and under the forward edge of all levels of the masseter, enveloping them anteriorly. The origin of

FIG. 19. Masticatory musculature of *Odocoileus*. A, Lateral view with M. masseter fully removed to expose M. zygomaticomandibularis. B, Same aspect with zygomaticomandibularis and most of the zygomatic arch removed to expose M. temporalis to full view. Pars superficialis of M. temporalis is partially reflected to expose more of the pars profunda and the planum tendineum temporælis.



this tendon is from a little bony ridge that parallels the alveolar edge of the maxillary so that it runs beneath the deep portion of the masseter as far back as the level of the last molar.¹ Toldt's (1905) description and his Figure 12, pl. II, show precisely the same condition in the reh. Insertion is onto the well-defined postero-ventral edge of the angular process.

M. masseter, pars profunda originates from a large oval-shaped area beneath the orbit, behind the main origin area of the superficial masseter (figs. 18,A; 19,A). The origin is somewhat tendinous on its superficial surface and markedly so in its posterior region (fig. 18,B), especially at mid-depth where a separate division might well be designated. Otherwise it is fleshy. The muscle inserts in front of and above the insertion area of the superficial masseter onto a sizeable area on the lateral face of the jaw at the region of the junction of horizontal and ascending rami (figs. 18,B; 19,A). Insertion is both tendinous and fleshy. For the reh, Toldt distinguished three component parts of the deep masseter. For *Odocoileus*, I found suggestive evidence of these divisions, although they were not nearly as sharply defined as he found them to be. It does not seem likely that the young age of my specimen would account for this difference, for the prepared skulls of adult animals show only a two-fold division judging from the muscle scars. In *Odocoileus*, using Toldt's terminology, division no. 3 is distinct, and nos. 1 and 2 are fused. In addition to this difference in degree of division within the deep masseter, I find one other minor difference between *O. virginianus* and *C. capreolus*. Actually, this may be more apparent than real, and may result from the nature of Toldt's illustrations. In his Figure 12, in the area between the origin of the ventral flange of the superficial masseter and the origin of the main mass of the masseter, there is shown an exposed area of bone which does not serve as an origin attachment site for any part of the muscle. In *O. virginianus* the corresponding area is entirely filled with origin fibers of the anterior part of the deep masseter. Toldt's text makes no mention of such a gap in the origin field as his figure shows, and this fact, plus my observation of the area in another member of the Cervidae, suggests the possibility to me that his Figure 12 may be somewhat in error.

¹ This statement is based upon observations of the location of the origin scars on numerous other prepared skulls in the FMNH collection, and not upon the juvenile animal dissected.

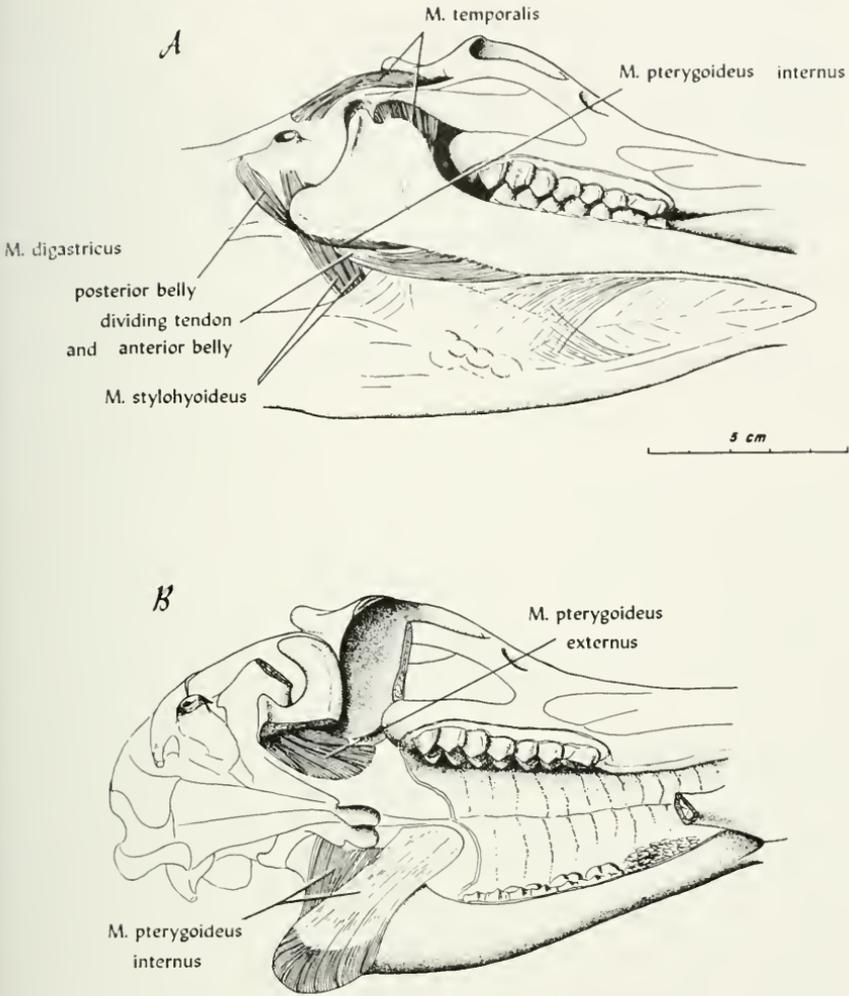


FIG. 20. Masticatory musculature of *Odocoileus*. A, Ventro-lateral view of a dissection showing Mm. temporalis, pterygoideus internus, digastricus and stylohyoideus. B, Deep dissection in ventro-lateral aspect showing M. pterygoideus externus.

M. zygomaticomandibularis is covered by the masseter except for its postero-dorsal third that lies exposed immediately behind and above the masseter, beneath the greater part of the zygomatic arch (figs. 18,A,B; 19,A). Its origin is from the ventral and slightly ventro-lateral surface of the zygomatic arch, and from low on the medial side of the arch in front. The origin is more massive and fleshy behind

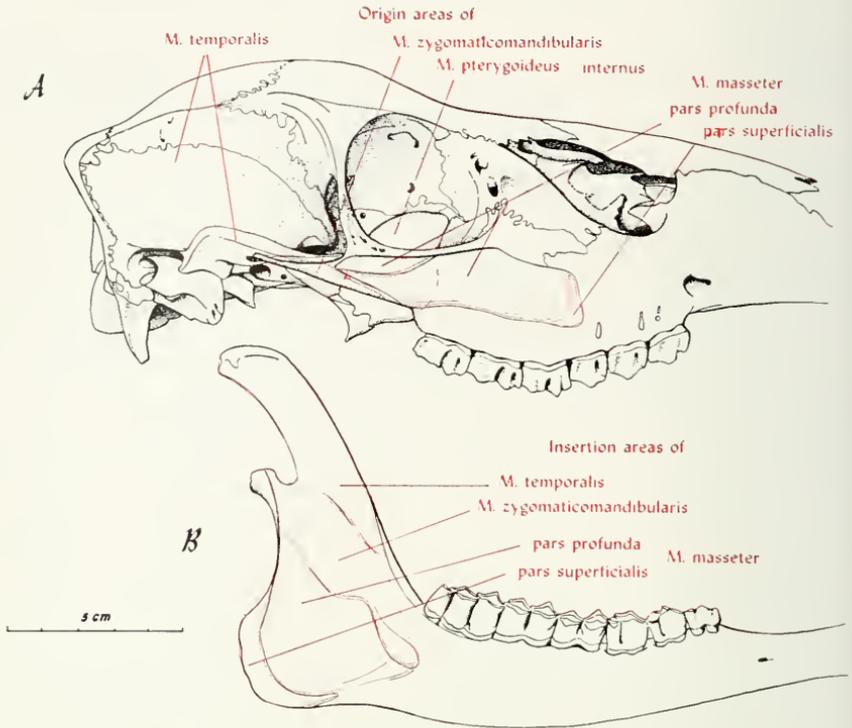


FIG. 21. Lateral view of a skull (A) and a jaw (B) of *Odocoileus* showing the various origin and insertion attachment areas of the masticatory musculature (mapped in red).

than in front, where it becomes tendinous and sheety. It lies in intimate contact with both the temporalis and deep masseter in its anterior portion. A slight cleft in the muscle allows for the passage of the N. massetericus, and makes a rather indistinct division into anterior and posterior portions. Most of the fiber bundles descend nearly vertically, roughly parallel to one another except that those in the back of the muscle are inclined slightly forward. All are of approximately the same length; the somewhat longer anterior ones originate lower on the skull but at the same time insert lower down on the jaw than those located more posteriorly. Insertion is onto the lateral face of the ascending ramus immediately adjacent to the insertion of the deep masseter, mostly above, but somewhat in front of it. The insertion fills the area from the linea obliqua up to the base of the coronoid process, which in turn serves for the insertion of the temporalis.

M. temporalis is covered by a light tendinous aponeurosis over most of its surface (fig. 18,A). Removal of this covering permits one

to observe the convergence of the muscle fibers from all sides of the temporal fossa, except from its front (fig. 19,A). The muscle is tendinous distally in its anterior and central portions, just above the coronoid process. Some of its origin comes from the covering aponeurosis. It perhaps could be divided into two component parts that would be comparable to the superficial and deep layers of many other mammals. Under this interpretation, the lateral zygomatic portion of the muscle that takes origin from the entire length of the medial face of the zygomatic arch, except for its ventral edge, together with the most superficial of the converging fibers that attach to the tip of the coronoid process, would all have to be considered as the superficial portion (fig. 19,A,B). However, in the posterior half of its origin, behind the top of the coronoid process, there is a complete mixing of these "superficial" and "deep" portions. Therefore, I am inclined to follow Toldt (1905), who did not consider such a division to exist in the reh. Insertion is onto both sides of the coronoid process by primarily fleshy attachment. The top of the coronoid receives the tendinous fibers that converge upon it, as described above. The fleshy insertion is more extensive on the medial side of the coronoid process and ascending ramus than on the lateral side of the process. It contacts the internal pterygoid muscle just in front of the inferior dental canal medially and the zygomaticomandibularis at the base of the coronoid process laterally.

Most of the posterior belly of *M. digastricus* can be seen in lateral view (fig. 18,A). It lies at a deeper level, behind the masseter and beneath the temporalis and the auditory canal, approximately in the plane of the cheek teeth. In this view, the anterior digastric can be glimpsed in front of and beneath the level of the angular process in the saddle between it and the horizontal ramus. The digastric is best viewed ventrally (fig. 20,A), where the tendinous division between the two bellies is partially visible, though for the most part it is obscured by its passage through the *M. stylohyoideus*. (This condition was not mentioned by Toldt in his description of the reh; otherwise I find the conditions of the digastric in *O. virginianus* fit well with *C. capreolus*, even to the extent of intermingling of the most superficial layers of the anterior digastric and the mylohyoideus, which Toldt described. In function, these intermingled layers would appear to work more with the mylohyoideus than with the rest of the anterior digastric.) The posterior belly originates from the paroccipital process (= proc. jugularis of Toldt (1905), Ellenburger and Baum (1943), and others). After forming a distinct belly, it goes into a slender tendon that passes between two layers of the *M. stylohyoideus*. An-

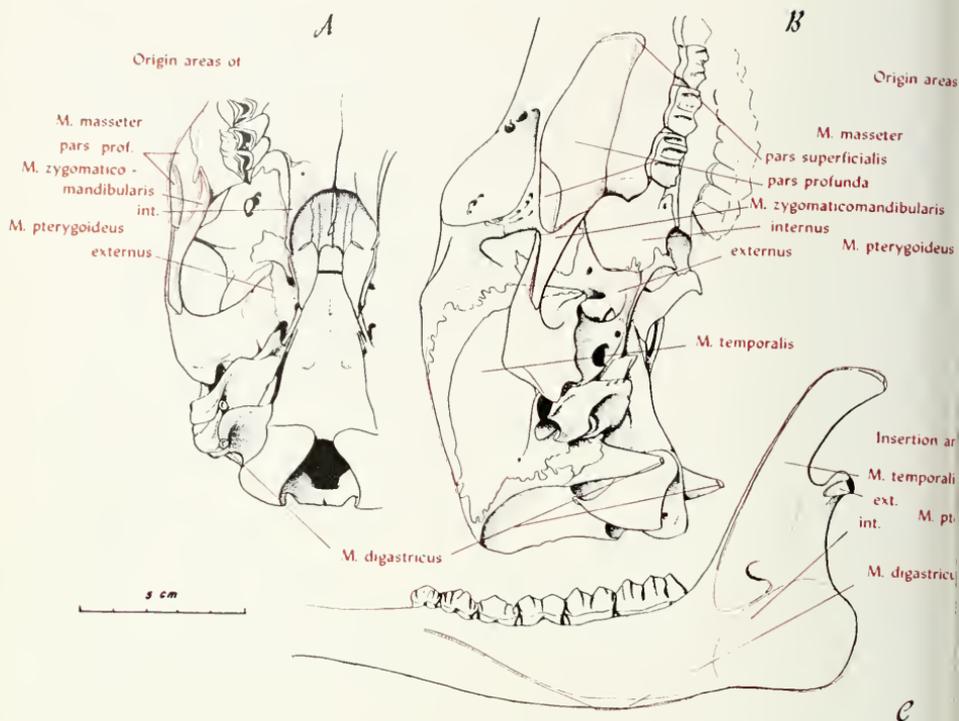


FIG. 22. Ventral (A) and ventro-lateral (B) views of a skull of *Odocoileus*, and the medial aspect of a lower jaw (C) showing the attachment areas as in Figure 21.

terior to this, the anterior belly originates from the dividing tendon, continues forward fleshy to insert in part directly onto the ventro-medial border of the mandible in front of the insertion of the internal pterygoid, and, in smaller part, to continue on and mix with the mylohyoideus and, finally, insert more anteriorly on the medial side of the ramus.

M. pterygoideus internus is a relatively large muscle (fig. 20, B). It takes origin from an extensive area in front of the origin area of the external pterygoid, from most of the lateral surface of the wing of the palatine bone as well as from a limited area on its ventral surface and from the sphenoid (orbitosphenoid). It is many-layered, the deepest layers come off from the ventral facet of the palatine bone, and it is covered tendinously from its origin for three-quarters of its length. The fleshy mass is much more extensive than the tendinous part, and it takes origin from the entire lateral face of the palatine wing. The insertion is fleshy, on the entire medial face of

the angle of the jaw, onto an area that is otherwise similar in size and proportion to that which serves as the insertion for the masseter. The most medial layers have a fiber direction that runs about 45° to the horizontal. The muscle runs downward and backward to its insertion. The next, more superficial layers also have a light tendon associated proximally. They take a more nearly vertical path downward than did the deepest part, and they arise somewhat behind it. A third, almost entirely fleshy portion lies in the most superficial position, and it originates from farthest back. Its fiber direction is nearly vertical. These various portions of the internal pterygoid are not truly distinct divisions in any sense: they cannot be divided, but they do serve as landmarks. There is a considerable lateral component of force to the posterior fibers.

M. pterygoideus externus is a small muscle, though it is one with a marked lateral direction to its pull (fig. 20,B). It has a double origin from the squamosal and alisphenoid (one part) and from the alisphenoid and lateral wing of the pterygoid (the other part), both from the area in front of the foramen ovale and from that which partially surrounds the foramen rotundum. It inserts antero-medially on the slight rugosity of the condyle.

TABLE V.—Weights and percentages of masticatory muscles: *Odocoileus*

Muscle	Weight (in grams)	%	% (without digastric)	
M. masseter	16.3		34.0	35.9
pars superficialis	7.9	16.5		17.4
pars profundus	8.4	17.5		18.5
M. zygomaticomandibularis	4.6	9.6		10.2
M. temporalis	13.3	27.8		29.3
M. digastricus	2.6		5.5	—
anterior belly	1.9	4.0		—
posterior belly	0.7	1.5		—
M. pterygoideus externus	1.7	3.5		3.8
M. pterygoideus internus	9.4	19.6		20.8
Totals	47.9 g.	100.0%		100.0%

Ovis aries

Figures 23,A,B; 24,A,B; 25,A-C; 26,A,B.

The specimen dissected, FMNH 57539, was obtained from the Armour Packing Company, Chicago, in June, 1953, through Messrs. E. H. Zamon and R. C. Wheeler. Mr. Wheeler made it possible for me to select the individual animal on the killing floor, so that I was able to obtain the head of a fully adult sheep for this study. The osteological drawings and muscle attachment maps were based on a

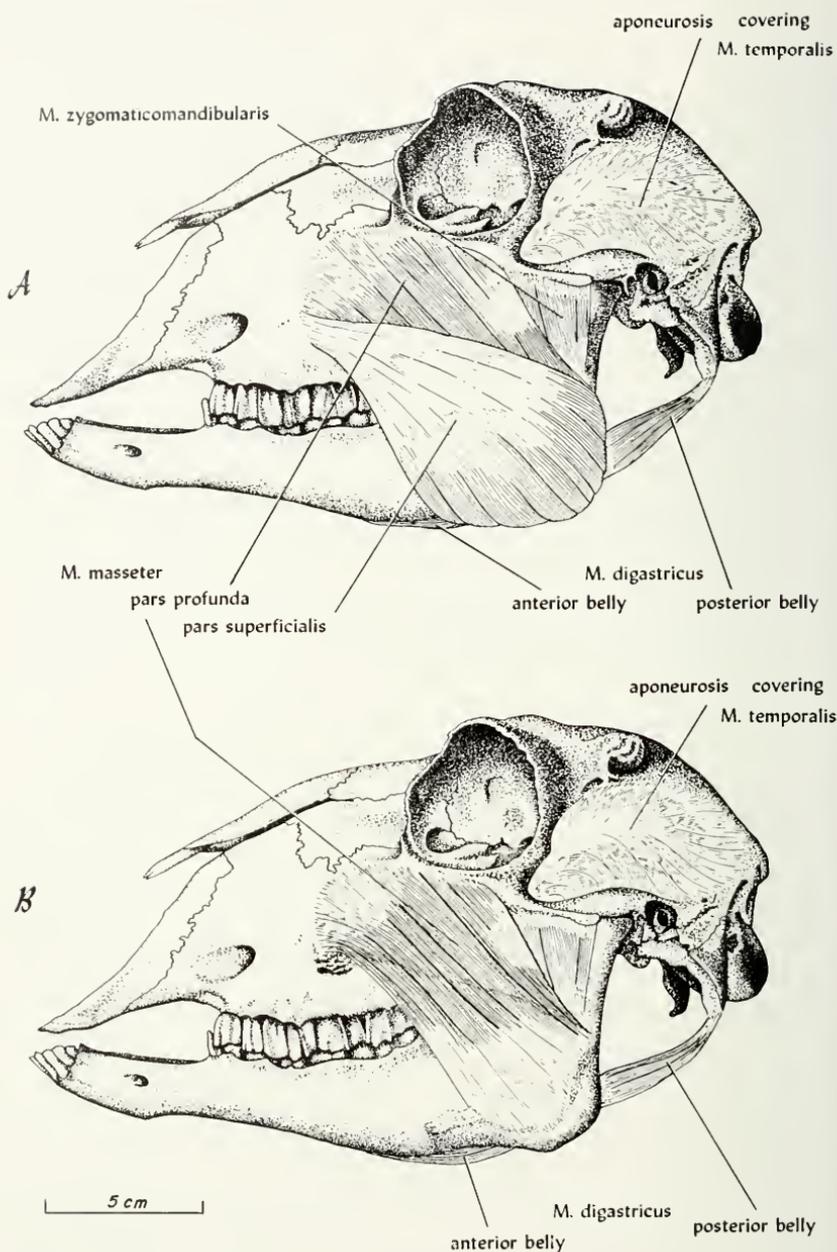


FIG. 23. Masticatory musculature of *Ovis*. A, Superficial dissection in lateral aspect showing the aponeurosis of M. temporalis and showing M. masseter and M. zygomaticomandibularis. B, Slightly deeper dissection showing M. masseter, pars profunda exposed to full view.

skull collected near Freeland, Wyoming, in 1948, FMNH 57540. Drawings are the work of Dr. Tibor Perenyi and Mrs. Maida Wiebe Leibhardt, based on my dissections and sketches.

Toldt did not include a sheep in his classic study, but Zey (1940) has made a detailed study of the changes in the developing masticatory apparatus of the sheep, through various post-natal stages from the newborn to the fully adult. I found conditions in the specimen I studied to be nearly identical to those that Zey described. However, it is most unfortunate that Zey was unable to publish his illustrations along with its detailed text. He states in a footnote (p. 7) that 28 drawings and one illustration were omitted because of the cost. Zey did not treat the depressor musculature of the jaw. Thus, there is no mention or description of the digastric muscles, and consequently his tables of weights and percentages reflect this omission. Zey used Toldt's muscle terminology, which I have also followed throughout. The following is a free translation of the pertinent portions of Zey's text (pp. 11-15) with my comments interjected and a description of the digastric muscle added.

M. masseter. After removal of the skin, subcutaneous fatty tissue and the facial musculature, a fascia-covered surface is exposed which separates the masticatory musculature and the parotid gland, a fascia which corresponds to the parotid-masseteric fascia of man. When one removes it, the whole of the powerful *M. masseter* dominates the picture. The largest part of the surface of the muscle is covered by a delicate tendinous plate that extends from the origin tendon of the muscle and expands backward over almost the entire surface of the masseter. As has been long known, the *M. masseter* is divided into a superficial layer (*pars superficialis*) and a deep layer (*pars profunda*), which are held together by fascia, though each is distinguished by a separate origin and insertion as well as by fiber direction.

Pars superficialis. This arises by a heavy compact tendon from above the third molars from a protruding, rough eminence of the maxillary bone (*crista facialis*).

I find the *crista facialis* to be located above M^2 , or even the back edge of M^1 . Perhaps Zey was counting the teeth from behind instead of in the usual manner.

. . . The tendon is not just situated on the outer margin, but it also engulfs the *crista* and forms a backwardly opening groove in which the fleshy front part of the *pars profunda* lies. This same tendon spreads backward and downward in a firm glistening tendon and serves as the origin for a powerful fleshy mass, in which the fibers diverge slightly in passing backward and downward to insert in part on the underside of the body of the mandible, including its angular process, and in part to fuse with the *pars profunda*.

Concerning the relationship between tendons and muscles, part of this superficial portion of the masseter goes through a considerable change during postnatal development. In the newborn, this tendon forms about one-third of the pars superficialis; in the lamb it apparently approaches half; and in the adult it forms two-thirds of the muscle. Indeed, with advancing age of the animal the pars superficialis always reaches farther forward on the lower jaw so that its straight forward fleshy part is strongly developed. This causes a change in the average fiber direction in the muscle. In the newborn it is very flat, and is inclined slightly from the horizontal plane, then it becomes increasingly steep as the lamb grows to adulthood.

Pars profunda. The deep portion of the masseter is covered in its forward and lower portions by the superficial layer, while the larger, higher and posterior parts stand exposed. It arises from a long, arched, clearly recognizable line on the skull that begins at the origin of the superficial layer on the maxillary bone, passes backward onto the jugal, runs back along this close to the edge of the orbit and ends somewhat in front of the junction of the jugal and zygomatic process of the temporal bone.

Actually, Zey has not described the complete area of origin of the muscle, but rather has defined its upper border. It should be added that the trace of the outline of the origin area makes a tight turn at its posterior limit, runs a short distance toward the midline, then runs nearly straight forward to the base of the crista that gives origin to the superficial masseter. Thus, the highly arched dorsal border and the straight ventral edge of the area of origin delimit a very sizeable surface region of the face. In depth, most of the origin is fleshy.

... The muscle fibers run obliquely posteroventrally, going over at midlength to a tendon that inserts on the external surface of the ascending and horizontal jaw rami. The muscle breaks down into an anterior and a posterior part. The line of demarcation runs in a vertical direction through the most forward point of the orbit. The fleshy portion of the anterior muscle mass arises fan-shaped from the maxillary bone. The posterior part arises tendinously from the underside of the jugular, and goes over into a muscular mass that inserts again tendinously on the lower jaw.

A grouping of these muscles into two principal parts is not yet distinct in the newborn. First, in the lamb, there is a preparation for the division. The tendon of the deep portion of the masseter that inserts on the lower jaw amounts to at most one-third in the newborn; in the adult animal, however, it is one-half the total muscle length. The tendon of the posterior part of the muscle that arises from the zygomatic arch remains fairly unchanged in all of the developmental stages of the sheep, whereas the fiber direction of the entire muscle changes considerably with age. With increasing age of the sheep, the fiber direction becomes more and more steeply inclined with respect to the horizontal.

I found several differences in detail (probably individual variations) from the conditions that Zey has described for the pars pro-

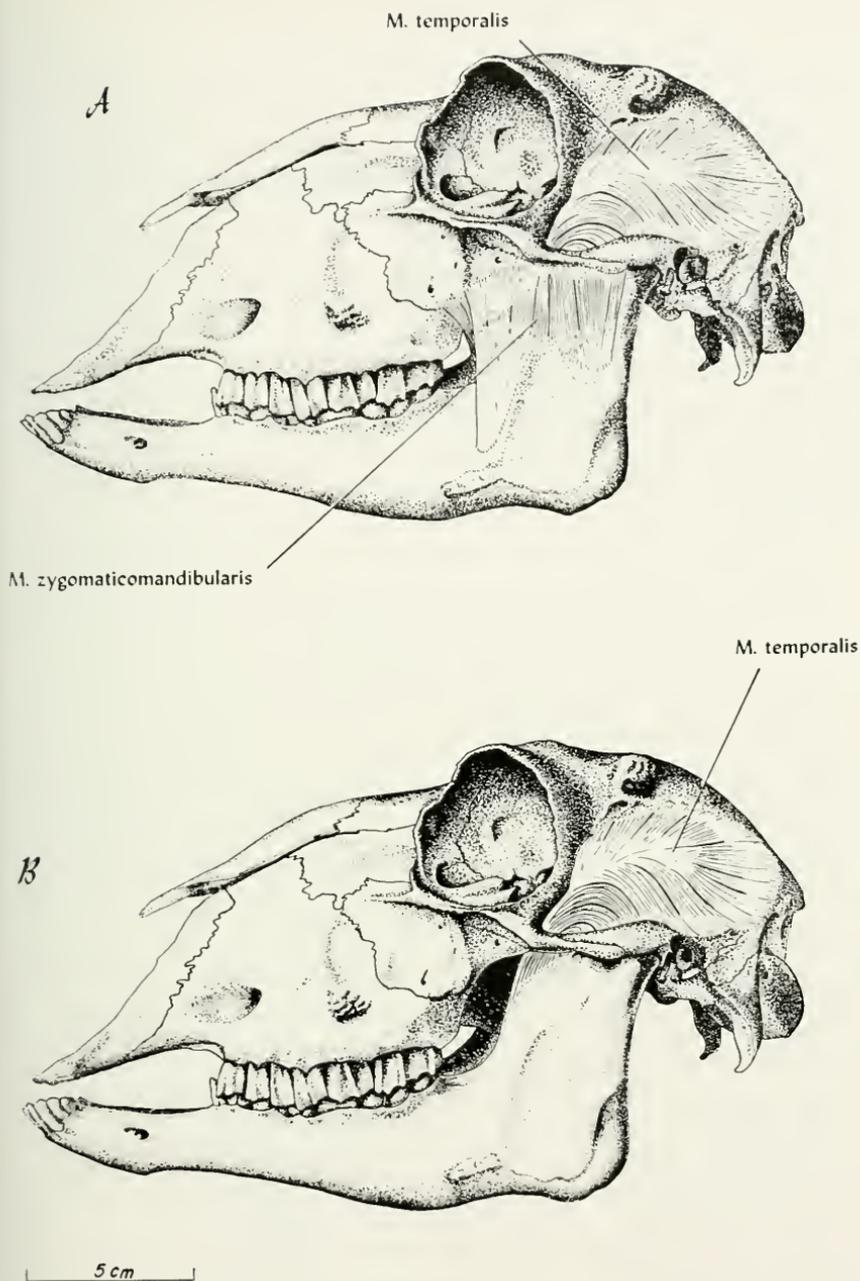


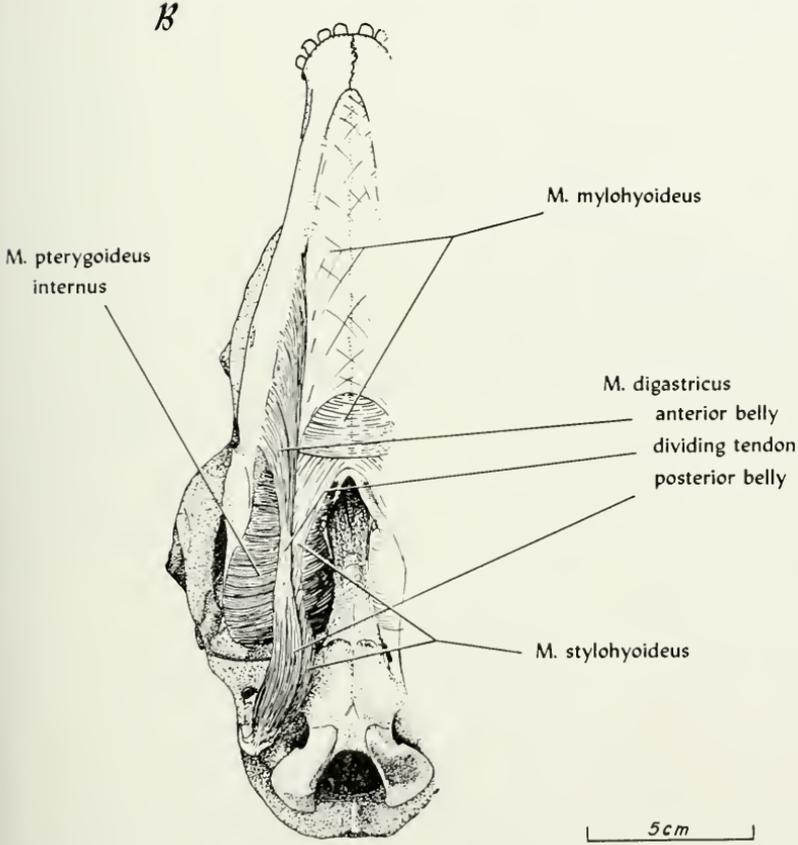
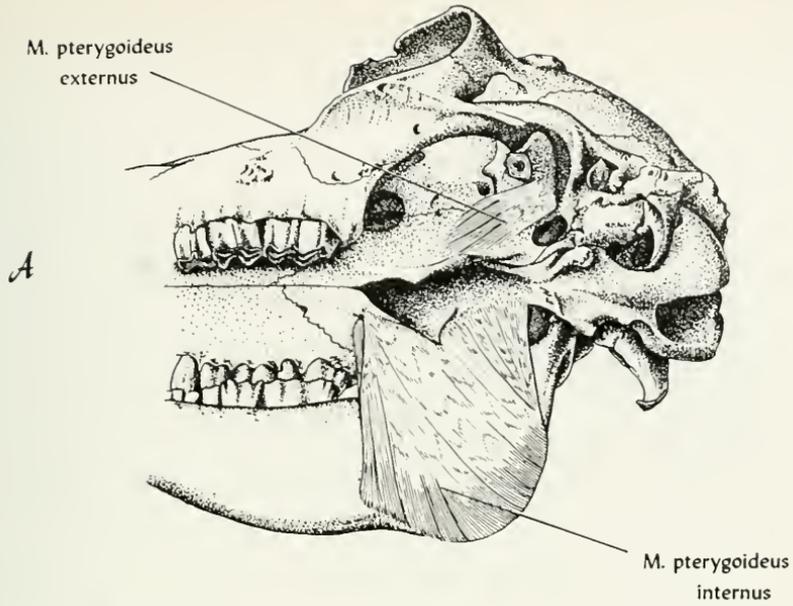
FIG. 24. Masticatory musculature of *Ovis*. A, Deep dissection in lateral aspect showing *M. temporalis* after removal of superficial aponeurosis, and showing *M. zygomaticomandibularis* exposed to full view. B, Deep dissection, same aspect, showing *M. temporalis* in full view after removal of entire masseter complex.

funda: 1) There is no clear-cut separation of the muscle into anterior and posterior divisions. 2) The anterior portion does have a mostly fleshy origin as Zey said, but it has a thin tendinous surface superficially for perhaps one-third the length. The insertion of that portion is almost entirely tendinous, and continuous with that of the posterior portion. As one traces the insertion tendon posteriorly into the region of the posterior portion of the muscle, it splits at the junction to allow for a sizeable fleshy insertion of the posterior portion between the backward and upward diverging arms of the insertion tendon. Also, a thin sheet of muscle has a fleshy insertion at greater depth, above the deepest of the tendon sheets. 3) I found an even more intimate fusion of pars superficialis and pars profunda than Zey noted. This is also true of the contact of pars profunda and the zygomaticomandibularis.

M. zygomaticomandibularis. After one removes the deeper layers of the masseter, there appears a distinct, powerful muscle mass, separable from the masseter, which, like the deep masseter, stretches between the zygomatic arch and the jaw bone, the *M. zygomaticomandibularis*. The upper limit of the muscle draws from the posterior edge of the crista facialis in an arch-shaped bend, to the underside of the zygomatic arch, and extends along this to the region of the jaw articulation capsule. The insertion of the muscle lies half on the ascending ramus, while that of the other part extends onto the body of the mandible. The dissection shows that the muscle consists of three layers. The two upper ones are half tendinous, while the third and deepest is fleshy. The individual layers are so arranged that tendon comes to lie on muscle. Also, the separate portions are bound together by fibers. In cross-section the muscle is shown to be tripartite. While the middle portion pulls approximately vertically, the anterior and posterior portions proceed to converge vertically toward the mandible.

The tripartite muscle of the grown animal is a bipartite one in the newborn and the lamb. The first (anterior) half is only slightly developed in the newborn. In the lamb it begins to extend out farther onto the maxillary bone and the body of the mandible. The muscle fibers of the third (posterior) portion increase considerably so that the average direction of the fibers of the entire mass comes to be at an angle of 90° to the horizontal plane. The tendinous part becomes further developed, until it amounts to half of the muscle in the adult sheep. Also, significant weight changes become established for each of the developmental stages, of which further note will be made in later sections.

FIG. 25. Masticatory musculature of *Ovis*. A, Deep dissection in ventrolateral view showing *Mm. pterygoideus internus* and *pterygoideus externus*. All of one jaw except its neck and articular condyle are cut away for viewing the musculature. B, Dissection in ventral view showing *Mm. pterygoideus internus*, *digastricus*, *stylohyoideus* and *mylohyoideus*.



I did not observe a definitely tripartite division of the muscle. The posterior third was found to be more or less distinct, but the anterior two-thirds (at the surface, actually more nearly half of the bulk of the muscle) showed no suggestion of a division.

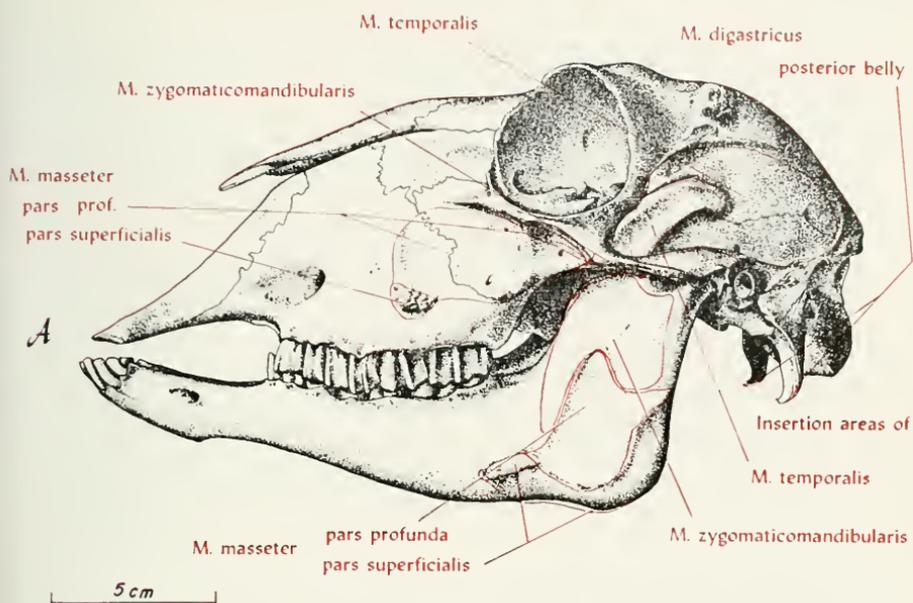
M. temporalis. A thin fascia covers this muscle. One takes it away so as to show the origin from the parietal and squamosal bones. At first the fibers run forward and downward quite flat-lying, but then they pass over a bony elevation of the squamosal and run partly in an arched curve down onto the coronoid process, and partly they proceed along it on the internal surface of the ascending ramus down to just above the mandibular foramen in back, and attach there to a bony flange which appears to correspond to the lingula of man's lower jaws. In the course of the descent of this last muscle portion, it takes on some additional fiber-bundles, which arise from the anterior, lower edge of the squamosal.

In addition to the relatively decreased weight in the young, the principal differences in these muscles in the individual developmental stages of the animals are that the tendinous origins slowly grow, and the course of the fibers in the young individual is flatter than in the adult sheep.

Zey did not mention the extent of lateral development of the muscle which arises, continuous with the rest of the temporalis, from the dorsal, slightly inward-facing surface of the posterior half of the zygomatic arch. It runs medially and forward, then downward to insert onto the lateral surface of the coronoid process.

M. digastricus. The digastric is a distinctly two-bellied muscle with a dividing tendon (fig. 25 A). Its anterior belly is by far the larger of the two. The posterior belly arises from the tip of the paroccipital process, and to a limited extent from the postero-ventral edge of the process, entirely tendinously. It remains largely tendinous, even at midlength where the fleshy bundles are most extensively developed. It soon passes into a dividing tendon that keeps a slight fleshy band attached to itself. The dividing tendon in turn gives rise to the anterior digastric, which is largely fleshy throughout except for some few tendinous insertion fibers. The insertion is onto a somewhat rugose area low on the medial surface of the horizontal ramus. The insertion area is very elongate and narrow, nearly as long as the length of the cheek tooth row that lies directly above it, except perhaps for the anterior premolar. Part of the origin of the mylohyoideus is by a thin but stout tendon that comes off from the front of the dividing tendon of the digastric. The stylohyoideus lies immediately adjacent to the posterior digastric and its dividing tendon where it originates by a gathering of slight tendinous bands from the surface of the occipito-hyoideus. In contrast to the condition in

Origin areas of



Origin areas of

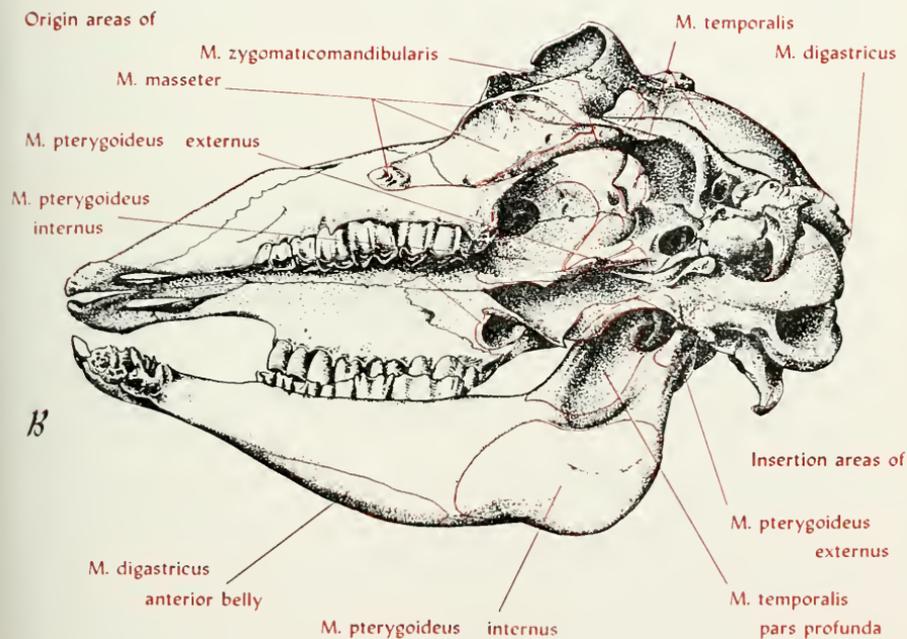


FIG. 26. Skull and jaws of *Ovis* with the masticatory muscle attachment areas (mapped in red). A, Lateral view of skull and jaws. B, Vento-lateral view of skull and one jaw ramus.

the deer and horse, there is no passage of the digastric's dividing tendon through a cleft in the tendon of the stylohyoideus.

M. pterygoideus internus. The inner chewing muscles (mm. pterygoidei) were dissected after the head was bisected. The internal pterygoid, which according to Toldt is made up of two portions in the deer, is in the sheep a single muscle mass in which four groups of muscle bundles can be only artificially distinguished. The superficial portion arises by means of a compact, flat tendon, in part from the under-edge of the lamina pterygoidea, in part from the under-face of the palatine bone. This tendon runs back at first, in the line of the hard palate, then turns downward in a concave flexure, so that it forms the anterior edge of the muscle. From this tendon, and from its radiating aponeurosis, the fiber-bundles go forth diverging; the anterior ones descend almost straight down to the lower edge of the body of the mandible, while the posterior, smaller ones run to the edge of the ascending ramus. The deepest section arises tendinously on the lower jaw and runs to the lamina lateralis of the sphenoid bone. The two middle portions unite into one muscle mass, in such a way that tendinous part comes to lie against fleshy part.

In the newborn animal, the individual layers are not yet clearly developed. At first, the tendinous portion covers about half of the muscle, but amounts to two-thirds of the total in an old animal. The angle which the muscle fibers make with the horizontal approaches nearer to a right angle, and the number and strength of the fibers increases (with age).

When Zey discussed the deepest section of the internal pterygoid, he reversed the identification of origin and insertion. More detail may be added to the description of the attachment areas as follows. Origin is from a sizeable area of complex outline, situated on the wing of the palatine and the ventral edge of the pterygoid wing, and to a limited extent from the orbitosphenoid. Insertion is onto a large sub-circular area at the junction of the horizontal and ascending jaw rami, including the entire median surface of the angular process.

M. pterygoideus externus. This muscle, seen in medial view, lies hidden deeply beneath the internal pterygoid. In order to dissect it, one must remove the internal pterygoid, and part of the lamina pterygoidea. The sphenoid and palatine bones, as well as the posterior edge of the processus alveolaris maxillae, serve as the origin area. From there on the muscle draws into two portions, in which the medial covers the lateral, that run to the inner surface of the condyle, the joint capsule, and the discus articularis. The muscle converges upon its insertion, and is entirely fleshy.

In the newborn, the directional course of the external pterygoid is inclined only slightly from the Frankforter Plane, while in the lamb, and finally in the adult animal, the angle of the fibers becomes increasingly greater. In the newborn, the total mass of this muscle is relatively large but in the adult animal it is proportionately less massive.

The following can be added to Zey's description of the external pterygoid: 1) The two portions of the muscle are fused with one another throughout their length, and 2) there is a considerable fusion of this muscle with the internal pterygoid in the region of their origins.

TABLE VI.—Weights and percentages of masticatory muscles: *Ovis*

Muscle	Weight (in grams)	%	% without digastric
M. masseter	61.0	42.2	44.4
pars superficialis	21.6	14.9	15.7
pars profundus	39.4	27.3	28.7
M. zygomaticomandibularis	11.2	7.7	8.2
M. temporalis	32.2	22.3	23.5
M. digastricus	7.4	5.1	—
M. pterygoideus internus	28.5	19.7	20.8
M. pterygoideus externus	4.3	3.0	3.1
Totals	144.6 g.	100.0%	100.0%

SPECIALIZED GROUP III, "rodent-gnawing" or "anterior shift" type.

For this group I dissected three forms, one from each of the classic Brandtian rodent suborders¹ to assure that the major adaptive modifications be examined. The three species dissected for this work were chosen so as to check the data in existence at the time the choice was made, and an overlap with those studies which predate Schumacher (1961) was planned. With the appearance of that work, further checks have been provided and a broadened base for comparative studies has been gained, but the group is still poorly represented.

Sciurus niger

Figures 27,A-D; 28,A-E.

Toldt (1905, pp. 62-65) gave detailed descriptions of his dissection of the jaw musculature of *Sciurus* and *Marmota*, but he did not identify the species studied. Inasmuch as I found differences in my *Sciurus* from Toldt's specimens (presumably species differences; see below), I present a description of the masticatory musculature of *Sciurus niger* based on a specimen from northwest Indiana FMNH 57538. The osteological illustrations are based on FMNH 47748. Drawings are by Dr. Tibor Perenyi from my sketches.

¹ Most students of the rodents no longer use Brandt's (1855) suborders, yet no substitute has become widely accepted (see Wood, 1959, for discussion). I am not advocating a return to these classic suborders; I merely use them because they are well known and are both adequate and convenient for my present purpose of dealing with a very small representation of the vast number of rodent taxa.

Both *M. masseter* and *M. temporalis* have a covering aponeurosis. This was removed and it was found that the origin tendon of *M. masseter*, pars superficialis arises from a small but pronounced bony protuberance located just beneath the infraorbital foramen (fig. 27,A). This is in contrast to the condition which Toldt reported for his *Sciurus* specimen; he noted a "roughened flat area" similarly located. Although Toldt did not give a specific identification for his squirrel, it is likely that he examined an individual of *S. vulgaris*. A quick check of a dozen skulls in the Field Museum collection showed this difference to be quite consistent between the two forms. The tendon to some extent envelops the front end of the tendinous anterior border of the deep masseter; i.e., that portion of the deep masseter which originates farthest forward on the maxillary and premaxillary bones, from the area that serves as the origin for the *M. maxillomandibularis* in those rodents possessing this distinct muscle. The tendon also differs from that which Toldt described as "a well isolated flat tendon." This difference appears to be consistent with the above mentioned difference in detail of the areas of origin. A few of the superficial fibers of the superficial masseter originate from the aponeurosis, and it is necessary in making a dissection to approach the origin area from the inner tendinous surface. As one proceeds with the dissection toward the posterior end of the muscle, its fibers are found to be more intimately associated with those of the next deeper muscle, *M. masseter*, pars profunda and a separation has to be forced to some extent. The insertion is, in large part, onto the roughened border of the posterior edge of the angular process. This part of the insertion is quite tendinous. The more anterior fibers run under the jaw to insert on the medially inflected margin of the process, beneath the insertion of *M. pterygoideus internus*. A distinct pars reflexa can be distinguished superficially, but there is no clear-cut separation between it and the adjacent portions of the rest of the superficial masseter, either in the region of their origins or their insertions on the medial side of the inflected edge of the angular process. However, in general, the insertion of the pars reflexa is the farther forward and higher of the two.

It was necessary to remove the *M. digastricus* in order to proceed with the dissection of the masseter, and the description of this muscle will be given in its usual sequential order following that of *M. temporalis*. The deep masseter is considerably stronger than the superficial masseter that covers its lower half. Its origin in *Sciurus niger* is (much as Toldt found it to be in *S. ?vulgaris*) for the most part

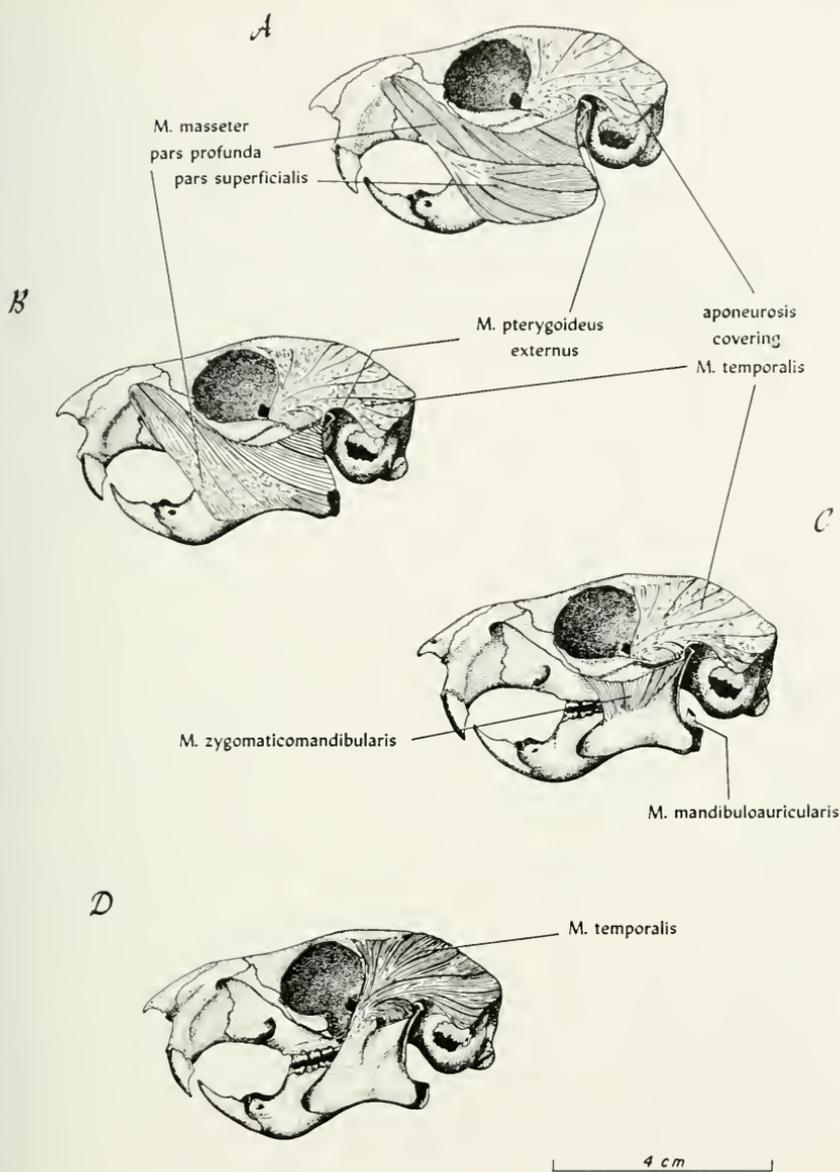
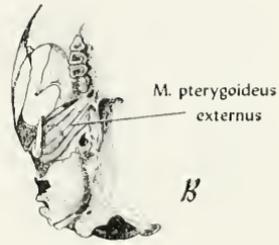
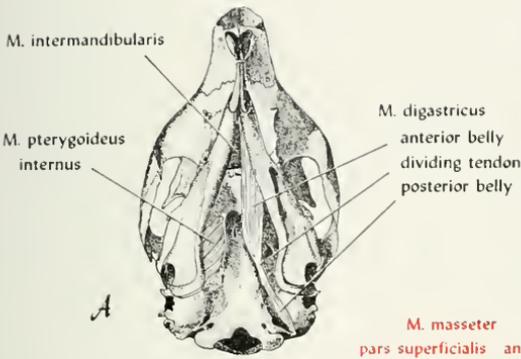


FIG. 27. Masticatory musculature of *Sciurus*. A, Most superficial aspect of Mm. temporalis, masseter and digastricus in lateral view. B, Lateral view with Mm. masseter, pars superficialis and digastricus removed to expose M. masseter, pars profunda in full view. C, Lateral view of deeper dissection after removal of entire M. masseter to expose M. zygomaticomandibularis. D, Lateral view of deep dissection with the zygomatic arch and M. zygomaticomandibularis cut away to show M. temporalis in full view.

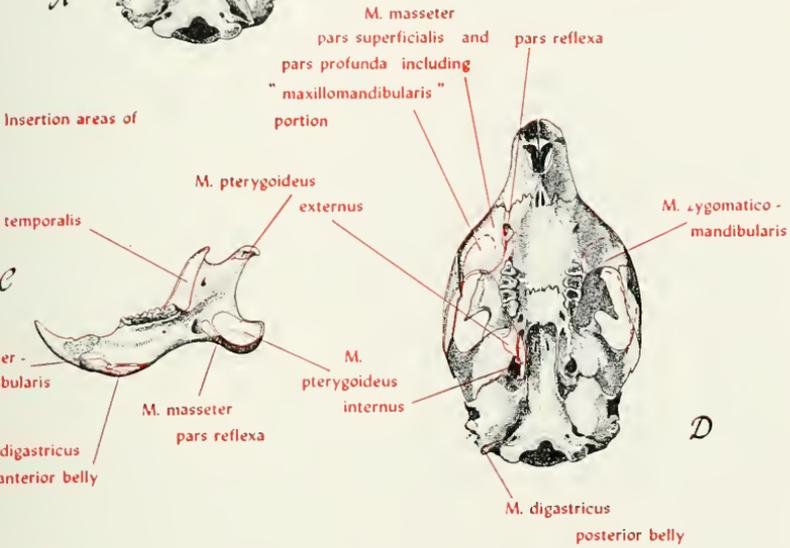
fleshy, from the lateral and ventral surfaces of the zygomatic arch (fig. 27,B). The area of origin also extends upward and forward from beneath the orbit onto the front of the anterior buttress and the side of the snout. Most of this anterior area of origin is from the maxillary bone, but its anterior end comes from the premaxillary above and in front of the opening of the infraorbital foramen, i.e., from that area which gives rise to the *M. maxillomandibularis* in those rodents possessing this muscle as a distinct and separate entity. It also arises in small part from the tendinous aponeurosis posteriorly. This Toldt did not observe. In describing *M. zygomaticomandibularis*, Toldt considered its anterior portion to be a fleshy muscle mass that originates from an area on the front face of the anterior buttress of the arch above the infraorbital foramen, but that lies beneath the origin area of the deep masseter. It is true that the *M. zygomaticomandibularis* proper, i.e., that part originating from the inner face of the arch, is continuous with this muscle lying immediately anterior to it. However, this same muscle is even more intimately united with the anterior edge of the deep masseter through its own anterior edge. At the anterior edge of each, the two merge in a fleshy fold that becomes tendinous toward its insertion, and no easy separation of the two can possibly be made. I have, therefore, forced the easiest separation at the back end of this muscle mass that I arbitrarily call the "maxillomandibularis" portion, and I include it as a portion of the deep masseter. In Figure 28,D the solid line within the common origin field indicates the extent of easy separation; the dashed line the trace of a forced separation. Anterior to the forward end of the solid line, the two layers fold into one another. The insertion, which is tendinous, is mostly in front of the junction of the linea obliqua and crista masseterica, but in back it is united with that of the zygomaticomandibularis.

The *M. zygomaticomandibularis* takes a fleshy origin from the entire medial face of the zygomatic arch and from the postero-dorsal area of the anterior buttress of the arch (fig. 27,C). The muscle is mostly fleshy throughout and becomes tendinous only toward its in-

FIG. 28. A and B. Ventral views of masticatory musculature of *Sciurus*: A, Showing *M. digastricus*, *M. pterygoideus internus* and *M. intermandibularis*. B, Showing *M. pterygoideus externus* with all of the jaw except the condyle and neck cut away. C, D and E. Skull and jaws of *Sciurus* showing the origin and insertion attachment areas (mapped in red) of the masticatory muscles. C, Medial view of jaw. D, Ventral view. E, Lateral view of skull and jaws and a postero-ventral view of the back end of a jaw.

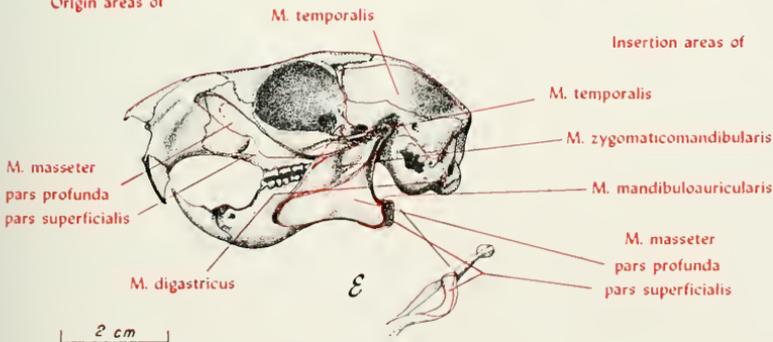


Origin areas of



Origin areas of

Insertion areas of



sersion in the anterior and superficial regions. The insertion is onto a lens-shaped area that runs diagonally forward and downward from the capsule at the articulation in back, to join with the tendinous insertion of the "maxillomandibularis" portion of the deep masseter in front. Its ventral edge follows along the linea obliqua almost to its junction with the crista masseterica and it inserts what tendinous fibers it has along this line. I looked for but did not find either the cleft for the passage of the masseteric nerve that Toldt reported, or the nerve itself at this level. Probably Toldt's dissection of the innervation was considerably more thorough than mine.

M. temporalis originates from the whole dorso-lateral wall (fig. 27,A-D) of the cranium. More precisely, it runs from the occipital crest behind, where it reaches nearly to the sagittal plane; and from this point forward it comes off from the cranium in such a manner that its most superficial fibers follow a faint ridge of bone that proceeds diagonally forward and laterally to the postorbital process of the frontal bone. Then the trace of its margin drops rapidly, so that the muscle in this area forms a posterior wall to the eye socket, follows a faint rugosity in a laterally-directed curve and runs out onto the dorsal surface of the posterior buttress of the arch where it lies adjacent to the posterior part of the origin of the zygomaticomandibularis. Its origin area then follows along the posterior part of the buttress, onto the ridge of bone that leads back, just above the external auditory meatus, to the lateral point of the occipital crest. In order to complete the dissection of the temporal muscle, and to describe its insertion, it was necessary first to sever the jaw ramus just anterior to the cheek tooth series. This in turn necessitated the prior dissection and removal of the *M. intermandibularis*, which will be discussed below. The insertion of *M. temporalis* is onto the whole of the small coronoid process, in large part tendinously, especially so onto its tip and from the antero-lateral surface of the muscle. The lateral surface of attachment is relatively small, but the medial surface is more sizeable, and extends down nearly to the edge of the alveoli of the last two molars. No sharp separation into superficial and deep portions is evident, though it is suggested in a general way—those layers originating more peripherally tend to converge upon the outer surface of the coronoid process.

M. digastricus is a two-bellied muscle with a distinct dividing tendon (fig. 28,A). The posterior belly arises from the antero-lateral edge of the paroccipital process and is largely fleshy. It forms a distinct belly that becomes tendinous anteriorly, and finally grades into

the dividing tendon. The dividing tendon is bound by fascia to the *M. stylohyoideus*. The anterior belly is flattened, and inserts quite far forward, low on the medial side of the ramus, just behind the symphysis.

M. pterygoideus internus originates from within the deep rugose fossa of the pterygoid bone just lateral to its ventral wing, and from the lateral surface of the wing itself (fig. 28,A). It is primarily fleshy and inserts by means of a bulky mass on the greater part of the medial surface of the angular process. Its structure appeared to be simple, with no indication that either origin or insertion was by more than one head.

M. pterygoideus externus arises from the area antero-lateral and above that of the internal pterygoid (fig. 28,B). The forward portion of this attachment, i.e., that situated immediately behind the last molar, is somewhat tendinous. The muscle is relatively very large (7 per cent of the total masticatory musculature), and it, too, appears to be simple in structure and largely fleshy. It inserts in part onto the joint capsule, though mostly onto the medial edge of the ridge of the condylar head and onto the neck of the ascending ramus just beneath the ridge.

TABLE VII.—Weights and percentages of masticatory muscles: *Sciurus*

Muscle	Weight (in grams)	%	% (omitting digastric & intermandibular)
<i>M. masseter, pars superficialis</i> (incl. <i>pars reflexa</i>)	0.563	18.1	19.1
<i>M. masseter, pars profundus</i> (incl. <i>maxillo-mandibularis</i>)	0.910	29.4	31.0
<i>M. zygomaticomandibularis</i>	0.322	10.4	10.9
<i>M. digastricus</i> (anterior and posterior)	0.137	4.4	—
<i>M. temporalis</i> (<i>superficialis</i> and deep)	0.570	18.4	19.4
<i>M. pterygoideus internus</i>	0.360	11.6	12.3
<i>M. pterygoideus externus</i>	0.215	7.0	7.3
<i>M. intermandibularis</i>	0.023	0.7	—
Totals	3.100 g.	100.0%	100.0%

M. intermandibularis has much the same appearance in *Sciurus* as its homologue in *Rattus*, although it is a fleshy mass of somewhat greater significance. It is covered, superficially, almost entirely by the anterior (insertion) portion of the anterior belly of the digastric (fig. 28,A). The body of the muscle takes origin from low on the medial surface of the horizontal ramus, just above the insertion area

of the digastric. Its fibers run directly toward the midline, i.e., transverse to the long axis of the body, to meet with their counterparts in a midline raphe. I did not attempt to split the two muscles apart at the raphe, but instead removed the pair together and have given the weight as one-half of that of the pair.

A distinct *M. mandibuloauricularis* is present (fig. 27,C). It has the usual attachment areas; it arises from the dorsal edge of the backwardly projecting angular process. Its fibers converge so that it inserts by a fine band of subcircular cross-section onto the front of the ear cartilage.

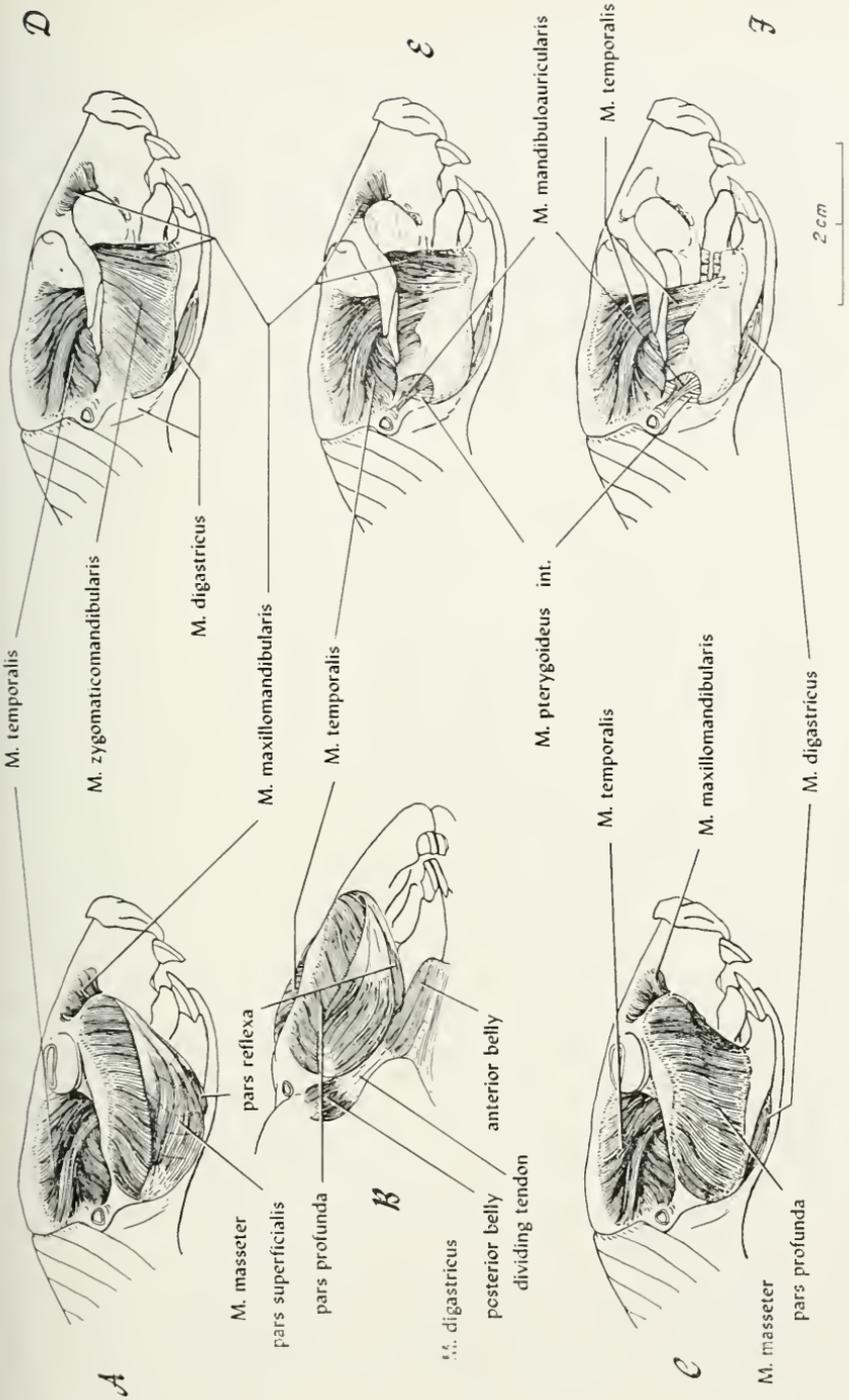
Rattus norvegicus

Figures 20, A-F; 30, A-E.

As in the preceding section, the description and illustrations of the masticatory musculature is based on my dissections. Toldt treated *Mus* and *Rattus* only briefly. He used the dormouse (*Myoxis*) as the myomorph representative, and only very occasionally did he compare *Mus* and *Rattus* with it. He gave no illustrations for any myomorph. Neither Green's (1935) "Anatomy of Muridae," Howell's (1926) "Anatomy of the Wood Rat," nor Parson's (1896) "Myology of Rodents—Part II, Myomorpha" does an adequate descriptive or illustrative job for my particular comparative purpose. Skull drawings are by Charles Joslin.

The specimen dissected was FMNH 15444, *Rattus norvegicus*. The osteological illustrations were based on a prepared skull, FMNH 57151, *Rattus norvegicus* (albino). A significant temporal aponeurosis is present. In lateral view, the cheek teeth are completely covered by the masseter complex. The most superficial portion of *M. masseter* originates by a stout tendon from a small oval area beneath the infraorbital foramen (fig. 29,A-D). It runs downward and backward, bowing out around the deeper tissues, fanning as it does. From near its anterior edge, it is split. The greater posterior portion, *pars horizontalis*, fans out as it proceeds backward and downward. It inserts along the posterior edge of the angular process for nearly its

FIG. 29. Masticatory musculature of *Rattus*. A, Superficial dissection exposing *Mm. temporalis*, masseter, maxillomandibularis and digastricus to lateral view. B, The same in oblique ventral view. C, Lateral view of *M. masseter*, *pars profunda* as seen after removal of *pars superficialis*. D, Lateral view of *Mm. maxillo-mandibularis* and *zygomaticomandibularis* as exposed by removal of *M. masseter*. E, Deep dissection of masseter complex in which *M. zygomaticomandibularis* has been removed exposing *M. maxillomandibularis* to full view. F, *M. temporalis* exposed to full view following removal of entire masseter complex.



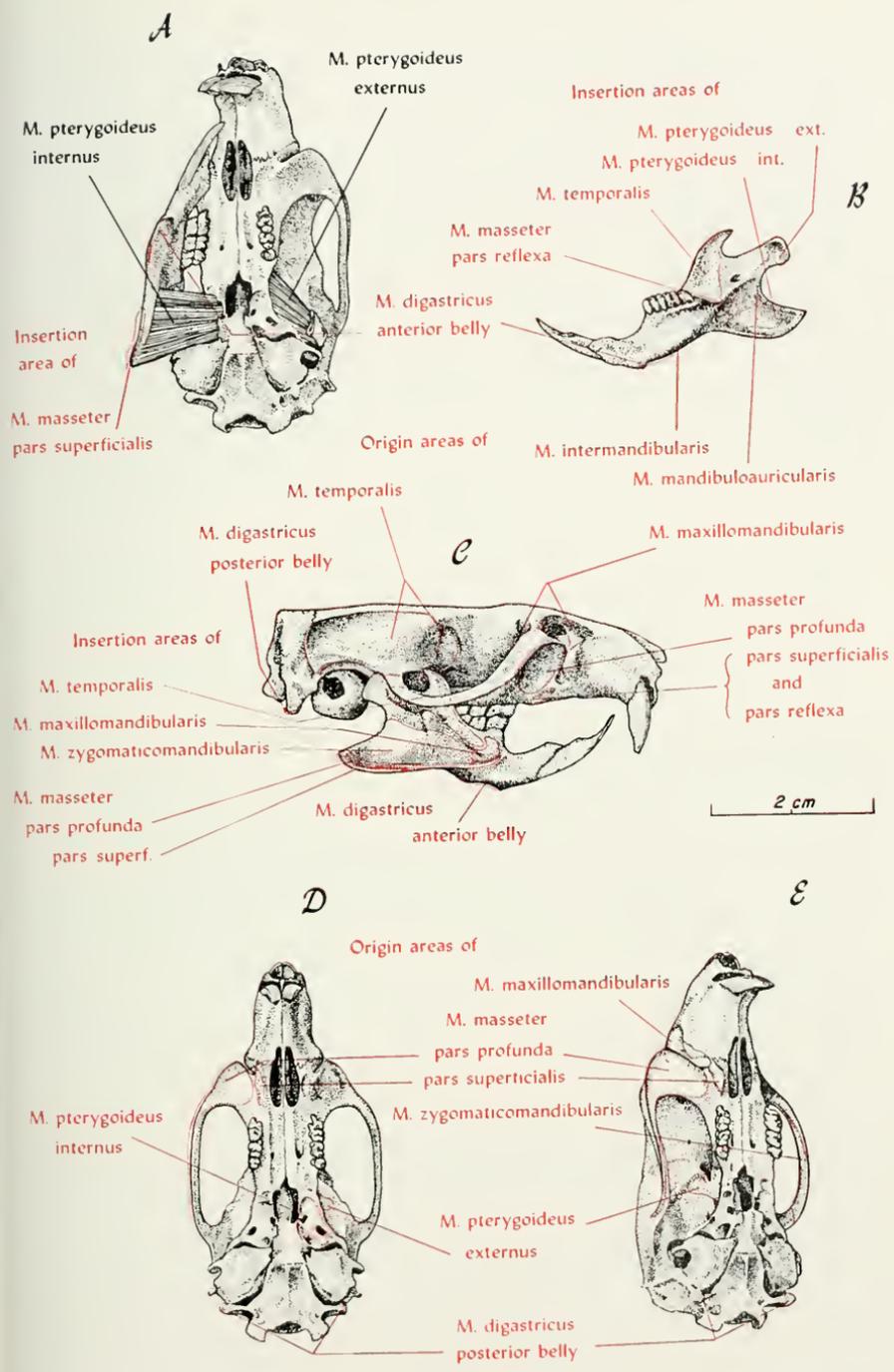
entire length. The anterior portion forms a considerable pars reflexa (fig. 29,A,B) that curves ventrally and inwardly around the lower edge of the mandible in its middle, and then ascends along its inner face to insert immediately behind the bulge for the "root" of the incisor tooth, anterior to the insertion area of *M. pterygoideus internus*.

The deep portion of the masseter, *M. masseter, pars profunda* (fig. 29,A,C) is relatively very large, surpassing *M. masseter, pars superficialis* (including both pars reflexa and pars horizontalis) in bulk. It takes its origin from the entire ventro-lateral edge of the zygomatic arch and from the antero-ventro-lateral face of the anterior buttress of the arch, beneath and in front of the orbit, and behind and beneath the infraorbital foramen. Its fibers descend nearly straight with only a slight backward inclination, fanning more toward the rear, to insert tendinously along the lower edge of the jaw onto the crista masseterica for its entire length. Its lower third is covered by the superficial masseter.

The *M. maxillomandibularis* is small but distinct (fig. 29,E). It originates from high on the medial wall of the infraorbital foramen as well as from a fine strand that extends backward from the foramen along the top edge of the anterior third of the zygomatic arch on its medial surface. The main mass passes through the infraorbital foramen, joins with the fibers that originate from the arch, and descends nearly straight downward with its fibers converging slightly and forming into a more tendinous mass. It inserts above the forward end of the crista masseterica, just beneath the first two cheek teeth at the junction of the crista masseterica with the linea obliqua. Just at the insertion, some of its fibers become mixed with some of the insertion fibers of the adjacent and deeper *M. temporalis*.

M. zygomaticomandibularis is located just behind *M. maxillomandibularis*, and slightly overlaps it superficially (fig. 29,D,E). It originates from the posterior two-thirds of the medial face of the zygomatic arch and inserts broadly above the insertion area of the deep masseter from the insertion area of the maxillomandibularis back to the posterior edge of the jaw, well below the condyle. It is a small muscle, and is fleshy throughout. Its fiber bundles are di-

FIG. 30. Masticatory musculature of *Rattus*. A, Oblique ventral view of the skull, one jaw ramus and the neck and condyle of other jaw showing *M. pterygoidei*. B, C, D and E. Skull and jaws of *Rattus* showing the origin and insertion areas (mapped in red) of the masticatory muscles. B, Medial aspect of jaw. C, Lateral view. D, Ventral view of skull. E, Vento-lateral view of skull.



rected almost directly downward to their insertion. Anteriorly it is contiguous with *M. maxillomandibularis*, though there is no difficulty in separating the two by working from their areas of origin.

M. temporalis arises from the lateral wall of the cranium and from deep within the orbital area (fig. 29,E,F). Nearly the entire area is delimited by bony crests. These are especially pronounced along the occipital and dorsal edges. (The dorsal crests are not in the sagittal plane, but are quite removed from it laterally.) Some of the more superficial fibers arise from the aponeurosis, but the origin is for the most part fleshy. The fibers converge forward and downward onto both sides of the coronoid process, and are more tendinous where they attach to its anterior edge from its apex down to the region of insertion of the *M. maxillomandibularis*. The more fleshy portions of the insertion are subequally divided between the lateral and medial surfaces of the coronoid process.

M. pterygoideus internus originates from the pterygoid fossa, anterior to the bulla (fig. 30,A). It proceeds postero-laterad to insert onto the entire inner face of the angular process. It is largely fleshy. Neither it nor the external pterygoid displays a very massive development.

M. pterygoideus externus takes origin from the lateral face of the pterygoid, from the maxillary in the region behind the tooth row, and from that part of the pterygoid that extends up onto the antero-ventral wall of the braincase (fig. 30,A). It runs outward and backward to its insertion on the internal surface of the neck of the condyle and laps up onto the joint capsule itself (fig. 30,B).

M. mandibuloauricularis (figs. 29,E; 30,B) originates from the posterior edge of the medial face of the jaw above the insertion area of the internal pterygoid, and below that of the external pterygoid, from a wedge-shaped area. It ascends to its insertion on the ear cartilage, anterior to the auditory meatus.

The anterior belly of the digastric (fig. 29,B) lies in a slightly more superficial plane than the *M. intermandibularis*, and it is entirely distinct from this small but well-formed muscle (fig. 30,B). A branch of the facial nerve escapes from between the anterior bellies on the medial side. The anterior bellies are distinct from one another in front of this point, but become increasingly fused behind. The tendency for fanning out toward the midline and for a fusion of the fibers of right and left digastric goes beyond the confines of the digastric, and involves a slight mixing with fibers of *M. mylohyoideus*. In the

main, the anterior digastric inserts onto the ventral edge of the jaw ramus from immediately behind the symphysis for a distance nearly equal to that of the cheek-tooth row (fig. 30,A,B). The posterior digastric (figs. 29,B; 30,D,E) originates from the paroccipital process and descends rapidly at first, then bends anteriorly and goes into a dividing tendon that in turn gives rise to the more antero-posteriorly-directed anterior belly.

A pair of *Mm. intermandibulares* is present (fig. 30,B). They run directly transverse between the rami, immediately behind the symphysis and meet in a midline raphe. The total bulk of the muscle is so small and a dissection separation at the raphe is so difficult that I removed both together leaving the raphic union intact, weighed both together, and entered half this amount in the weight chart. The same procedure was used in *Sciurus*.

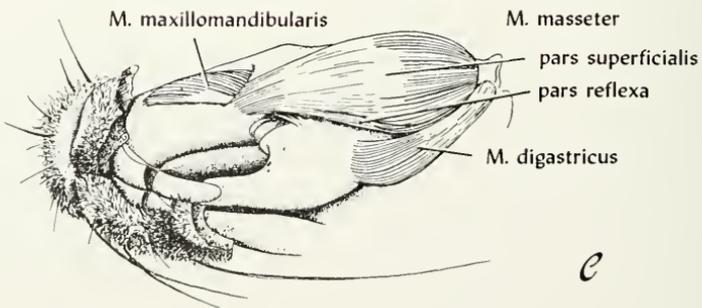
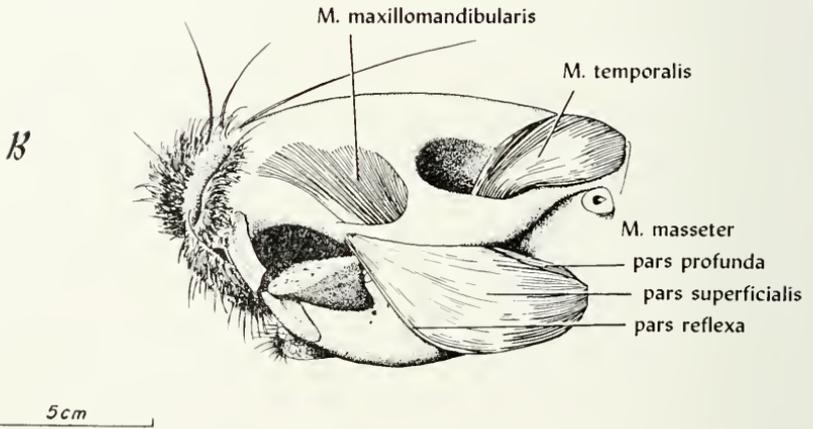
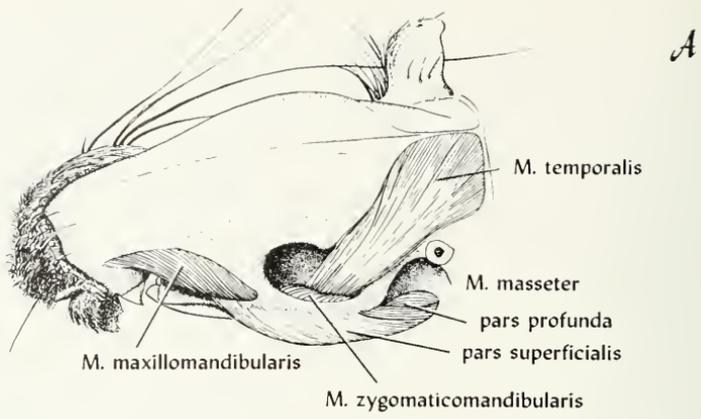
TABLE VIII.—Weights and percentages of masticatory muscles: *Rattus*

Muscle	Weight (in grams)	% with digastric and intermand.	% without digastric and intermand.
<i>M. masseter superficialis</i> (incl. pars horizontalis and pars reflexa)	0.34	17.6	18.8
<i>M. masseter profundus</i>	0.40	20.7	22.1
<i>M. zygomaticomandibularis</i>	0.12	6.2	6.6+
<i>M. maxillomandibularis</i>	0.12	6.2	6.6+
<i>M. temporalis</i>	0.59	30.6	32.6
<i>M. digastricus</i>	0.10	5.2—	—
anterior belly 0.06			
posterior belly 0.04			
<i>M. intermandibularis</i>	0.02	1.0	—
<i>M. pterygoideus externus</i>	0.08	4.2—	4.4+
<i>M. pterygoideus internus</i>	0.16	8.3	8.8+
Totals	1.93 g.	100.0%	99.9%

Hystrix sp.

Figures 31, A-C; 32, A-C; 33, A-C.

Toldt's work will serve as a starting point for my expanded description of the jaw apparatus in the hystricomorph rodents. His description of *Hystrix* (1905, pp. 57-60) is repeated below in translation, followed by a list of comments, emendations, and additions as based on my dissections of a specimen of this genus, FMNH 57212. FMNH 57170 the skull of a young adult female served for the attachment area maps and FMNH 41337 for the teeth (other specimen had diseased and damaged dentition). The drawings were made by Mrs. Maidi Wiebe Liebhardt from my sketches or photos.



Porcupine (*Hystrix cristata*). In the *M. masseter*, which while not as massive as in any of the small rodents mentioned thus far, the superficial portion forms by far the largest part of the exposed fibrous layer, and all of the molars, with the exception of the first lower, are covered by it in side view. It arises, not with a sharply delimited tendinous cord, but by means of a wide tendinous sheet that adheres to the forward part of the zygomatic arch on the lateral surface and its lower edge and continues contiguous with it, nearly straight backward from the zygomatic process of the maxillary bone. The anteriormost, thickest part of this tendinous layer arises from the underside of the maxillary, in front of the first molar and from the root of the flange of the zygomatic arch. From there on, fleshy bundles arise from the tendinous plate of the superficial portion, taking a straight course in a backward sloping direction, forming an angle of about 20° with the origin tendon. They converge on the angular process, inserting on its lateral surface and posterior edge. The few more deep-lying and backward-sloping fiber-bundles descend down toward the lower edge of the ascending ramus, spread out onto this and beneath it, to attach to the narrow surface of bone there, which extends to the back edge of the angular process. Only in the anteriormost portion of the muscle do the fiber-bundles find no immediate bony insertion, but instead form a very considerable *pars reflexa*, which curves around the bend between the body and the ascending ramus of the jaw, and ascend on the medial surface of the ascending ramus behind the forwardly directed swelling alveolus of the incisor. It reaches to the part covered by the *M. pterygoideus internus*, onto the insertion of *M. pt. externus*, and backward to the neighborhood of the posterior edge of the ascending ramus. Those fleshy bundles that originate closest to the *pars reflexa* run to the median side of the lower edge of the ascending ramus in a straight (diagonally) backward direction, to insert along this edge below the *M. pterygoideus internus* as far back as the angular process. The deep portion of the *M. masseter* arises from the entire lower edge of the zygomatic arch, in large part fleshy, and runs parallel throughout with slightly backward inclined fiber-bundles, down to the *crista masseterica*, to insert in this area and as far back as the posterior edge of the angular process. The most posterior arising parts of the deep portion run in a horizontal direction to the posterior edge of the ascending ramus, where they insert in the area above the angular process that extends up to behind the articulation process. Only in this region does the deep portion lie exposed at the surface, while its entire forward and lower part is covered by the superficial portion.

The *M. maxillomandibularis* is proportionately strongly developed (fig. 5), its flat elliptical fleshy body extends forward to the bone at the edge of the nasal opening. It arises from the lateral surface of the premaxillary and maxillary bones where it lies clearly exposed, and from the thick upper flange of the zygomatic process. It passes through the wide infraorbital foramen

FIG. 31. Masticatory musculature of *Hystrix*. A, Superficial dissection showing *Mm. temporalis*, *maxillomandibularis*, *zygomaticomandibularis* and *masseter* in dorso-lateral view. B, Lateral view at same level of dissection showing *Mm. maxillomandibularis*, *masseter* and *temporalis*. C, Vento-lateral view of superficial dissection showing *Mm. maxillomandibularis*, *masseter* and *digastricus*.

with its fiber-bundles converging from front to back, bends downward behind the lower flange of the zygomatic process and proceeds on in a strong flat tendon which inserts on the lateral surface of the lower jaw at the angle formed by the junction of the crista masseterica with the linea obliqua.

The *M. zygomaticomandibularis* appears as a powerful muscle plate (fig. 5), which arises from the medial surface of the zygomatic arch in immediate contact with the preceding muscle, together with which it forms a considerable part of the orbital wall. Its anteriormost fiber-bundles descend approximately perpendicular, the hindmost always more obliquely forward-sloping, to the lateral face of the lower jaw, where they insert along the linea obliqua. The fusion of this muscle plate with the *M. maxillomandibularis* into a uniform mass appears here to be complete, for both combine on their medial surfaces into a common tendinous plate by means of which insertion follows along the linea obliqua. The posterior end of this tendon sheet lies against the tendon of *M. temporalis*. The portion of the *M. zygomaticomandibularis* which arises from the most posterior part of the zygomatic arch is to some degree separated from the larger forward part of the muscle, in part near its origin by a gap for the passage of the *N. massetericus*, in part by its insertion also. Its entirely forward-sloping fiber-bundles lie exactly along the incisura mandibulae on the lateral face of the ascending ramus, and attach on this immediately beneath the coronoid process and partly on the edge of it, in contact with the *M. temporalis*. Both the *M. zygomaticomandibularis* and the *M. maxillomandibularis* are well separated from the deepest portion of *M. masseter*.

The *M. pterygoideus internus* is comparatively very small, composed of a superficial portion and a deep portion, the first of which is the stronger and grows downward with parallel, slightly backward-sloping fibers to the lower edge of the ascending ramus, and inserts tendinously directly above the insertion line of the superficial portion of *M. masseter*. Its posterior end does not reach the angular process. The deep portion is fused only in front with the superficial layer, and runs with slightly diverging fiber-bundles downward to its insertion somewhat above the lower edge of the ascending ramus and on the medial face of the angular process near its posterior edge.

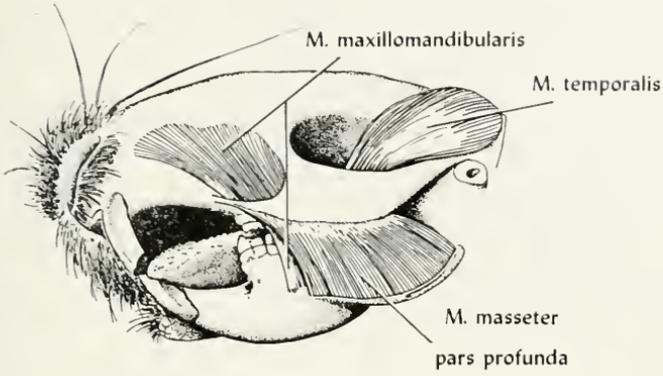
The *M. pterygoideus externus* is, in comparison with other rodents, rather powerful. It proceeds in a horizontal, slightly backwardly-inclined direction to the neck of the jaw articulation capsule, the entire medial side serving for its insertion.

Although Toldt's description is quite generally adequate, the following modifications, based on my dissections, clarify some points.

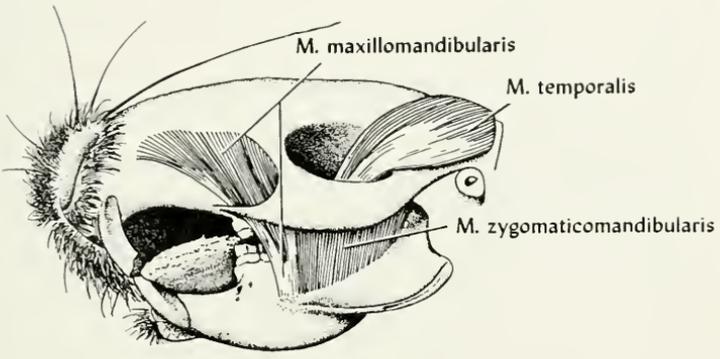
1) Anteriorly, the deep portion of the masseter is not only covered by the superficial portion, but it also fuses with it so that separation

FIG. 32. Masticatory musculature of *Hystrix* in lateral view. A, After removal of pars superficialis of *M. masseter*, pars profunda is exposed. B, The same view, but with *Mm. maxillomandibularis* and *zygomaticomandibularis* exposed by removal of *M. masseter*. C, Deep dissection showing entire masseter complex and most of the zygomatic arch removed to expose *M. temporalis* to full view.

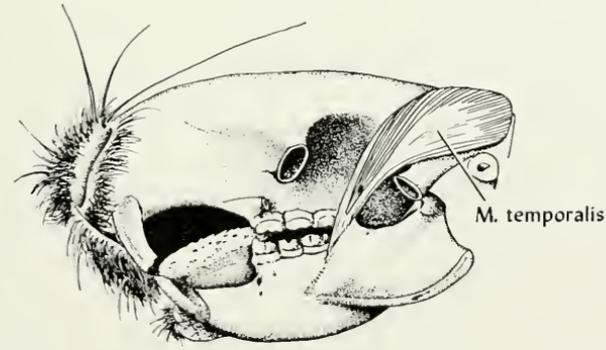
A



B



5 cm



C

of these two is difficult in this region and at best somewhat arbitrary (figs. 31,A,B; 32,A).

2) The two divisions of the superficial masseter have not been separated from one another, though they are clearly recognizable distally, because any division proximally appears to be so arbitrary as to be nearly meaningless.

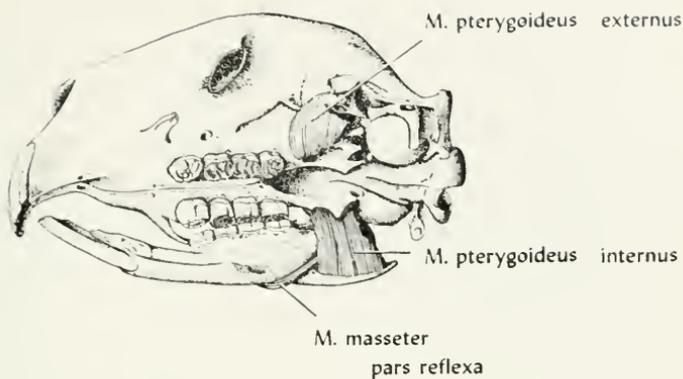
3) *M. temporalis* (not discussed by Toldt) is fleshy and originates as a relatively thin sheet from the broad temporal area above the ear and behind the eye (figs. 31,A,B; 32,C). It is thinnest near the midline, and becomes thicker laterally. Superficially, the fleshy bundles insert on a long stout tendinous plate that in turn inserts on the coronoid process. The muscle forms a very appreciable portion of the posterior wall of the orbit, and in its deep layers it arises by two tendinous bands buried within the more fleshy portions of its origin. These two tendons come off from two bony prominences located immediately behind the orbit, the anterior of which is rough and elongate, the other is but a rough hummock of bone.

4) Toldt did not give the area of origin of the *M. pterygoideus internus*. The muscle comes from a rugosity on the rim of the elongate oval-shaped foramen located immediately below and medial to the area of origin of the external pterygoid, from a region about half way from the end of the tooth row to the anterior end of the bulla (fig. 33,A). It takes its origin from alisphenoid, palatal, and pterygoid bones, from deep within this foramen, from its anterior, internal, and lateral walls, in addition to the rugosities of its rim. I did not find a division as complete as the one Toldt reported, and since virtually all the pull exerted where the muscle contracts is between the very closely placed points, I consider the muscle as a unit.

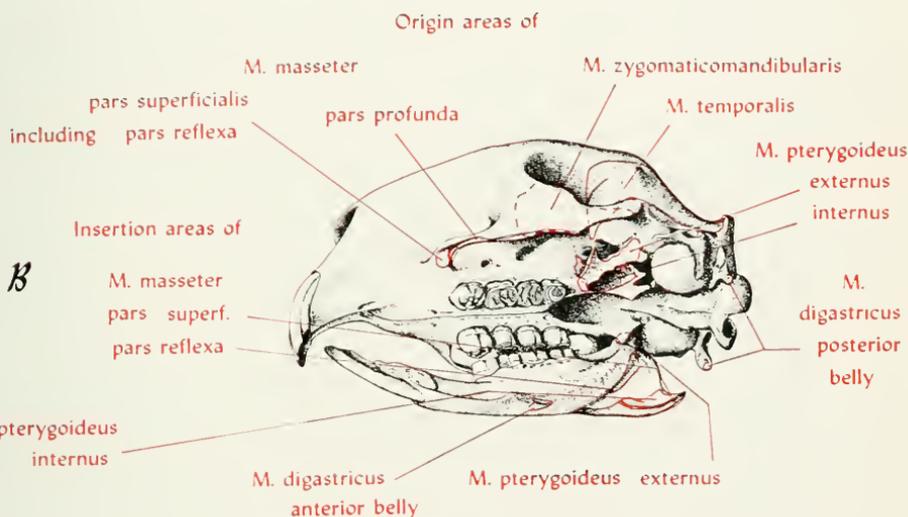
5) A very small *M. intermandibularis* is present, located immediately anterior to the insertion areas of the *Mm. digastrici* and running between the two rami. There is some tendency for its fibers to interlace rather than run parallel to one another, especially in its anterior and superficial portions. No attempt was made to include it within the table of weights and percentages as its total weight would be but a small fraction of that of *M. pterygoideus internus*, the small-

FIG. 33. Masticatory musculature of *Hystrix*. A, Vento-lateral view of a deep dissection of jaw muscles (with most of one jaw ramus removed) to expose *Mm. pterygoideus internus* and *pterygoideus externus*. B and C. Skull and jaws of *Hystrix* showing jaw muscle attachment areas (mapped in red). B, Vento-lateral view of skull and one jaw ramus. C, Lateral view of skull and jaws.

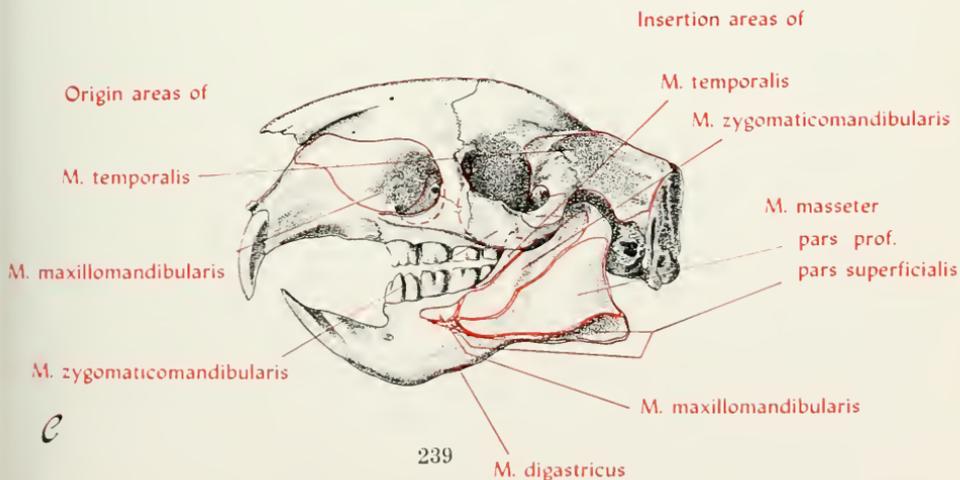
A



5 cm



B



C

TABLE IX.—Weights and percentages of masticatory muscles: *Hystrix*

Muscle	Weight (in grams)	%	% without digastric
M. masseter pars superficialis (incl. pars horizontalis and pars reflexa)	11.9	28.8	31.3+
M. masseter pars profunda	4.9	11.9	12.9—
M. maxillomandibularis	6.2	15.2	16.3+
M. zygomaticomandibularis	4.3	10.4	11.3+
M. temporalis	6.3	15.3	16.6—
M. pterygoideus internus	2.1	5.1	5.5+
M. pterygoideus externus	2.2	5.4	6.0
M. digastricus	3.3	8.0	—
Totals	41.3 g.	100.1%	100.0%

est of the muscles of mastication, and in terms of percentages, it would certainly be less than one percent of the total. One other accessory muscle is present and should be noted, though it has no function in chewing; the M. mandibuloauricularis. It is a slight fleshy cylindrical mass running from the posterior edge of the jaw about half way between the articular condyle and the apex of the angular process, and extending to the anterior face of the auricular cartilage.

Discussion and Comparisons

Assessments and Procedures

The foregoing descriptive materials provide a basis for interpretation of the generalized group and three specialized groups of mammals with respect to jaw structure and mechanism. Although there is a wealth of comparative information on cranial osteology and dentition (see appropriate columns of Table A (Appendix) and Osborn, 1907; Romer, 1945 and 1966; Gregory, 1951; Grassé *et al.*, 1955; Piveteau *et al.*, 1957, 1958, and 1961; and many others) a comparative treatment of cranial myology and function has been much less adequate. What is known is brought together in Toldt, 1905; Weber, 1927; Klatt, 1928; Bolk *et al.*, 1939; Becht, 1953; Fiedler, 1953, and Schumacher, 1961a. The full needs of comparative anatomy are therefore far from satisfied.

Table A (Appendix) shows in graphic form both what is, and what is not available. It is evident that the field has not been covered adequately for a broad systematic understanding to emerge. The basis for establishment of the three accepted specialized masticatory adaptive groups and the generalized one is made on a sampling that is drawn from only about half of the known mammalian orders, and some of these are quite inadequately sampled. To make the most out of the information available, and thereby to provide the broadest basis for comparative study there *must* be standardization. Operating on this premise, I have tried to select simple, fundamental data and mechanical units as standards that would use as much as possible of the information given in the literature. Hopefully, future workers will include comparable information in their reports, for these same data and mechanical units are requisites of any attempts to achieve broad comparative mechanics. As I have conceived them, the standards are: 1) muscle weights or mass given in per cent, which give an indication of relative muscle power (this has been one of the most consistently employed means of comparison); 2) muscle attachment maps, which provide a key to a determination of the manner and degree of utilization of available muscle forces, because much about

a muscle's structure, form, pull direction, and geometry can be deduced from them and from the surface modeling of the bone within them,¹; and 3) a formula (employing these data) for estimating the total maximum jaw-closing useful power as a method of achieving a simple and direct comparative mechanical analysis.

Other standards are not being judged, except in this broad comparative sense, and many should possibly be included in future goals. A case in point is the use of dry ash weights of muscles as superior and more reliable standards of comparison than wet weights (see Schumacher and Rehmer, 1960; Schumacher, 1961a, and others). Such a refinement is desirable, but it is not essential, and is not required here, since to do so would exclude most of the data from the literature. A great stride can be made by accepting the minimum uniform standards set forth here which encompass the broadest possible coverage that will at the same time permit a modest comparative mechanics to emerge. Therefore, in drawing upon the literature the most useful works were those that: 1) provided the broadest possible coverage taxonomically, and 2) that gave muscle weights or other data that might be directly applied to a straight-forward mechanical analysis, in preference to more intricate analyses. Works such as Stöcker's (1957) study of the masticatory muscles of *Elephas maximus*, for example, give sophisticated functional analyses which are in themselves desirable. However, they stand apart in their degree of refinement, and for comparative study are useful mainly as models and for their raw data because not enough work of such technical excellence has been done. In still other instances, fine studies such as Fiedler's (1953) broad taxonomic paper (which gives no muscle weights) have had to be almost ignored for comparative mechanical purposes because they are not applicable within the loosely standardized framework that has been most generally used by other authors, or that could be utilized here.

Many anatomists have, as an adjunct to their descriptions, given muscle mass or volume or weight data (or %) as one, often the only, fundamental basis of comparison. In a very few instances (Davis, 1955, 1964, for example) muscle attachment maps have been used, and occasionally very refined mechanical analyses have been attempted. What has not been done, and what I here do, is to assemble, augment, and integrate these data, and to extract a common

¹ Although many workers have not provided such maps, they can be made using an adequate comparative osteological collection by reference to the muscle scars. Thus one can utilize any work that provides muscle weight or percentage values.

denominator of fact in order to put this comparative study on the broadest possible base.

The muscle attachment maps, such as have been used by Davis, are fundamental data in every way equal in importance to muscle mass or weight data. Both are prerequisites for the mechanical analysis used here. When properly oriented, the attachment maps show both the working and resultant distances, and the direction and application of forces. In short, they provide the proportionately scaled portrayal of the placement, positioning, and other relationships of the functioning lever, or other mechanical systems involved. These muscle attachment maps, when combined with the muscle weight data (and with certain correction factors to account for force components which act outside of the plane of jaw-closure) give a simple (useful power) estimate of static jaw-closing mechanics.

LIMITATIONS

There are a number of shortcomings of the comparative method as employed here which are noted that their effects may be understood and minimized. These same shortcomings apply to direct comparisons of muscle weights, or muscle pull directions, as well as to any kind of an analysis of the mechanics involved which must utilize the first two. All are due to certain inter-related uncertainties about muscles generally:

1) Absolute force values (or even the range of these) are rarely known for an animal. Man is one of the few exceptions to this (see Mainland and Hiltz, 1933; Howell and Brudevold, 1950).

2) Muscle pull is not necessarily always directly proportional to muscle weight (or mass). Duyff and Bouman (1927) found that even when contracted powerfully, muscles vary considerably in their ability to exert force.¹ Further, there is no adequate way to judge the extent to which maximum contractile ability is actually put to use during normal chewing, let alone the extent to which this might vary. Nor has the significance at the ultra-structure level of the double overlap of the thin filaments from each end of the sarcomere (which must reduce the pull tension achieved) been fully studied or understood (Huxley, 1965). Still, there is evidence that in general there is an approach to direct proportionality between muscle mass and

¹ Difficulties with this sort of test lie in the fact that while actual resultant forces are readily measurable, the true effort forces rarely are being governed by difficult-to-measure (if not by unmeasurable) factors such as tension, motivation, fatigue, pain, etc.

force and that this is a reasonable first approximation of the actual condition. That assumption is implicit in the mechanical treatment in this work.

3) Muscles, of course, take quite different forms (i.e., some are cylindrically straight with parallel fibers, others are fanning sheets, some pennate, etc.) all of which give different force values per muscle mass. The simplest, straight, and compact ones are the easiest to assess mechanically. Fanning sheets of muscle, with pull forces applied in a variety of directions are more complex, and in the cases of broadly fanning sheets wherein the pull is in quite divergent directions, an averaging of these gives only the crudest sort of an idea of the direction of application and amount of force possible during powerful contraction.¹ Pennate muscles usually tend to have tendon cords or bands upon which forces become concentrated for their application. Other types have their own peculiar characteristics each of which must ideally eventually be considered. As yet I have not been able to refine satisfactorily correction factors to compensate for these possible errors which remain "built in" in the efficiency formula. One compensatory adjustment which has been consistently made is an estimate of the point of action for each muscle mass. This has been selected according to a muscle's cross-section, and its average pull-direction vectors, and not merely by using the midpoints of its attachment fields.

4) Knowledge of the neurological patterns of triggering and firing of muscular nerves, and the subsequent contraction of muscle fibers is another area wherein our general knowledge is weak. Electromyographic studies by Swinyard *et al.* (1953), Carlsöö (1956, a, b), and Basmajian (1959) among others give insights into these aspects, but at present there is no way to assess whether any particular muscle acts at once, by a wave of contractions, or in some other manner, except in a very few instances for man and a few laboratory animals. For the present the mechanical analysis must assume average, overall, simultaneous contraction for each muscle. This could well be the most important limitation to comparative studies—especially to those of a comparative mechanical nature.

¹Furthermore, during lesser contractions, and perhaps even during powerful ones, whole portions of a muscle may be relaxed, and not utilized at all, which could not only alter the total resultant force, but could also drastically change the direction of pull. My efficiency formula (p. 270) takes no account of this possibility, but rather assumes for the present that the conditions of total contraction apply during powerful closure of the jaws.

5) The length of muscle fibers varies. It has long been known that long-fibered muscles provide speedy action with relatively the greatest power available in the fully extended condition, and that they usually operate over considerable distances. Short-fibered muscles, on the other hand, provide powerful forces, but only over short operating distance spans. At this stage, it did not seem feasible to attempt to work out the possible permutations and combinations, and to attempt to account for this variable. Thus there is no factor for it in the efficiency formula.

6) The relative amounts of contractile and noncontractile tissue of muscles varies. Superficial fascia and fat are readily removed upon dissection, but such tissues which do no contractile work, often are not readily measured when incorporated within a muscle or its tendons and ligaments. There is no accounting for them in the formula either. Mollier (1937) has made a detailed study of some of these aspects.

7) For the vast majority of mammals, we do not know much about how the jaw muscles are used. The extent of antagonistic and protagonistic action, and even the extent and degree of unilaterality, is generally poorly known, although some reasonable assumptions can be made. MacMillan (1930) discussed unilateral vs. bilateral balanced occlusion, and concluded that unilaterality is the rule, but the matter is not quite as simple as he stated it, for he did not attempt a really comprehensive coverage of the mammalia.¹ More recently, Ardran *et al.* (1958) and Ride (1959) have used cinematographic and cineradiographic techniques to record and study actual jaw movements in domestic rabbit and *Protemnodon rufogrisea*. If more of this sort of work were to be done with a wide variety of mammals an important advance in our knowledge of comparative masticatory adaptation would result.² My formula has no factors for any of these uncertain variables, but I generally think of unilaterality as the rule.

8) Muscles vary in their vascular supply, and hence in fatiguing and recuperative speed (see Duyff and Bouman, 1927). As yet there is no factor in the formula to correct for this variable. Still, it should not be lost sight of, and it may someday be possible to correct for it.

9) Weight measurement errors of the muscles of the smaller mammals especially, and desiccation during dissection are each errors which cannot be accounted for in the formula. Both of these short-

¹ He considered directly a canid, a bovid, an equid, a rabbit, and an elephant in comparison with man. From the literature he expanded his considerations by adding representatives of Sciuridae, Tapiridae, and Artiodactyla to the list.

² Hiemae (pers. comm.) has recently employed the technique effectively using *Rattus* and *Didelphis*.

comings have been minimized by using care and repeated and frequent soaking of the specimens in their preserving fluids whenever work was being done, and by working quickly when making the weight measures. It is felt that this does not constitute a serious drawback.

After contemplating this list of the known uncertainties regarding muscle activity—and realizing that there are probably others—one might well question the practicality of attempting a functional analysis in the face of such an array. Actually, the situation is not quite as bad as this implies, because some of these are quite certainly relatively minor considerations which will not alter results in any major way. Others were mentioned so that the need for correction factors to account for them could be kept in mind and adjustments made as soon as the necessary information becomes available. Furthermore, one can only work with the information presently available, and I think that enough is known to permit our comparative studies to be extended to the mechanical level by means of the useful power formula. Doubtless, direct muscle comparisons such as have been employed prior to this work will remain as valid first bases of comparison, although most of the uncertainties listed here apply equally to them, too. Just as such comparisons are of value in our understanding of the diversity of the masticatory apparatus of mammals, so, too, will the comparative mechanics be useful, I believe. As it is used here (p. 270), the formula incorporates muscle mass (as a measure of potential effort force) and the geometry of the operative lever arms (as the simple mechanical system). These are the major variables, and, in addition, the formula incorporates certain correction factors in order to compensate for power loss resulting from imperfect muscle alignments, but it is not refined beyond this level.

The stimulating work of Gans and Bock (1965) brings a fresh and sophisticated approach. They make a theoretical analysis of the functional significance of muscle form—an approach that may eventually lead to a considerably improved understanding of fundamentals. Hence, their approach brings promise of future refinements in my formula by providing additional correction factors. Several aspects of their work apply to many of the limitations discussed here.

COMPARISONS

Having assessed the most pertinent considerations relating to a broad comparative treatment, and having at hand detailed discussions and descriptions of the masticatory apparatus for at least one

representative of each of the major successful mammalian adaptive groups, we can now make comparisons. Tables X - XIII and the graphs (figs. 34-37) combine all of the acceptable¹ jaw muscle mass (or weight, or volume) data from the literature with the new data given here. The tables and graphs extend the comparative studies of Becht (1953) and Schumacher (1961a) by including a broader taxonomic spread.² I have standardized the entries and have included, when known, such information as age group, sex, side examined, number of specimens sampled (N), range and confidence limits (where sample size makes these pertinent), in order to make clear the basis and significance of each entry. Appended to Table X (as part B) and the graph (fig. 34), which pertain to the forms of the Generalized Group, are the few miscellaneous forms that have been studied and reported upon. These are the only ones from this subcategory for which adequate comparative data have been given.

The tabulations (Tables X - XIII) are standard enough that they require no general comment.³ The graphs for each of the adaptive groups, by virtue of the method of interconnecting the adjacent (systematically ordered) comparable entries, form patterns that point up quite strikingly any hyperdevelopment of one muscle group within any single genus or species relative to the others. At the same time, and equally effectively, these patterns show the related compensatory reaction(s) by the other muscle group(s) that is(are) responsible. This results, of course, from the use of a closed system of percentages for the jaw-closing musculature, whereby any one change has to be

¹ Much of the data from other sources had to be interpolated because different muscle designations, or muscle divisions, or muscle groupings were used by the several workers. Wherever possible these data have been made comparable to the rest; in instances where no reasonably clear-cut resolution could be arrived at the data had to be excluded. All such changes are indicated in footnotes to the tables and graphs. All data are presented as percentage of the adductor musculature (both tables and graphs). The tables also give percentages (in italics) for the total jaw musculature wherever possible.

² These tables give greater detail (especially muscle subdivisions) than Becht's, and they utilize more of the information from the literature. Schumacher's work is meticulously detailed, but he chose to include only data from his own dissections within his tables, so again these tables and graphs are the more comprehensive.

³ After this was in press two rather neglected, important works became available, Kuhlhorn (1939) and Fabian (1925). Both give muscle weight data which adds significantly to the coverage of the Mammalia, and I have added this information to Tables X-XIII. This data does not enter into the discussions, or in a major way into the associated graphs. In general, there is sufficient agreement between the new entries and the older ones, that no major changes or regroupings seem to be required. The jaw muscle proportion data for the kangaroo correlates well with its way of feeding, and with that of other browsers and grazers, hence placement in Specialized Group II.

offset (compensated for) elsewhere in the system (i.e., percentage total must always be 100%). The advantage to such a graphic presentation is that a mirror image pattern of the lines in the graph tends to result, an effect which greatly facilitates seeing the general trends of changes as well as the major compensatory (not biological compensation—see above) reaction(s). The Specialized Group I forms show this mirror image pattern in its clearest and simplest expression (fig. 35) because most of the compensatory changes are made by but one muscle group. Comparisons of overall graphic patterns from one adaptive group to another also are aided by this visual method, with the result that some of the fundamental differences may be instantly recognized, and in fact become a part of the differentiation and characterization of the groups.

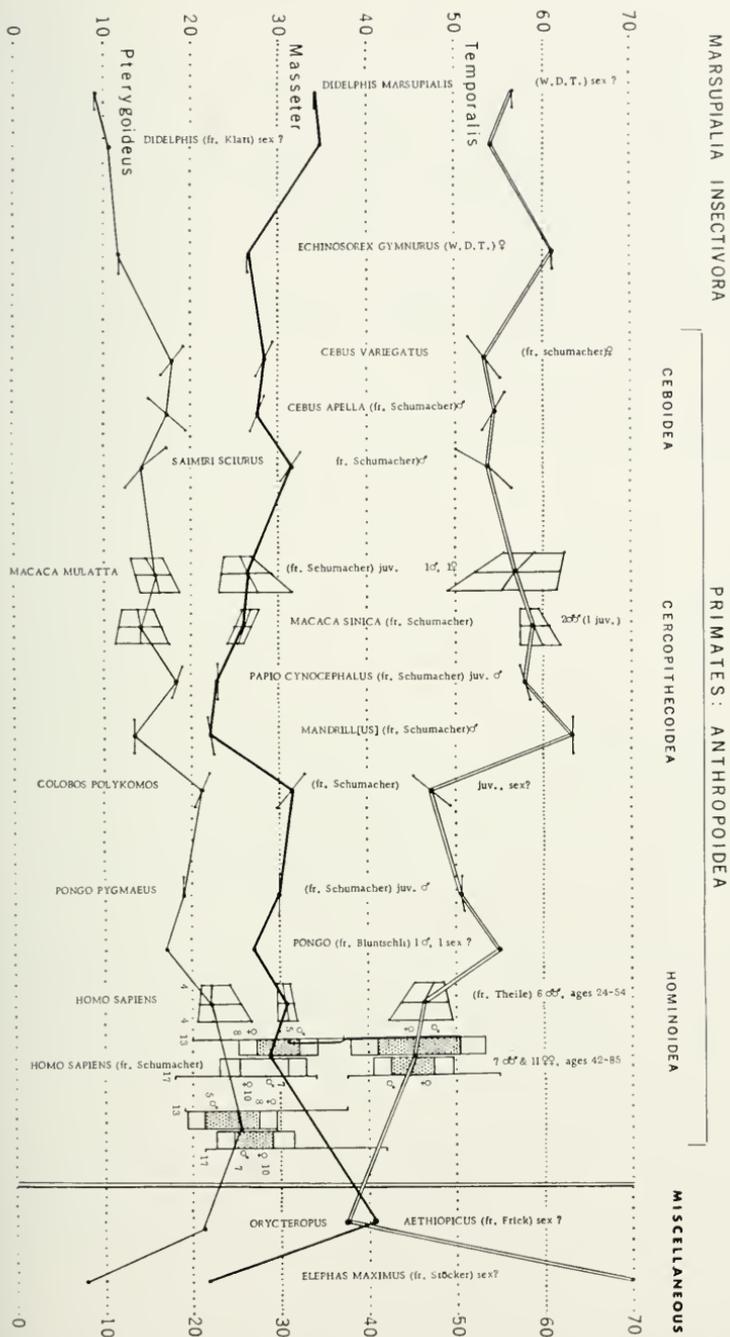
GENERALIZED GROUP

This group, containing those living forms (*Didelphis* and *Echinosorex*) which on both paleontological and morphological grounds represent a very close approach to the phylogenetic stem groups of the higher mammals, can be characterized in a variety of ways. First is the relative importance (to judge by mass) of the major jaw-closing muscle groups, based upon a comparison of the mean values for each taxon (Table X, fig. 34). These are summarized as follows: 1) Temporalis Group is dominant and generally amounts to over 50% of the total, with a range of 45 to 60%. It is in the upper (55–60%) region of this range for the more primitive and generalized members of the lot. 2) Next in importance is the Masseter Group, which usually

FIG. 34. Graph showing the relative proportions of mass of the various jaw-closing muscle groups in percentage, for forms belonging to the Generalized Adaptive Group. Represented are Marsupialia (Didelphoidea), Insectivora (Erinaceoidea), and Anthropoid primates (Ceboidea, Cercopithecoidea, and Hominoidea). Included as an appendage at the end are the few representatives of the miscellaneous category (with respect to adaptive groupings).

Key: Scales given on the edges are in percentage. Single points located in the central position, with respect to the line of any taxon, represent the mean value of that measure or the only value known. These means or values for each muscle group are interconnected from taxon to taxon by coded lines. Whenever the side (or sides) dissected has (have) been reported, the entries are accordingly offset to left or right from the center line for that taxon. When the sex is known, it, too, is indicated on the graph. Dot-sized tick marks connected by a vertical line show individual entries and their range where a sample of two or more is available. Open rectangles indicate one standard deviation from the mean and the contained stippled areas show the 95% confidence interval for the mean (a modified Dice-Leraas diagram). The *M. Pterygoideus* Group entries for *Homo sapiens* are offset to avoid a confusing overlap with those of the *M. Masseter* Group. The graphs (figs. 34–37) do not include data from Fabian (1925) and Kuhlhom (1939) which were added to the corresponding tables (X–XIII) in press.

GENERALIZED GROUP



amounts to about 30% of the total jaw-closing musculature, with a range of 22-35%. Again it is in the upper region of the range for the more generalized animals of the group (27-35%). 3) The Pterygoideus Group trails in importance among the jaw-closing muscles in that it is consistently the smallest, usually amounting to less than 20% of the total, with a range of 9-26%, being at the low end of this range in the more generalized forms (9-12%).

The second and equally important means of characterizing the group is by comparison of its relative jaw muscle development pattern with the corresponding patterns in the Specialized Groups. Discussion of these broader (intergroup) comparative aspects is deferred for they will be handled in subsequent sections of the work devoted to treating in turn each of these adaptively Specialized Groups in relation to the Generalized Group, and in other sections devoted to intergroup comparisons between the Specialized Groups.

The third and different sort of manner of characterization of the Generalized Group is one dealing with intragroup comparisons of the degree of jaw muscle development, from taxon to taxon within the group. These variable intragroup relationships are represented by changes and trends seen in the extent and manner of development of the mirror image pattern on the graph (fig. 34—discussed above). For the Generalized Group, in moving from taxon to taxon, it appears that the Pterygoideus and Masseter muscle groups share in the compensatory response which offsets the variably developed Temporalis Group. However, one can also see that this results, in large measure, from the fact that the representation of the group is so completely dominated by the Primates.¹ If one excludes the higher Primates and looks at that section of the graph pertaining to the less advanced members of the Generalized Group, the Marsupialia, Insectivora, and Ceboidea representatives, this tendency disappears. Therefore, the trend for the Pterygoideus and Masseter groups to share in the compensatory response to the Temporalis Group changes may be more a characteristic of the Cercopithecoidea and Hominoidea than a characteristic of the entire Generalized Group. The latter may perhaps be best characterized as showing a variable and irregular pattern as regards which muscle group (Masseter or Pterygoideus) is involved in these compensatory responses, with, however, the developing tendency for both muscle groups consistently to come to share

¹ In fact, the Order Primates is the only well represented one in the Generalized Group (see Schumacher, 1961a), and its representation is solely by the more advanced superfamilies.

the compensatory response within the higher Primate segment of the group.¹

The jaw-opening musculature (M. digastricus and various associated or derived muscles) should be included in any comprehensive treatment of the masticatory apparatus. It has not been as consistently treated as has the jaw-closing musculature because many students have been concerned exclusively with the jaw-closing functions and not with total jaw movements. Enough is known, however, to define limits for the digastric for the Generalized Group at between 4 and 8% of the total jaw musculature.

Now that some distinguishing features of the Generalized Group have been set forth, and without anticipating the comparisons between this group and each of the three adaptively Specialized Groups which are to follow, it may be well to note again that each group does have its own very distinctive characteristics.

The characteristics that mark the Generalized Group are morphological features that are intermediate between those of the other groups. However, they are much more like those of one of the Specialized Groups (Group I—"carnivore-shear" group) than those of the others.

To facilitate comparisons between groups, the same system of presentation of detailed data will be followed for the various Specialized Groups as has been used here for the Generalized Group. Also a short summary, key characterization of each of the Specialized Groups, will precede the more detailed account, so that the primary criteria characterizing each may be easily singled out.

SPECIALIZED GROUP I—The "carnivore-shear" or "scissors" type

In this, the most studied of the groups, there are many parallels with conditions in the Generalized Group. Outstanding is the fact that the Temporalis Group musculature is also characteristically extensively developed (see Klatt, 1928; Becht, 1953; Davis, 1955;

¹ Speculation as to the significance of this tendency in the Primates is tempting. Perhaps the tendency results from putting the dentition and, even more importantly, the masticatory musculature to other uses besides the usual food gathering and processing ones—uses that in turn make their own other demands. Activities such as fighting, assuming upright posture, grooming, and vocalizing, none of which is unique to the higher Primates, of course, come immediately to mind in this regard. It may be that in addition to (or corollary with) possible changes in food, the degree to which the advanced Primates have shifted the functioning of that apparatus which is fundamentally a food gathering and processing one, to one that also serves these other functions is the key reason for this trend. Various pertinent aspects of this are discussed by DuBrul and Sicher, 1954, and DuBrul, 1958.

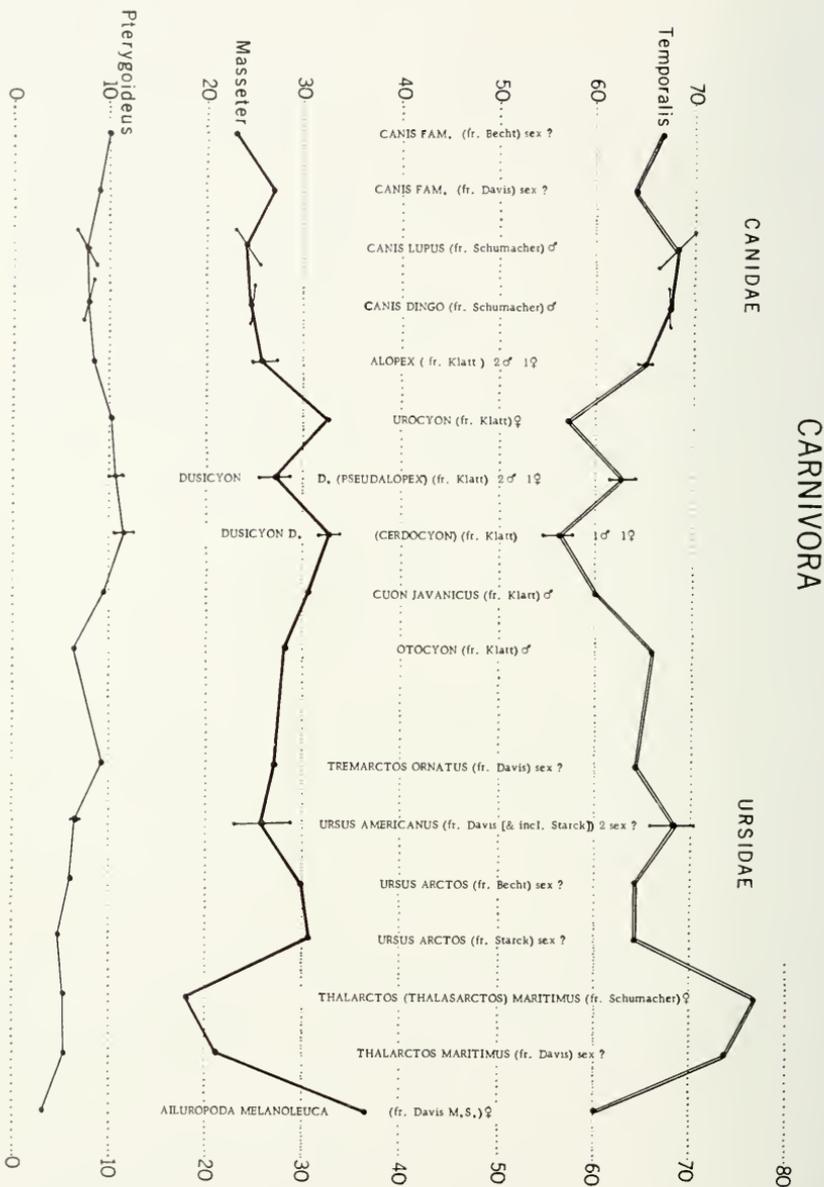
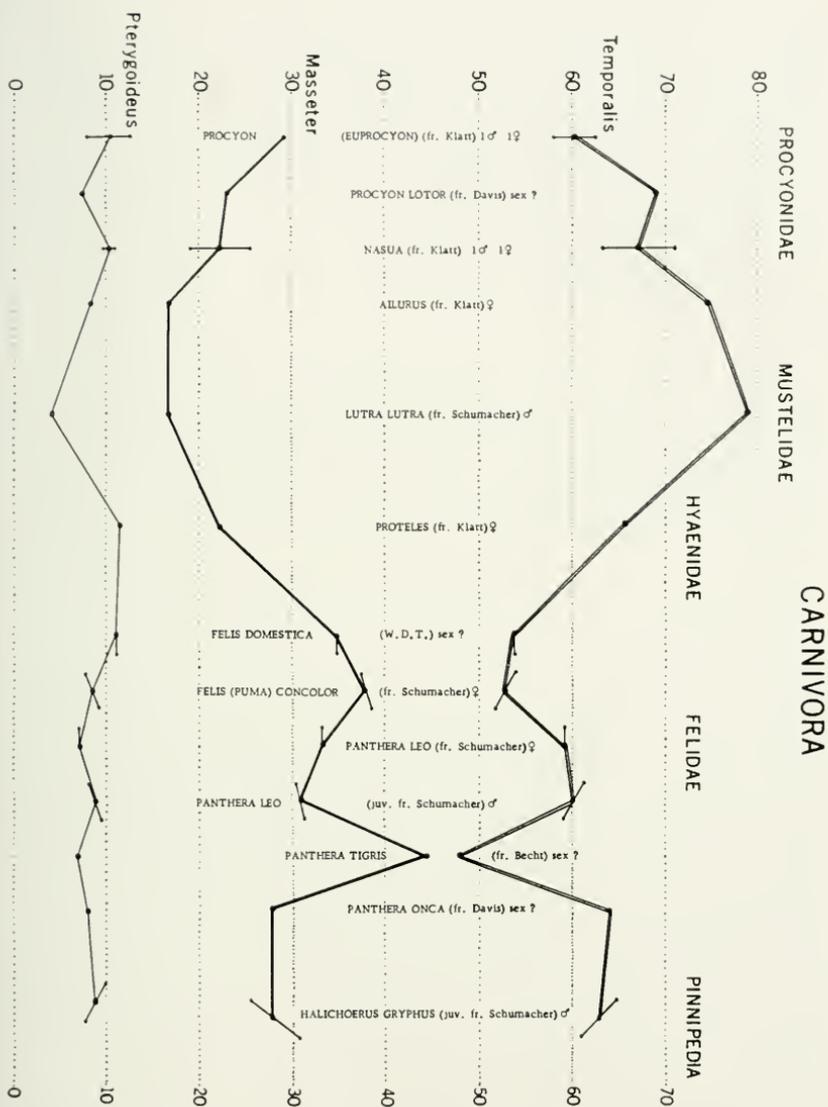


FIG. 35. Graph showing relative proportions of mass of the jaw-closing muscle groups expressed as percentage for the Specialized Group I "Carnivore-shear" forms. Represented are six families of Fissipedia (Canidae, Ursidae, Procyonidae, Mustelidae, Hyaenidae and Felidae) and one of the Pinnipedia (Phocidae).



Key: Scales given on edges are in percentage. The midpoint values for each jaw-closing muscle group are interconnected by lines coded as in Figure 34. The caption to Figure 34 also gives notations that apply here. Scapino (personal communication) has as yet unpublished, comparable data for seven mustelid genera. These do not appear in the graph or in Table XI.

Schumacher, 1961a; and in this work Table XI and fig. 35). Here the degree of development is so marked and apparent a condition that it has long been noted. Also, more students have studied the masticatory apparatus of the carnivores than in most other groups, so that the representative taxonomic spread is quite broad.

The detailed summary of those features that characterize the group follows, beginning as before with an assessment of the relative importance of the jaw-closing muscle groups as the first consideration: 1) The Temporalis Group is decidedly the dominant one, and it usually amounts to about 64% of the total. The full range is from 53%¹ to 79%, and well over two-thirds of the individuals fall within the 58% to 70% range. 2) Consistently next in position of dominance is the Masseter Group, which amounts to about 28% of the total of the jaw-closing musculature on the average. The range for this group lies between 17% and 38%,¹ and within this range over two-thirds of the individuals are found between 23% and 33%. 3) The Pterygoideus Group trails with an average of about 8% of the total. Its range of variation is quite a narrow one being from 3.6 to 11.7%, although in terms of its variation in proportion to its own size scale it is comparable to the other groups.

Comparisons of the adductor musculature of the Specialized Group I forms with that of the Generalized Group show basically that the pattern and ranking are the same, although the degree of development of the Temporalis Group is more extreme and the Pterygoideus Group is more reduced. There is no tendency either for any change in the order of ranking, or for any two of the muscle groups to approach one another in degree of development. These last conditions are well displayed by comparison of Figures 34 and 35. It will be noted, too, that Figure 35 shows the mirror image pattern between the Temporalis and Masseter Groups; the Pterygoideus Group being reduced to such an insignificant proportion of the total that almost no opportunity for the amount of variation necessary to compensate for changes in the Temporalis Group is left for it. Thus, Pterygoideus Group reduction is seen to be of equal significance in characterizing the Specialized Group I forms, as is extensive temporalis development, although it is generally not so credited.

¹ Becht's recordings for *Panthera tigris* are, I suspect, not comparable. Forty-eight per cent for the Temporalis group appears to be an unduly low value, and 45% for the Masseter group seems to be proportionately too high. It is possible that he interpreted and recorded part of the M. Temporalis as M. Zygomatico-mandibularis. This would cause the switch of a significant fraction from the Temporalis group to the Masseter group.

Intragroup comparisons of Specialized Group I show only a few trends of interest. The canidae, ursidae, procyonidae, mustelidae, and hyanenidae all show quite similar patterns in the degree of variation from one taxon to the next. The ursids show the most consistent degree of reduction of the Pterygoideus muscle group of the lot. That family and the mustelidae, to judge by its single representative here (*Lutra*), show the greatest compensatory reduction of the Masseter Group in correlation with the great development of the Temporalis Group. The felidae tend to have a relatively large Masseter Group development and correspondingly a lesser Temporalis development.

The jaw-opening musculature in the Specialized Group I forms varies between 7.5 and 14% (but is generally about 10%) of the total of the entire masticatory musculature. This represents between 50 and 100% average increase over the proportions for the Generalized Group, but there are a number of exceptions that do not conform to this average trend.

SPECIALIZED GROUP II—The “ungulate-grinding” or “mill” type

In this Specialized Group, in spite of rather limited representation, enough is known that we are able to see a number of significant features which serve to characterize it (see Becht, 1953 and Schumacher, 1961a, as well as Table XII and fig. 36 in this work). The most striking of these are the differences in relative proportion to be seen in the ranking of the jaw-closing muscle groups. Here, in contrast with the conditions in the Generalized Group and in Specialized Group I, the Masseter muscle group exhibits a decided tendency to be the dominant one (at about 50% of the total). The Temporalis Group is generally far removed from a position of dominance, being either about equal to the Pterygoideus Group, or smaller than that group (sometimes much smaller). The Pterygoideus Group averages quite high (at very nearly 30% of the jaw-closing musculature), but it is surpassed (i.e., on the graph, is crossed) by the Temporalis Group in four taxa (fig. 36). Perhaps the best quick characterization of the group (in addition to Masseter dominance) is by this crossing over, and by the co-ordinate fact that no muscle group consistently gains a position of overwhelming dominance.¹

¹ Here masseter maximum is 60%—in the other two Specialized groups the maximum for the dominant muscle group is commonly 70% and occasionally approaches 80%. In the Generalized Group although the dominant muscle group seldom exceeds 60% it rarely falls below 50% so that consistency characterizes it.

In greater detail the Masseter muscle complex is quite consistently dominant. The only exception (*Camelus*) is suspect, and will only become less so when a better Tylopoda representation becomes available. The masseter averages nearly 48%, with a range extending from 30 to 60%. (The drop to 30% is the *Camelus* entry.) No marked tendency for clustering at any level is apparent. The Pterygoideus Group ranks second on the average, although it is surpassed by the Temporalis in four of the eight genera (albeit only marginally in three instances), and in one instance where it ranks higher it only slightly exceeds the Temporalis Group. This is due, not so much to its own variability as it is to that of the Temporalis complex. The Pterygoideus Group averages 27% with a range of 23 to 40% and all entries but one are between 23 and 32%. The Temporalis Group varies so greatly, by a factor of about 3 $\frac{1}{2}$, that its average of 24% can have little meaning taken by itself. The range for it is 13 to 44%, with some tendency for a clustering in the middle segment between 23 and 31%.

Intergroup comparisons with both the Generalized and the Specialized Group I forms are striking because the significant shift in relative importance between Masseter and Temporalis complexes is so marked. This contrast, long noted between the forms of Specialized Group II and those of Specialized Group I, is almost as striking between the Specialized Group II forms and those of the Generalized Group. (Although since the latter has not received common recognition it, of course, hasn't been compared.) Also, other at least partially dependent, but less pronounced, differences exist. For example, Pterygoideus development is more pronounced in forms of this group than in either Generalized or Specialized Group I forms. Yet it is more comparable with Pterygoideus development within the Generalized Group than it is to that of the latter, which shows specialization of the Pterygoideus complex trending in the opposite direction (reduction). Another example of a dependent difference between the forms of this Specialized Group and the other two groups is in the nature of the compensatory adjustments made by the lesser muscle groups in response to the dominant one. Here the two minor muscle groups, instead of tending to share the compensatory response as is the case with forms of the Generalized Group, or having one take over almost completely as is the case in the Specialized Group I forms, show considerable variation in their responses. The mirror-image pattern demonstrates this, for it is less clear cut. Sometimes one, sometimes the other, and sometimes both together do the com-

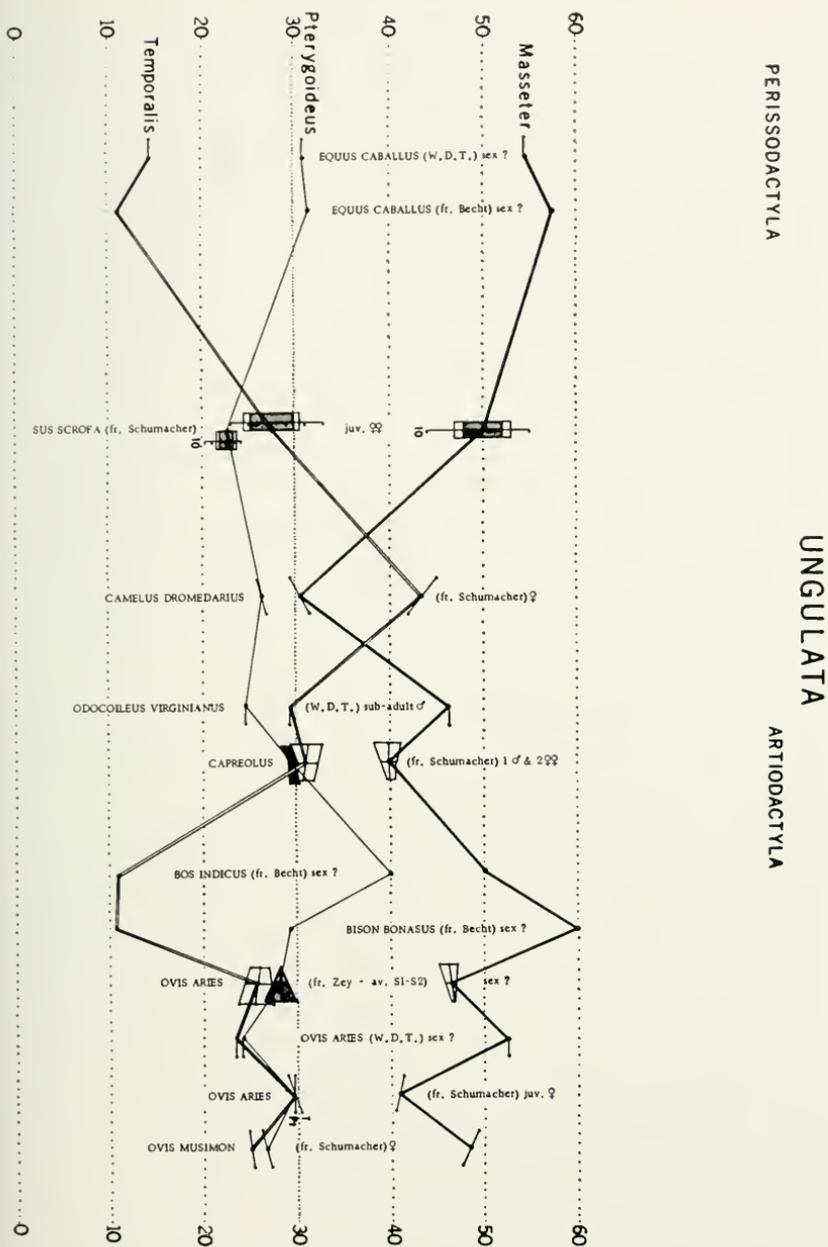


FIG. 36. Graph showing relative proportions of mass of the jaw-closing muscle groups in per cent for the Specialized Group II "ungulate-grinding" forms. Represented are one Perissodactyl family (Equidae) and four Artiodactyl families Suidae, Camelidae, Cervidae and Bovidae. For key to notations, see caption to Figure 34.

pensating. Hence there are crossovers at various positions on the graph (fig. 36), features of the pattern that do not occur in the other groups (figs. 34, 35).

Intragroup comparisons of jaw muscle development are restricted by the limited sampling of those taxa known to belong to the "mill" type Specialized Group. For the Perissodactyla, only for *Equus* has the jaw musculature been dissected and weighed. Such poor representation militates against making generalizations about that order. One can merely note that in *Equus* the jaw-closing muscle groups are about as widely spaced as are any on the graph and are thus as clearly separable from one another as are those of any of the "mill" type forms. This separation is achieved with the masseter complex dominant at about 56%, the pterygoideus ranking next at about 31%, and the temporalis at about 13% (fig. 36). Within the Artiodactyla (i.e., all of the other taxa shown in fig. 36), where representation is somewhat improved, the masseter complex varies between 30 and 60% of the total of the jaw-closing musculature, and except for *Camelus* is in the 40 to 60% range. Even here the representation is far from ideal as there is only a single representative each for Sui-formes and Tylopoda, and there are but two representatives of the cervoid branch of Ruminantia. Within this broad segment of the Artiodactyla, the Temporalis Group exceeds the Pterygoideus Group by from 2 to as much as 18% of the total of the jaw-closing musculature. In contrast to this, for the remaining taxa which are in the bovoid division of the Ruminantia, the Pterygoideus Group again (as in *Equus*) ranks second to the Masseter. In them it ranges from about an equal degree of development with that of the Temporalis Group (at 25 to 30% of the jaw-closing musculature) up to nearly four times that proportion (at 40% for *Bos*, where Temporalis Group is down to 11%). Thus, for the Specialized Group II forms as a whole, as can be seen in the irregularities of the mirror-image responses of the minor jaw-closing muscles to the dominant Masseter complex, there is little consistency as to which of the minor ones makes the compensatory response; sometimes both share in this, and sometimes one or the other even joins the dominant group and thereby opposes the reciprocating one.

The jaw-opening musculature of the forms within Specialized Group II shows a very uniform degree of development. It varies only between 5 and 7.4% of the total jaw musculature for those forms for which a record of its mass has been made known. This represents most of the same major taxa as are represented by muscle mass data

for the jaw-closing musculature, although it does so with a less consistent coverage at the generic level. The most serious omission results from the fact that the Typopoda are unrepresented since no weight or mass data is given for *M. digastricus* of *Camelus*.

SPECIALIZED GROUP III—The "rodent-gnawing" or "anterior-shift" type

This, the last of the three well-recognized, adaptively specialized groups, is represented by a systematic coverage that is at the same time both fairly broad but relatively very thin at the general level (see Becht, 1953; Schumacher, 1961a, and this work, Table XIII and fig. 37). It is the most highly specialized of the lot in terms of the modification of the jaw musculature (Wood, 1955, 1959, 1965). The masseter complex is again dominant, as in Group II, but here this dominance is quite complete. With an average of 66% of the total of the jaw-closing musculature, and a range of 55 to 77%, the masseter complex so overshadows the other muscle groups that nothing else is needed as a means of briefly characterizing the forms of Specialized Group III, although the well-defined compensatory mirror image pattern (fig. 37) is noteworthy, too.

Nothing of significance in the nature of added detail can be offered at this point concerning mass of the dominant masseteric muscle complex. However, for the secondary muscle groups, the averages and ranges for each (which are very similar to one another) are informative. The Pterygoideus Group average is very slightly the higher of the two, at 18%, with a range of 12 to 28%. The temporalis is nearly 17%, with a range of 7 to 29%. Neither is consistently in the second-ranking position, and there is a strong tendency for one by itself, or the other by itself, to provide the reciprocal response to fluctuations of the masseter complex. This can be seen in the mirror image pattern in the graph (fig. 37).

Intergroup comparisons show this specialized group to have a closer similarity to Specialized Group II than to either of the others, in that the fundamental shift from a dominant temporalis muscle group to a dominant masseter muscle complex is accomplished by both. They also show a similar degree of alternation in rank among the minor muscle groups, i.e., these two muscle groups cross over one another on the graphs (figs. 36, 37). There the similarities end; the overwhelming dominance of the masseter complex in Specialized Group III is a notable distinction that has already been mentioned. Also, in the degree to which one muscle group outshadows the other.

Specialized Group III corresponds most closely with Specialized Group I, where, however, it is the temporalis instead of the masseter complex that is so hypertrophied.

In the area of intragroup comparisons within Specialized Group III, the Lagomorpha are distinguished by a decided outranking of the temporalis muscle by the pterygoideus. The converse situation holds for the Myomorpha. The Sciuromorpha and Hystricomorpha are alike in being intermediate between the others, and in having these two muscle groups so nearly equally developed that neither consistently outranks the other, hence the crossing over of the lines representing the proportions of these two muscle groups (fig. 37).

The relative percentage of the jaw-opening musculature is not known for the Lagomorpha, but again as for the forms of Specialized Group II, most other major taxa have some representation. Values ranging from 4.4 to 9.2% are reported.

SUMMARY

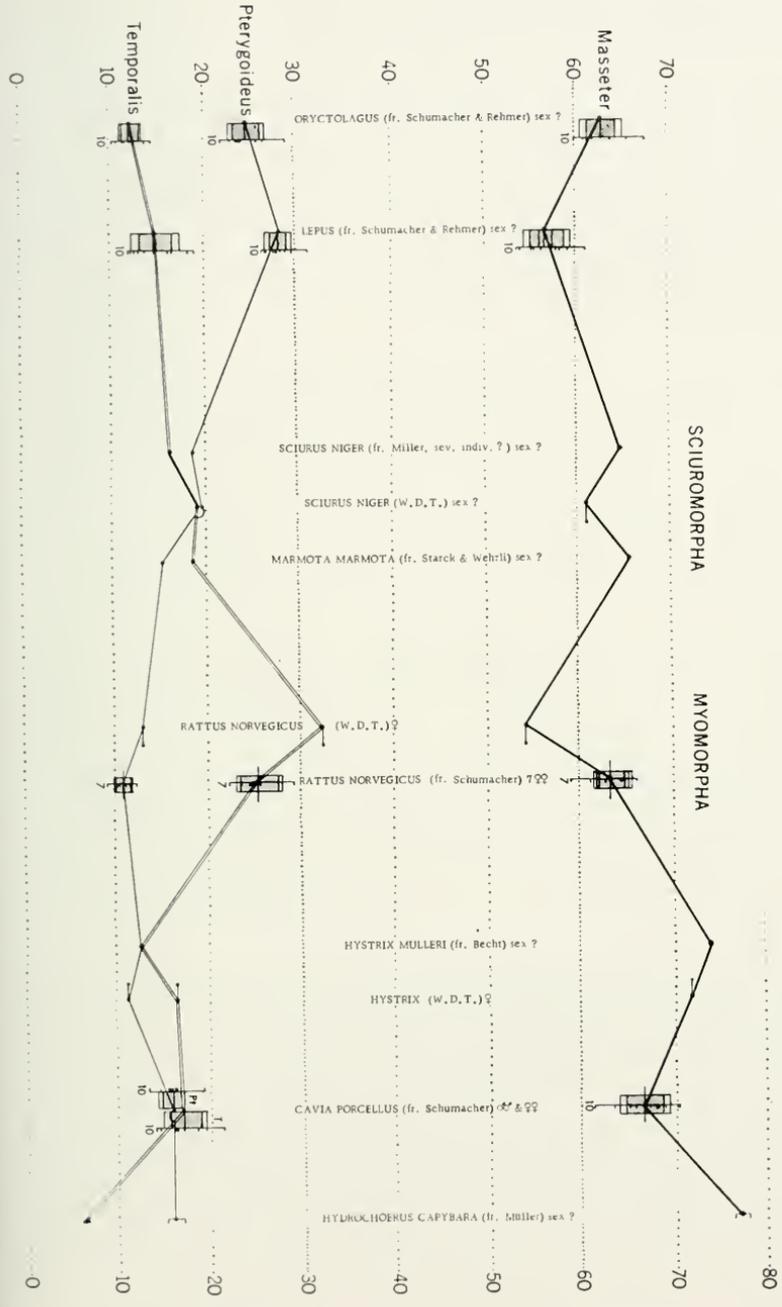
The compilations made here are more inclusive than are any others currently available. Thereby a broader basis of comparison for the usual kinds of comparisons—direct muscle weight or mass comparisons, and the average vectoral pull direction comparisons—can be made, and can be made in somewhat greater detail than previously. Figure 38 provides a schematic summary of this data for the three Specialized Groups. In it, the average percent of the total jaw musculature, and the approximate pull direction vectors for each muscle group are shown as though projected onto the two perpendicular planes that are related in their orientation to the major chewing movements: the vertical parasagittal plane of the skull and the vertical transverse plane through the jaws. As will be shown in the following functional treatment, both aspects should be considered simultaneously. This approach which has only rarely been used by other workers focuses attention not only upon the fundamental differences in muscle mass, but also shows the characteristic directions of the contractile forces used to move the jaws, both in the plane of closure, and in the “plane of grinding.”

FIG. 37. Graph showing the relative proportions of the jaw-closing muscle groups in percentage, for the Specialized Group III, “rodent-gnawing” forms. Represented are two genera (both Leporidae) of Lagomorpha and some representation of each of the rodent suborders of Brandt: Sciuromorpha (Sciuridae), Myomorpha (Muridae), and Hystricomorpha (Hystricidae, Caviidae, and Hydrochoeridae). For key to other notations, see caption to Figure 34.

LAGOMORPHA

RODENTIA

HYSTRICOMORPHA



Schematic Vector Diagrams of Jaw Muscles

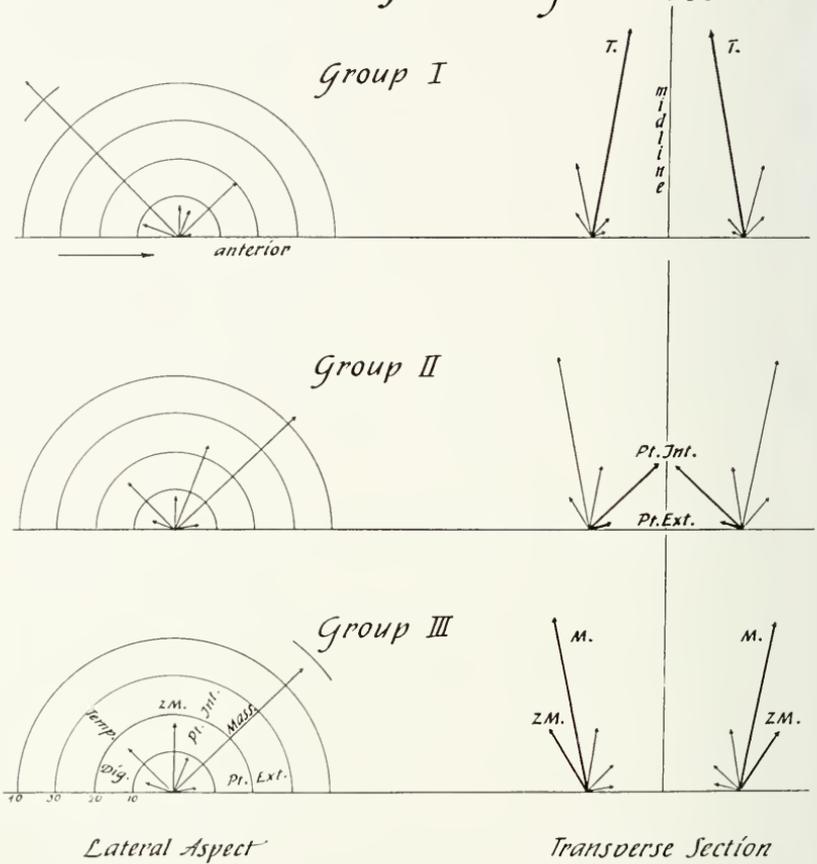


FIG. 38. Schematic vector diagrams showing a uniform generalized approximation of the mean muscle pull directions and the relative mass of each of the various jaw muscles (vector length in σ_1) for the three successful adaptively specialized groups.* The origin points of action have been superimposed on a single point in the lateral aspect diagrams, and on two single points (one corresponding to each jaw ramus) in the transverse section diagrams. Group I = "carnivore-shear" or "scissors" type. Group II = "ungulate-grinding" or "mill" type. Group III = "rodent-gnawing" or "anterior-shift" type. In the lateral views, the anterior of the head of the animal is to the right. The abbreviations designate the appropriate masticatory muscle, which is oriented in the same direction in each set of diagrams. The Generalized Group (not shown) has a vector pattern quite like that of Group I.

* Data from Fabian (1925), Kuhlhorn (1939), and Schumacher (1961) are not included.

TABLE X-A.—Relative weights (%) of the masticatory muscles in mammals of the Generalized Group.

Form and worker	Dig.	Temporalis group		Masseter group		Pterygoideus group		
		Superf.	Prof.	Sup.	Prof.	Int.	Ext.	
<i>Didelphis</i> data f. Fabian '25	3.86	←	54.13 52.04 →	←	35.71 34.33 →	9.12 ←	10.16 9.76 →	0.64 →
<i>Didelphis</i> data f. Klatt '28	7.8	←	54.5 50.2 →	←	35.1 32.4 →	←	10.4 9.6 →	→
<i>Didelphis virginiana</i> new data, this work	4.7	←	56.9 54.3 →	14.3 ←	34.1 9.3 32.5 →	7.0 ←	9.0 8.6 →	1.6 →
<i>Cenolestes caudatus</i> data f. Fabian '25	5.32	←	74.33 70.38 →	←	17.91 16.95 →	5.94 ←	7.77 7.35 →	1.41 →
<i>Echinosorex gymnaurus</i> new data, this work	7.7	←	61.2 56.5 →	11.0 ←	27.0 10.4 24.8 →	9.4 ←	11.8 11.0 →	1.6 →
<i>Perodicticus potto</i> data f. Fabian '25	10.36	←	48.28 43.28 →	←	32.50 29.14 →	13.72 ←	19.21 17.23 →	3.51 →
<i>Cebus variegatus</i> data f. Schumacher '61a	—	—	53.7	—	28.4	(12.7)	18.0	(5.3)
<i>Cebus apella</i> data f. Schumacher '61a	—	—	54.7	—	27.8	(12.0)	17.5	(5.5)
<i>Saimiri sciureus</i> data f. Schumacher '61a	—	—	54.2	—	31.3	(11.1)	14.5	(3.4)

TABLE X-A.—Relative weights (%) of the masticatory muscles in mammals of the Generalized Group (Continued).

Form and worker	Dig.	Temporalis group		Masseter group			Pterygoideus group	
		Superf.	Prof.	Sup.	Prof.	Zm.	Int.	Ext.
<i>Callithrix pennicillata</i> data f. Fabian '25	4.02	←	45.51 43.68 →	←	35.33 33.90 →	→	(13.17) 12.64 ←	(5.99) 19.16 5.75 18.39 →
<i>Macacus rhesus</i> data f. Fabian '25	6.16	←	54.32 50.98 →	←	27.80 26.09 →	→	(12.72) 11.93 ←	(5.16) 17.88 4.84 16.77 →
<i>Macaca mulatta</i> data f. Schumacher '61a	—	—	57.4	—	26.6	—	(11.3)	(4.8) 16.1
<i>Macaca sinica</i> data f. Schumacher '61a	—	—	59.5	—	26.0	—	(11.4)	(3.3) 14.6
Kleinkopf-Favian [? <i>Papio</i> sp.] data f. Fabian '25	4.35	←	48.93 46.80 →	←	31.82 30.43 →	→	(13.64) 13.04	(5.61) 19.25 5.37 18.41
[<i>Papio cynocephalus</i> <i>mormon</i>] data f. Fabian '25	8.14	←	48.28 44.34 →	←	31.03 28.51 →	→	(16.26) 14.93 ←	(4.43) 20.69 19.00 → 4.07
<i>Papio cynocephalus</i> data f. Schumacher '61a	—	—	58.2	—	23.2	—	(12.8)	(5.8) 18.6

TABLE X-A.—Relative weights (%) of the masticatory muscles in mammals of the Generalized Group (Continued).

Form and worker	Dig.	Temporalis group		Masseter group			Pterygoideus group		
		Superf.	Prof.	Sup.	Prof.	Zm.	Int.	Ext.	
Mantel-Pavian (<i>Hamadryas</i>) [? juvenile] data f. Fabian '25	3.59	←	50.42 48.61 →	←	27.49 26.50 →	←	(17.05) 16.44	22.09 21.30	(5.04) 4.86
<i>Hamadryas</i> [<i>Comopithecus</i> (<i>Papio</i>) <i>hamadryas</i>] av. 7 ♂, data f. Fabian '25	2.49	←	70.39	←	19.95	←	(7.43)	9.66	(2.23)
Sphinx-Pavian [<i>Mandrillus</i> (<i>Papio</i>) <i>sphinx</i> ? juv.] data f. Fabian '25	5.38	←	42.64 40.34 →	←	36.69 34.72 →	←	(15.50) 14.67	20.67 19.56 →	(5.17) 4.89
<i>Mandrillus</i> (<i>Papio</i>) <i>sphinx</i> data f. Schumacher '61a	—	←	63.6	←	22.7	←	(9.3)	13.8	(4.5)
Dschelada [<i>Theropithecus</i> (gelada)], av. 1 ♂, 1 ♀ data f. Fabian '25	3.93	←	60.69	←	25.31	←	(10.44)	14.01	(3.57)
<i>Cercopithecus diana</i> data f. Fabian '25	4.81	←	58.30	←	24.31	←	10.03	13.46 →	3.43
<i>Erithrocebus patas</i> data f. Fabian '25	5.78	←	42.53 40.48 →	←	39.08 37.20 →	←	(14.94) 14.22	18.39 17.50 →	(3.45) 3.28
		←	57.67 54.34 →	←	27.61 26.01 →	←	(11.04) 10.40	14.72 13.89 →	(3.68) 3.49

TABLE X-A.—Relative weights (C_1) of the masticatory muscles in mammals of the Generalized Group (Continued).

Form and worker	Dig.	Temporalis group		Masseter group		Pterygoideus group	
		Superf.	Prof.	Sup.	Zm.	Int.	Ext.
<i>Colobus</i> sp. data f. Fabian '25	6.28	←	43.25 40.53 →	←	28.79 26.98 →	(18.70) 17.53 ←	27.96 8.68 26.21 →
<i>Colobus polykomos</i> data f. Schumacher '61	—	—	47.7	—	31.2	(15.9)	21.1 (5.2)
<i>Pongo</i> sp. av. 1 ♂, 1 sex? data f. Bluntschli '29b	—	—	55.5	—	27.0	—	17.5 —
<i>Pongo pygmaeus</i> data f. Schumacher '61a	—	—	50.7	—	30.1	(13.8)	19.3 (5.5)
<i>Homo sapiens</i> data f. Theile 1884 av. 6 adult ♂♂	7.5	←	47.1 43.6 →	←	30.7 28.4 →	12.1 ←	22.3 8.6 20.6 →
<i>Homo sapiens</i> av. 19 ♂ & ♀ data f. Schumacher '61a	—	—	45.5	—	28.9	(11.4)	25.7 (14.3)

Note.—Data from Fabian, 1925 has been added in press and is not considered in text.

TABLE X-B.—Relative weights (%) of the masticatory muscles in mammals of a Miscellaneous Group (unassigned as to the other designated masticatory groups).

Form and worker	Dig.	Temporalis group		Massefer group		Pterygoideus group	
		Superf.	Prof.	Sup.	Prof.	Int.	Ext.
<i>Myrmecophaga jubata</i> data f. K�hlhorn '39		33.49			42.76	(11.91)	23.75 (11.84)
<i>Tamandua tetradactyla</i> data f. K�hlhorn '39		26.32			34.21	(28.95)	39.48 (10.53)
<i>Dasypus sexcinctus</i> [<i>Euphractus</i>] data f. K�hlhorn '39		48.61			32.64	(14.58)	18.75 (4.17)
<i>Tolypeutes conurus</i> data f. K�hlhorn '39		37.60			45.60	(12.80)	16.80 (4.00)
<i>Tatus noremscinctus</i> [<i>Dasypus</i>] data f. K�hlhorn '39		46.88			23.44	(21.88)	29.69 (7.81)
<i>Oryzctropus capensis</i> data f. Fabian '25	4.24	41.62 39.86	→		33.95 32.51	(16.75)	24.43 (7.68) 23.39 →
<i>Oryzctropus aethiopicus</i> 2? ♂♂, data f. Friek '51	4.1	38.1 36.6	→		40.3 32.5 → 38.6	16.3	21.6 4.5 → 20.8 →
<i>Elephas maximus</i> data f. Stocker '57	9.1	69.9 63.6	→		22.2 13.1 → 20.1	4.5	8.0 2.8 → 7.3 →
<i>Manatus</i> sp. data f. Fabian '25 av. 1 ♂, 1 ♀	8.37	42.96 39.37	→		34.62 31.72	(16.33)	22.42 (6.09) 14.97 5.58 → 20.55 →

Note.—Data from Fabian, 1925 and K hlhorn, 1939 added in press, and are not considered in text.

TABLE XI.—Relative weights (%) of the masticatory muscles in mammals of Specialized Group I—the “carnivore-shear,” or “scissors” type.

Form and worker	Dig.	Temporalis group		Masseter group		Pterygoideus group	
		Superf.	Prof.	Sup.	Zm.	Int.	Ext.
<i>Schakal-fuchs</i> [<i>Canis aureus</i>] data f. Fabian '25	8.03	←	→	←	→	(11.19)	(1.13)
		54.23		33.44		12.32	
		49.88		30.76		10.29	1.04
						←	←
<i>Canis familiaris</i> data f. Becht '53	10.8	←	→	←	→	←	←
		67.0		23.0		10.0	
		59.8		←	10.8	2.9	5.9
				←	20.6	←	8.8
<i>Canis familiaris</i> data f. Davis '55	9.5	←	→	←	→	←	←
		64.0		15.0	6.0	7.5	9.0
		58.0		←	←	←	8.0
				←	←	←	←
<i>Canis lupus</i> data f. Schumacher '61a	—	—	—	—	—	—	7.6
		68.2		←	←	←	←
<i>Canis dingo</i> data f. Schumacher '61a	—	—	—	—	—	(7.5)	(0.4)
		67.6		←	←	←	←
				←	←	←	←
<i>Alopex</i> av. 2 ♂♂, 1 ♀ data f. Klatt '28	8.0	←	→	←	→	←	←
		65.1		←	←	←	9.0
		59.9		←	←	←	8.3
				←	←	←	←
<i>Silbertfuchs</i> [<i>Vulpes</i>] data f. Fabian '25	8.67	←	→	←	→	(9.44)	(0.55)
		61.70		←	←	←	9.99
		56.35		←	←	←	0.50
				←	←	←	9.12
<i>Urocyon</i> data f. Klatt '28	8.6	←	→	←	→	←	←
		57.0		←	←	←	10.1
		52.1		←	←	←	9.2
				←	←	←	←
<i>Canis azare</i> [<i>Dusicyon</i>] data f. Fabian '25	9.88	←	→	←	→	(9.25)	(1.71)
		64.04		←	←	←	10.96
		57.72		←	←	←	1.54
				←	←	←	9.87

TABLE XI.—Relative weights (%) of the masticatory muscles in mammals of Specialized Group I—the “carnivore-shear,” or “scissors” type (*Continued*).

Form and worker	Dig.	Temporalis group			Masseter group			Pterygoideus group	
		Superf.	Prof.	Sup.	Prof.	Zm.	Int.	Ext.	
<i>Duscycyon D. (Pseudalopex)</i> data f. Klatt '28 av. 2 ♂♂	9.9	← 64.0 57.7	→	←	← 25.0 22.6	→	←	← 11.0 9.9	→
<i>Duscycyon D. (Cerdocyon)</i> <i>comericurus</i> av. 1 ♂, 1 ♀ data f. Klatt '28	11.9	← 57.4	→	←	← 31.7	→	←	← 10.9	→
<i>Canis javanicus</i> data f. Klatt '28	8.6	← 59.8 54.7	→	←	← 30.7 28.1	→	←	← 9.5 8.7	→
Löffelhund [<i>Otocyon caffer</i>] data f. Fabian '25	10.31	← 65.75 58.97	→	←	← 28.05 25.15	→	← (5.52)	← 6.21 4.95 5.57	→ (0.69)
<i>Otocyon</i> data f. Klatt '28	10.3	← 65.7 59.0	→	←	← 28.0 25.2	→	←	← 6.2 5.6	→
<i>Tremarctos ornatus</i> data f. Davis '55	10.0	← 64.0 58.0	→	←	← 27.0 2.5 24.0	→	←	← 9.0 7.0 8.0	→ 1.0
<i>Ursus americanus</i> data f. Davis '55 (incl. Starek data) & f. Davis '64, av. 1 juv. ♂, 1 sex?	9.7	← 67.9 61.4	→	←	← 9.7 2.6 23.4	→	←	← 6.2 5.6	→ 0.6
<i>Ursus arctos</i> data f. Becht '53	8.1	← 64.0 59.0	→	←	← 11.9 15.9 27.8	→	←	← 6.0 5.1	→
<i>Ursus arctos</i> data f. Starek '35	14.5	← 64.0 54.4	→	←	← 14.5 3.8 26.6	→	←	← 5.0 4.5	→ 0.5

TABLE XI.—Relative weights (%) of the masticatory muscles in mammals of Specialized Group 1—
the “carnivore-shear,” or “scissors” type (Continued).

Form and worker	Dig.	Temporalis group		Masseter group		Pterygoideus group	
		Superf.	Prof.	Sup.	Prof.	Int.	Ext.
Eisbär [<i>Thalarcos</i>] data f. Fabian '25	12.58	←	72.55 63.42 →	←	21.70 18.97 →	(5.24) 4.58 ←	5.75 5.03 →
<i>Thalassarctos (Ursus)</i> [<i>Thalarcos</i>] <i>maritimus</i> data f. Schumacher '61a	—	—	76.7	—	17.9	(5.1)	5.4
<i>Thalarcos maritimus</i> data f. Davis '64	10.0	←	73.3 66.0 →	←	21.1 12.0 → 19.0 →	4.0 ←	5.5 5.0 →
<i>Ailuropoda melanoleuca</i> data f. Davis '64	10.3	←	59.8 53.6 →	←	4.9 36.5 6.7 32.7 →	2.0 ←	3.6 1.2 3.2 →
Wachsbär [<i>Procyon</i>] data f. Fabian '25	12.98	←	57.83 50.33 →	←	29.49 25.66 →	(11.52) 10.03 ←	12.67 11.03 →
<i>Procyon (Euprocyon)</i> data f. Klatt '28 av. 1 ♂, 1 ♀	9.5	←	62.8 56.8 →	←	29.1 26.3 →	←	8.1 7.4 →
<i>Procyon lotor</i> data f. Davis '64	9.0	←	69.2 63.0 →	←	23.1 3.0 21.0 →	6.0 ←	7.7 1.0 7.0 →
Nasenbär [<i>Nasua</i>] av. 1 ♂, 1 ♀ data f. Fabian '25	9.40	←	68.31 61.89 →	←	21.46 19.45 →	(9.33) 8.46 ←	10.23 9.27 →

TABLE XI.—Relative weights (%) of the masticatory muscles in mammals of Specialized Group I—the “carnivore-shear,” or “scissors” type (Continued).

Form and worker	Dig.	Temporalis group			Masseter group			Pterygoideus group		
		Superf.	Prof.	Sup.	Prof.	Zm.	Int.	Ext.		
<i>Nasua</i> 1 ♂, 1 ♀ av. data f. Klatt '28	8.0	←	71.1 65.5 →	←	19.1 17.6 →	→	←	9.8 9.0 →	←	—
<i>Ailurus</i> data f. Klatt '28	8.2	←	74.8 68.6 →	←	16.8 15.4 →	→	←	8.4 7.7 →	←	—
Dachs [?] <i>Melops</i> data f. Fabian '25	12.52	←	77.43 67.74 →	←	17.08 14.94 →	→	(5.20)	5.49 4.54 →	(0.29)	0.25 ←
<i>Lutra lutra</i> data f. Schumacher '61a	—	—	78.9	←	17.0	←	(3.8)	4.2	(0.4)	←
<i>Suricata tetradactyla</i> data f. Fabian '25	10.18	←	65.33 58.68 →	←	28.33 25.45 →	→	(5.67)	6.34 5.09 →	(0.67)	0.60 ←
Fuchs-Manguste [<i>Cynictis</i> <i>penicillata</i>] data f. Fabian '25	9.31	←	68.79 62.38 →	←	24.64 22.35 →	→	(6.16)	6.57 5.59 →	(0.41)	0.37 ←
<i>Proteles</i> data f. Klatt '28	9.4	←	65.7 59.6 →	←	22.5 20.4 →	→	←	11.7 10.6 →	←	—
Hauskatze data f. Fabian '25	8.7	←	60.54 55.27 →	←	30.32 27.68 →	→	(8.76)	9.14 7.99 →	(0.38)	0.35 ←
<i>Felis (Felis) domestica</i> new data this work	8.5	←	54.0 49.7 →	←	35.0 24.0 →	→	←	11.0 9.3 →	←	0.4 ←
		←		←	32.2	→	←	9.7	←	→

TABLE XI.—Relative weights (%) of the masticatory muscles in mammals of Specialized Group I—the “carnivore-shear,” or “scissors” type (Continued).

Form and worker	Dig.	Temporalis group			Masseter group			Pterygoideus group	
		Superf.	Prof.	Zm.	Sup.	Prof.	Zm.	Int.	Ext.
<i>Felis (Puma) concolor</i> data f. Schumacher '61a	—	—	—	—	—	—	—	(8.6)	(0.1)
<i>Panthera leo</i> data f. Schumacher '61a	—	—	—	—	—	—	—	(7.3)	(*)
<i>Panthera leo</i> juv. ♂ data f. Schumacher '61a	—	—	—	—	—	—	—	(8.7)	(0.2)
Tiger data f. Fabian '25	10.24	←	→	←	←	→	←	(7.58)	(0.21)
<i>Panthera tigris</i> data f. Becht '53	7.5	12.7	←	31.5	29.2	←	←	←	←
<i>Panthera (Jaguaris) onca</i> data f. Davis '55	8.0	←	←	←	←	←	←	←	←
Seehund [<i>Phoca vitulina</i>] data f. Fabian '25	24.59	←	←	←	←	←	←	←	←
<i>Halichoerus gryphus</i> data f. Schumacher '61a	—	—	—	—	—	—	—	—	—

* Presumably less than 1/10 of 1%.

Note.—Data from Fabian, 1925 added in press and is not considered in text. Some of Klatt's data apparently taken from Fabian.

TABLE XII.—Relative weights (%) of the masticatory muscles in mammals of Specialized Group II — the “ungulate-grinding,” or “mill” type.

Form and worker	Dwg.	Temporalis group			Masseter group			Pterygoideus group		
		Superf.	Prof.	Sup.	Prof.	Zm.	Int.	Ext.		
Känguruh [species ?] data f. Fabian '25 av. 1 ♂, 1 ♀	5.03	←	36.42 34.59	→	←	41.71 39.61	→	(18.96) 18.01	21.87 20.77	(2.91) 2.76
Domestic horse data f. Fabian '25	** 5.55	←	12.60 11.90	→	←	56.87 53.71	→	(26.64) 25.16	30.54 28.83	(3.90) 3.67
<i>Equus caballus</i> data f. Becht '53	6.2*	←	11.1 10.4	→	←	57.5 53.9	→	25.0	31.4 29.4	4.4
<i>Equus caballus</i> new data, this work	6.5*	←	14.6 13.6	→	←	54.5 42.6	→	25.0	31.0 29.0	4.0
Zebra [species ?] data f. Fabian '25	** 5.81	←	16.31 15.36	→	←	53.87 50.74	→	(24.42) 23.00	29.82 28.09	(5.40) 5.09
Wildschwein [species ?] data f. Fabian '25	3.78	←	29.34 28.23	→	←	40.92 39.37	→	(23.11) 22.24	29.74 28.62	(6.63) 6.38
<i>Sus scrofa</i> av. 10 juv. ♀ data f. Schumacher '61	—	←	27.5	→	←	(32.4)	→	(17.0)	22.7	(5.7)

TABLE XII.—Relative weights (%) of the masticatory muscles in mammals of Specialized Group II—the “ungulate-grinding,” or “mill” type (Continued).

Form and worker	Dig.	Temporalis group			Masseter group			Pterygoideus group			
		Superf.	Prof.	Sup.	Prof.	Zm.	Int.	Ext.			
<i>Camelus dromedarius</i> data f. Schumacher '61a	—	—	43.4	—	—	30.4	—	(21.0)	26.3	(5.4)	—
Hirschkuh [♀ <i>Cervus</i>] data f. Fabian '25	5.48	←	21.33	→	—	43.29	→	(32.31)	35.39	(3.08)	—
<i>Odocoileus virginianus</i> new data, this work subadult ♂	5.4	←	29.4	→	16.5	46.1	→	←	24.5	3.5	→
Reh [<i>Capreolus capreolus</i>] data f. Fabian '25	4.17	←	27.8	→	←	43.6	→	(26.79)	30.37	(3.58)	→
<i>Capreolus capreolus</i> av. 3 adults, 1 ♂, 2 ♀ data f. Schumacher '61a	—	←	27.05	→	←	42.59	→	(26.1)	29.4	(3.3)	→
<i>Bos indicus</i> data f. Becht '53	7.4	←	25.92	→	←	40.81	→	←	25.67	3.43	→
<i>Bison bonasus</i> data f. Becht '53	6.9	←	31.0	→	←	39.7	→	(26.1)	29.4	(3.3)	→
			11.0	→	←	50.0	→	←	40.0	—	→
			10.2	→	←	43.0	→	←	37.1	—	→
			10.6	→	←	45.3	→	←	29.4	—	→
			9.9	→	←	60.0	→	←	27.4	—	→
			9.9	→	←	55.8	→	←	27.4	—	→

TABLE XII.—Relative weights (%) of the masticatory muscles in mammals of Specialized Group II — the “ungulate-grinding,” or “mill” type (Continued).

Form and worker	Dig.	Temporalis group		Masseter group		Pterygoideus group		
		Superf.	Prof.	Sup.	Prof.	Int.	Ext.	
Wasserbock [<i>? Kobus</i>] data f. Fabian '25	6.17	—	23.64	—	50.02 46.94	—	(24.18) 26.34 24.71	(2.16) 2.02
Zwerg-antilope [<i>? Cephalophus</i> or <i>? Neotragus</i>] data f. Fabian '25	9.08	—	22.57 20.52	—	48.25 43.87	—	(24.51) 29.18	(4.67) 4.25
<i>Onis aries</i> av. 2 adults (S ₁ & S ₂) data f. Zey '40	—	—	25.7	—	(9.8) 15.5 46.2	(21.0)	(23.1) 28.1	(5.0)
<i>Onis aries</i> (juv. ♀) data f. Schumacher '61a	—	—	29.6	—	40.9	—	(24.3) 29.6	(5.3)
<i>Onis aries</i> new data, this work	5.1	—	23.5 22.3	—	14.9 49.9	7.7	19.7 22.7	3.0
<i>Onis musimon</i> data f. Schumacher '61a	—	—	25.1	—	48.3	—	(23.3) 26.7	(3.4)

* Included *M. occipito-mandibularis*.

** Presumably includes *M. occipito-mandibularis*.

Note.—Data from Fabian, 1925 added in press and is not considered in text.

TABLE XIII.—Relative weights (%) of the masticatory muscles in mammals of Specialized Group III—the “rodent-gnawing,” or “anterior-shift” type.

Form and worker	Dig.	Temporalis group		Masseter group			Pterygoideus group		
		Superf.	Prof.	Sup.	Prof.	Zm.	Mm.	Int.	Ext.
<i>Lepus timidus</i> data f. Fabian '25	5.05	13.70	→	←	53.48	←	(28.02)	32.83	(4.81)
		13.01	→	←	50.78	←	←	26.60	4.56
<i>Lepus</i> av. 10 indiv. data f. Schumacher & Rehmer '60	—	15.0	—	—	56.9	—	(22.9)	28.1	(5.2)
		—	—	—	—	—	—	—	—
<i>Oryzologus</i> av. 10 indiv. data f. Schumacher & Rehmer '60	—	12.4	—	—	62.9	—	(19.9)	24.8	(4.9)
		—	—	—	—	—	—	—	—
<i>Sciurus niger</i> several indiv. data f. Miller (unpub. thesis U. of Chicago)	6.0	16.5	→	←	64.8	→	10.3	18.7	7.2
		15.5	→	←	50.5	→	←	17.5	→
<i>Sciurus niger</i> new data, this work	4.4 [+Im.=0.7]	19.4	→	←	61.0	→	11.6	19.6	7.0
		18.4	→	←	29.4	→	←	18.6	→
<i>Marmota marmota</i> data f. Starck & Wehrli '35	—	18.8	—	←	(7.0)	—	(10.3)	15.5	(5.2)
		—	—	←	65.7	—	—	—	—
<i>Rattus norvegicus</i> av. 7 adult ♀ data f. Schumacher '61a	—	25.6	—	←	(1.7)	(15.9)	(7.6)	11.1	(3.5)
		—	—	←	63.4	—	—	—	—

TABLE XIII.—Relative weights (%) of the masticatory muscles in mammals of Specialized Group III—the “rodent-gnawing,” or “anterior-shift” type (Continued).

Form and worker	Dig.	Temporalis group		Sup.	Masseter group		Pterygoideus group		
		Superf.	Prof.		Prof.	Zm.	Int.	Ext.	
<i>Rattus norvegicus</i> new data, this work	5.2 (+Im.=1.0)	32.6 30.6	→	17.6 ←	54.1 50.7	6.2 →	8.3 ←	13.3 12.4	4.1 →
<i>Hystrix cristata</i> data f. Fabian '25	7.62	14.61 13.49	→	←	72.97 67.41	→	6.04 ←	12.43 11.48	(5.89) 5.44
<i>Hystrix mulleri</i> data f. Becht '53	8.7	13.0 11.7	→	←	74.0 68.0	←	5.7 ←	13.0 11.7	6.0 →
<i>Hystrix</i> sp. new data, this work	8.0	16.6 15.3	→	←	71.9 66.3	15.2 →	5.1 ←	11.5 10.5	5.4 →
<i>Erethizon dorsatus</i> data f. Fabian '25	5.05	21.54 20.45	→	←	56.77 53.90	→	8.57 ←	21.69 20.60	(12.67) 12.03
<i>Caria porcellus</i> 10 adults ♂ & ♀ data f. Schumacher '61a	—	17.6	→	←	(54.2) →	(5.5)	(13.5)	16.0	(2.6)
<i>Hydrochoerus capybara</i> av. 2 adults, sex ? data f. Müller '33	9.2	6.8 6.2	→	←	77.1 70.0	18.3 →	11.6 ←	16.1 14.6	3.0 →

Note.—Data from Fabian, 1925 added in press and is not considered in text.

Functional Analysis

No single, well-established method of comparative functional mechanical analysis of the mammalian masticatory apparatus exists. Of the many gross mechanical studies that have been made, some focus attention upon motion at the occlusal surfaces, others upon the pressures that can be brought to bear, others upon the sequences of chewing movements, and still others upon the pressures resultant at the jaw joint. The following have all made significant contributions to our understanding along one or more of these lines: Ryder (1879), Lubosch (1907), Worthmann (1922), Hildebrand (1937), Loos (1946), Butler (1952), Becht (1953), Davis (1955), Stöcker (1957), Parrington (1959), Maynard Smith and Savage (1959,) Butler and Mills (1959), Butler (1961), Schumacher (1961a), Davis (1964), and Welsch (1967).

In discussing the jaw mechanics of *Tremarctos* and *Ursus*, Davis (1955) stated that the vertebrate jaw is customarily regarded as a Class III lever. This is understandable since the form and articulation relationships of the jaw, and the usual arrangement of its musculature corresponds quite well with the pattern of the Class III lever. Even in the Mammalia it does generally retain the form of that system (fig. 39), with the power or effort force (E) situated between the work or resultant force (R) and the fulcrum.

Davis also noted shortcomings of this view: namely, that it holds only in cases where the coronoid process is not appreciably higher than the capitulum of the jaw. (This with reference to the occlusal plane and with regard to the temporal muscle, of course.) He also implied that the same sort of limitation pertains where there is a well-developed angular process of the jaw with regard to the action of the masseter muscle. To this must be added yet one more limitation which also operates where there is a well-developed angular process, namely, one with regard to action of the internal pterygoid muscle.

Davis then proceeded to show how an interpretation of the mammalian jaw as a Class III lever is an oversimplification. For the

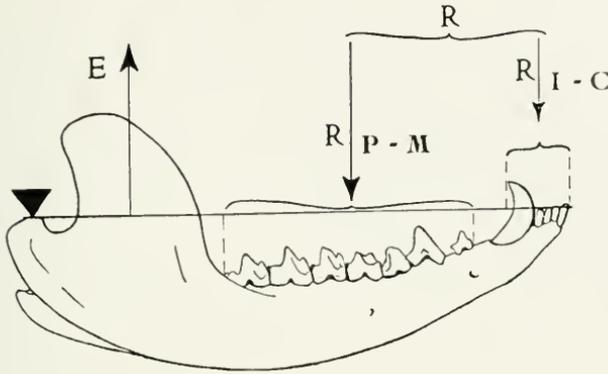


FIG. 39. The mammalian jaw as a Class III lever. Scheme shows the usual interpretation. E = effort force; R = resistance force; R_{P-M} = resistance (or work) force resulting at the midpoint of the Premolar-Molar area where mastication proper is effected; R_{I-C} = resistance (or work) force resulting at the midpoint of the Incisor-Canine area where incision, cropping, stabbing and grasping are affected.

Carnivora, at least, he showed that it is a combination of a couple system and a bent lever system that functions. Davis considered the bent lever to be a modified Class I lever.¹ Actually, both the couple and the bent lever can be considered to be modified Class I levers. For the bent lever, Davis demonstrated the point. Figure 40 shows the manner in which the couple is treated as a pair of bent levers—and hence as two modified Class I levers. In the subsequent muscle leverage diagrams the effort force and its lever arm and the force vector diagram for the fulcrum are set off in red to contrast with the resultant lever arm which appears in black (figs. 42-47).

Davis' system of analysis of the forces resulting upon the fulcrum (jaw joint) is here refined slightly. His bent lever diagram shows the fulcrum positioned and oriented by eye estimate. An improvement over such estimates is achieved by use of simple vector analysis diagrams, whereby a more precise measure of the direction of application of the various resistance forces at the fulcrum from the (average) contribution of each muscle group results. Also, since the internal pterygoid muscle acts synergistically with the masseter at one pole of the couple, and in counteraction (as far as pressures at the joint are concerned) to the temporalis at the other pole. I have included the pterygoid group contribution in Figure 40 along with that of the masseter group. In Figures 42-47, however, each of the three muscle

¹ He did not state his reason for this. One could, with equal logic, call it a modified Class III lever.

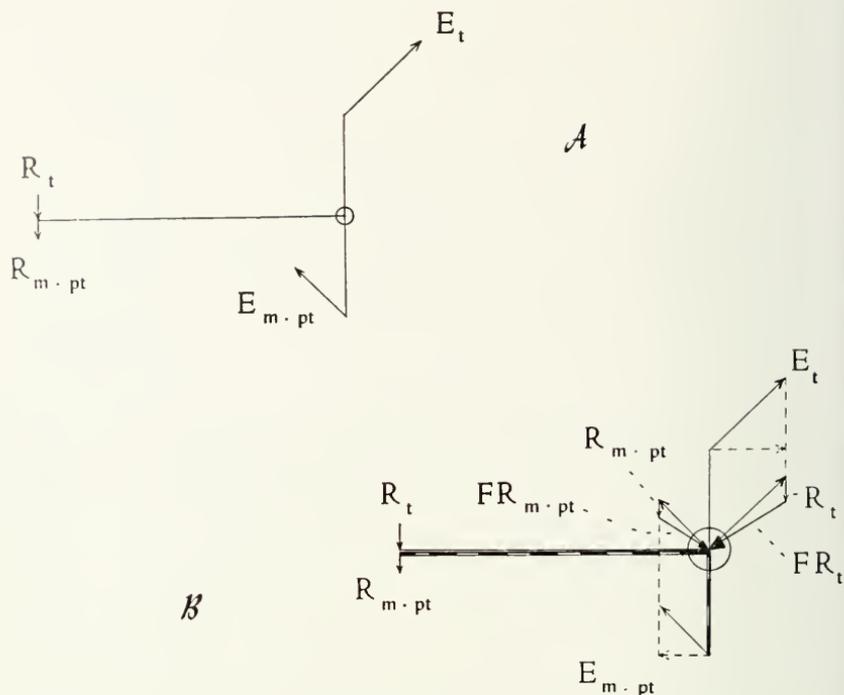


FIG. 40. Refinement of Davis' diagram of the couple lever system in the jaw apparatus of mammals. A, The couple with the forces designated according to the following scheme. E = effort force; R = resistance force; Subscripts t , m , and pt = forces resulting from the action of temporalis, masseter or pterygoideus musculature, respectively. B, The couple as two bent levers:—one, that pertaining to the temporalis muscle, is shown in thin solid line, and the other, that of the masseter and pterygoideus groups combined, is shown in dashed heavy line. The diagram also illustrates the vector method of determining both the directions of, and the resultant resistance forces acting at the fulcrum (FR), which result from the functioning of the various jaw-closing muscle groups. Broken-line arrows indicate force vector applicable to jaw closure (i.e., that applied at right angle to lever arm).

groups is shown separately. The result of this change in Davis' procedure is to show that the couple action is of even greater importance generally in the Mammalia (and especially in the Carnivora) as a means of reducing resultant pressures upon the joint than he had indicated. Note also (fig. 40, B) that the resultant resistance forces at the fulcrum are not exactly aligned in opposing directions (i.e., the temporalis resultant force at the fulcrum does not directly oppose that of the combined masseter and pterygoideus) but that they approach such a condition. Davis' main points, 1) that the rear of the

glenoid fossa has the greatest pressures directed against it, and 2) that this fact explains the enlargement of the carnivore post-glenoid process, are thus not only well taken, but are reinforced and further elaborated.

One other, relatively minor, example of the falaciousness of the notion that the mammalian jaw is to be considered a Class III lever is noted. To some extent, within a few of the forms belonging to Specialized Group III, the jaws actually tend to function more as a Class II lever with regard to the cheek teeth, as far as an important portion of their musculature is concerned. For example, with the masseter of *Hydrochoerus* the effort lever arm slightly exceeds in length the resistance (resultant at level of cheek teeth) lever arm—a condition that meets the definition of a Class II lever since the fulcrum is at one end of the lever system, and the resistance force is between it and the effort force. Thereby an increased mechanical advantage results because the factor operating in a Class II lever is greater than one, while in contrast a factor of less than one operates in the less efficient Class III lever. Other such examples may be found in Specialized Group III, and even very occasionally in Specialized Group II. Invariably such occurrences are correlated with an extreme degree of specialization of feeding habits, dentition, or both.

THE USEFUL POWER FORMULA

Lack of a comparative mechanics of the masticatory apparatus has already been discussed. One need is for a standard method of comparison of the relative useful power of the jaw closing apparatus between forms. Such a means of comparison necessarily involves many mechanical aspects. Direct comparisons of muscle mass (or volume, or weight, or of the lever systems of the various forms), serve as a first means of distinguishing resemblances and differences. However, such comparisons only provide glimpses into the mechanics of operation of the jaws, for they do not combine the basic mechanical factors in a manner that would account for the interplay of the various permutations and combinations among the factors concerned (such as forces and levers), even for a single muscle group, let alone for the entire complex. The following simple formula is proposed as a means of achieving just such an elementary level of (static) mechanical comparison. It draws upon 1) muscle mass (or weight or volume) proportions, 2) muscle position and cross-sectional thickness (including consideration of muscle shape and attachment positions),

3) leverages (taken from maps of muscle attachment to skull and jaws), and 4) direction of muscle pull. Thus, a measure of the useful power (E) of the jaw-closing mechanics for temporalis (t), or masseter (m), or pterygoideus (pt) musculature may be calculated as follows:

$$Et \text{ (or } Em \text{ or } Ept) = M \times F_L \times F_X \times r$$

M is the mass (weight or volume) of the muscle group expressed as percentage of the total jaw-closing musculature. Its weakness as a measure of actual proportionate muscle power has already been mentioned. Clearly, it is only an approximation and future studies will probably bring qualifying refinements.¹

F_L and F_X are correction factors. They are necessary to adjust for the fact that a muscle may be so aligned that not all of its contractile power can be utilized for jaw closure: either some of the force may be applied along an axis outside of the plane of closure, or at some other angle than a right angle to the functioning lever arm (the only fully efficient angle). The subscripts L and X designate the two perpendicular vertical planes onto which all of these three-dimensional muscle pull forces can be projected for our analysis. These are 1) the longitudinal (parasagittal) plane of the skull and jaws, and hence the plane of simple jaw closure, and 2) the idealized average cross-section plane through the midregion of the jaw musculature (i.e., functionally through the effort region of the jaws). In F_L only muscle pull forces within, or projected onto, the plane of jaw closure are considered. F_L provides adjustment for the angle of pull within

¹ Several refinements are now possible, but were not used because they contribute only very minor adjustments to the values concerned. Also they are out of keeping with the rest of the values or measures used. One of these is the possible use of dry ash weights of muscles instead of wet weights as a means of achieving a more accurate measure of the proportion of each individual muscle to the total jaw muscle complex. The procedure eliminates most of the errors resulting from differential evaporation which can occur during dissection, study, photography, illustration, and measuring or weighing procedures, but normal care to prevent desiccation gives results that do not differ very greatly in the final proportions. Furthermore, only Schumacher has consistently employed the method, and hence as a comparative base it is presently very restrictive. For these reasons it seems quite impractical at present. Another possible refinement is the use of the physiological cross-section values for each muscle as a means of arriving at muscle power (E. Weber, 1846 and 1851; Buchner, 1877; Fick, 1910; and Schumacher, 1961). Very likely this gives little improvement over the muscle map and weight technique used here at the level that is being studied. Thus, I made no attempt to incorporate it into the formula. These and other possible refinements relating muscle power to muscle type or form are discussed and elaborated upon by Gans and Bock (1965), but as yet these are not ready for application in the useful power formula.

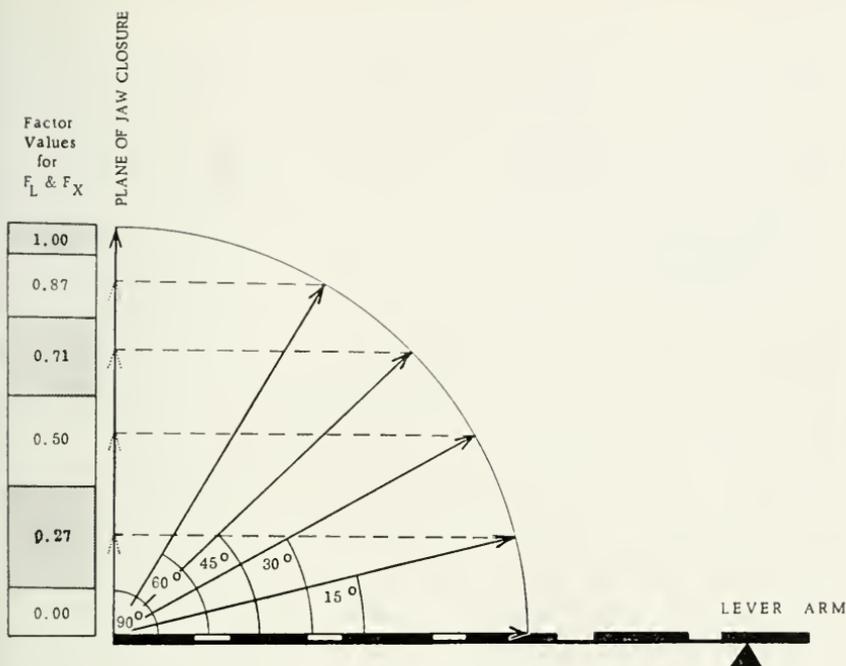


FIG. 41. Diagram illustrating the method used for selecting values of the correction factors F_L and F_X to be applied in the useful power formula. Since the forces operating in a lever system act perpendicularly, each to its own lever arm, when a muscle pulls at some angle other than a 90° angle, the useful effort expended in operation of the lever is reduced proportionately to the degree of departure from this optimum. A muscle pulling at 60° exerts but 87% of its total expended effort in a direction useful for the closing operation of the lever (i.e., this equals that force vector that is operating at 90°). In the same way, a muscle pulling at 45° exerts 71% of its effort in a direction perpendicular to the lever arm, etc. The six factor values to be applied in the formula (see text) are those that correspond to the discrete zones (alternating clear and stippled bands) whose midpoints are sine functions of the designated angles shown here. Arrows show average muscle pull direction. Dotted arrows show the appropriate proportion for the perpendicular vector for the lever arm for F_L or for departure from the plane of action for F_X .

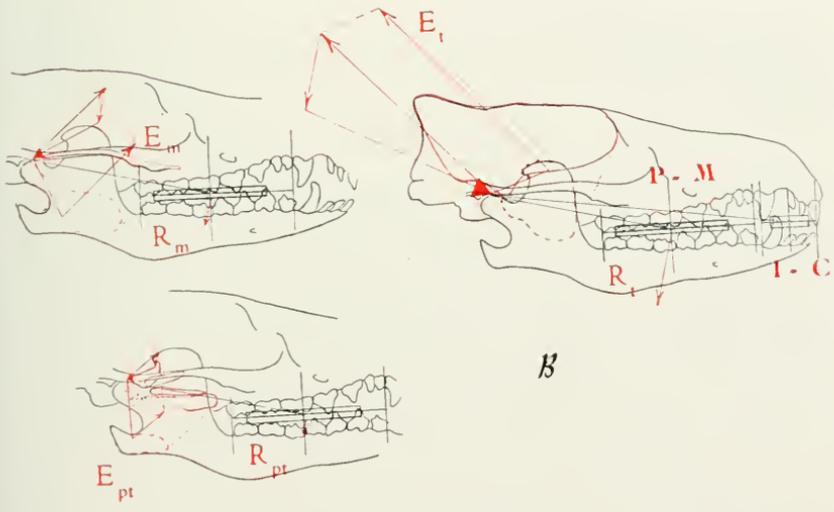
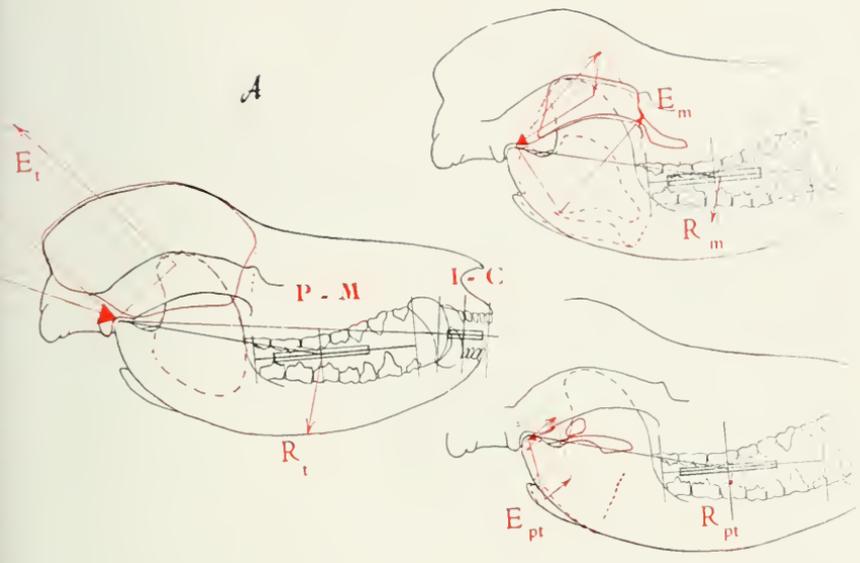
that plane as it relates to the effort lever arm of the muscle being considered. This pull is 100% efficient if it is directed normal to the lever arm, and is at 0% efficiency when it is exactly aligned in either direction with this lever arm. All variations between these extremes are possible. For application in the formula, this angle can be approximated with reasonable accuracy by sighting with a protractor, using mean fiber direction, and functional midpoints of the origin and insertion attachment fields for each muscle. In F_X muscle pull acting in the average vertical cross-sectional plane through the jaw musculature is considered in a similar way. Here, however, adjustment is made for the angle of muscle pull with regard to the degree

of divergence that it may take, medially or laterally from the axial plane of the head (i.e., deviation from the plane of jaw closure). Such a pull force is 100% efficient for closure if it falls exactly on the vertical line that represents the plane of closure,¹ and is at 0% efficiency when the pull is at a right angle to that line (plane) in either a medial or lateral direction. For use in the formula, the angular divergence from the plane of closure may be approximated by the same means that the angle was approximated for F_L . In F_X , because the sighting distances tend to be longer and because in this aspect the musculature is less flattened in its general configuration, perhaps the estimate is slightly less precise. For both correction factors I have selected a series of values (sine functions) to be applied in the formula according to whether the angle concerned is one that approximates more closely one of 0°, 15°, 30°, 45°, 60°, or 90°. In the case of F_L , the concern is with the angle in relation to the lever arm, while in F_X it is in relation to the plane of closure (see fig. 41). Thus, for each factor a choice of six values from 0 to 1.0 is used. In the future, a finer gradation may be employed to improve the accuracy of the result, but for the present this scale seems to be quite adequate.

The symbol r stands for the ratio of the mechanical advantage of the effort lever arm in relation to the resistance lever arm in the system. It follows from the law of the lever.

¹ For convenience this is usually a vertical line through a jaw ramus in the region of its musculature parallel to the axial plane, instead of in the mid-axial plane itself.

FIG. 42. Outline drawings of skull and jaws of *Didelphis* (A) and *Echinorex* (B). They serve as bases of the maps of the various jaw-closing muscle attachment areas, of the vector diagrams of muscle action during jaw closure, and of the lever systems. All are needed for calculating the jaw-closing efficiency for each muscle group. Solid red lines delimit origin areas; broken red lines, insertion areas. Straight black lines connect the jaw joint (fulcrum in the jaw lever system) with the functional dental regions (stippled areas—I-C=Incisor-Canine region, or P-M=Premolar-Molar region). These are the resistance arms of the lever systems. Similar straight red lines run from the condyle to the mean functional center of the attachment fields of each muscle group. These constitute the effort arms of the lever systems. Red arrows originating at the point of operation of the effort lever arms are proportioned effort vectors (E). They indicate both the mean direction of application, and the relative strength of the muscle force. However, they are not corrected for the muscle alignment factors F_L and F_X (see text). Red arrows originating at the functional center of the premolar-molar dental regions are proportioned resistance vectors (R), which show direction and extent of the resistance forces operating at that point, and resultant from the action of each muscle group. The red vector polygons at the condyle resolve the forces acting at the joint.



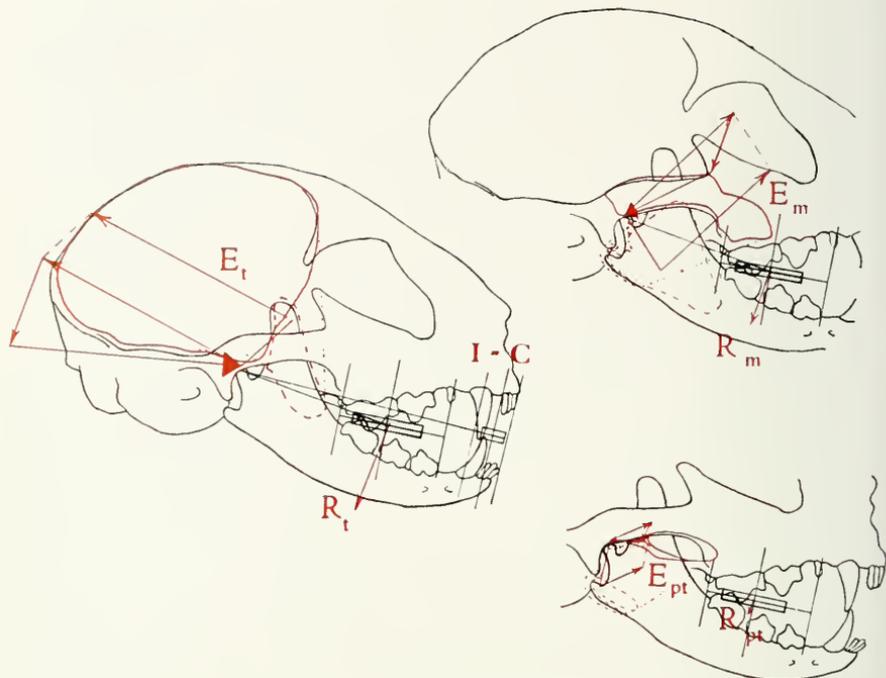


FIG. 43. Outline drawings of skull and jaws of *Felis* with other data pertinent to jaw lever mechanics shown superimposed. Details are explained in caption to Figure 42.

THE USEFUL POWER FORMULA APPLIED

Utilization of this formula is carried out for the forms dissected as follows: The procedure is straightforward, although lengthy. First, accurate outline drawings of skull and jaws are made for each species, and the resultant lever arms (fulcrum to the appropriate functional dental region, i.e., either I-C=Incisor-Canine, or P-M=Premolar-Molar region) are added. Each of these drawings is then triplicated in order to provide separate bases for illustrating features related to mechanics for each of the three main jaw-closing muscle groups (figs. 42-47). Then the muscle attachment maps, the appropriate effort lever arm for the muscle group being considered, and that muscle's force vectors with their resultants at the jaw joint are added (shown in red in figs. 42-47). By this procedure, the attachment positions are made to appear in a standard orientation for each muscle group, and are precisely recorded as an aid to determining 1) the muscle's alignment, 2) the functional midpoints of its attachment fields, and from these, 3) the effort-lever arm. Then, from the finished drawings

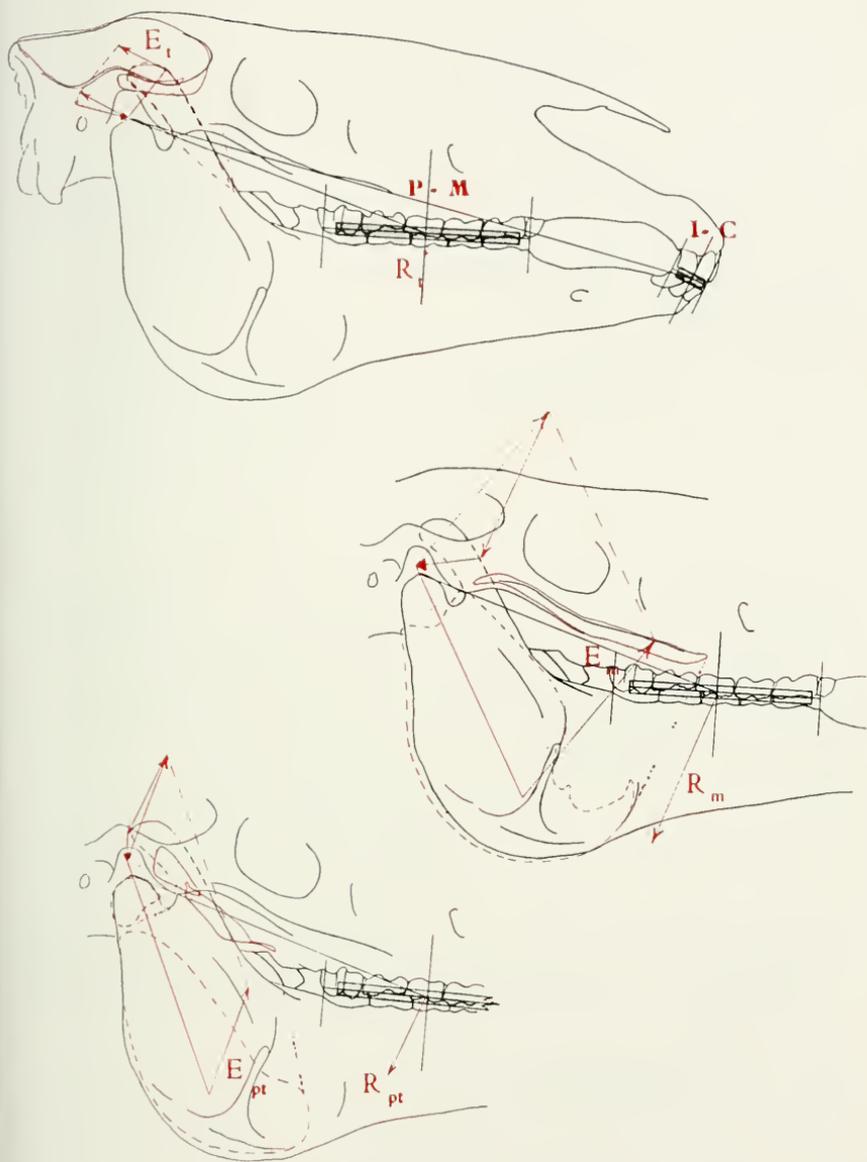


FIG. 44. Outline drawings of skull and jaws of *Equus* showing the jaw-closing muscles' attachment fields and the other features explained in the caption to Figure 42.

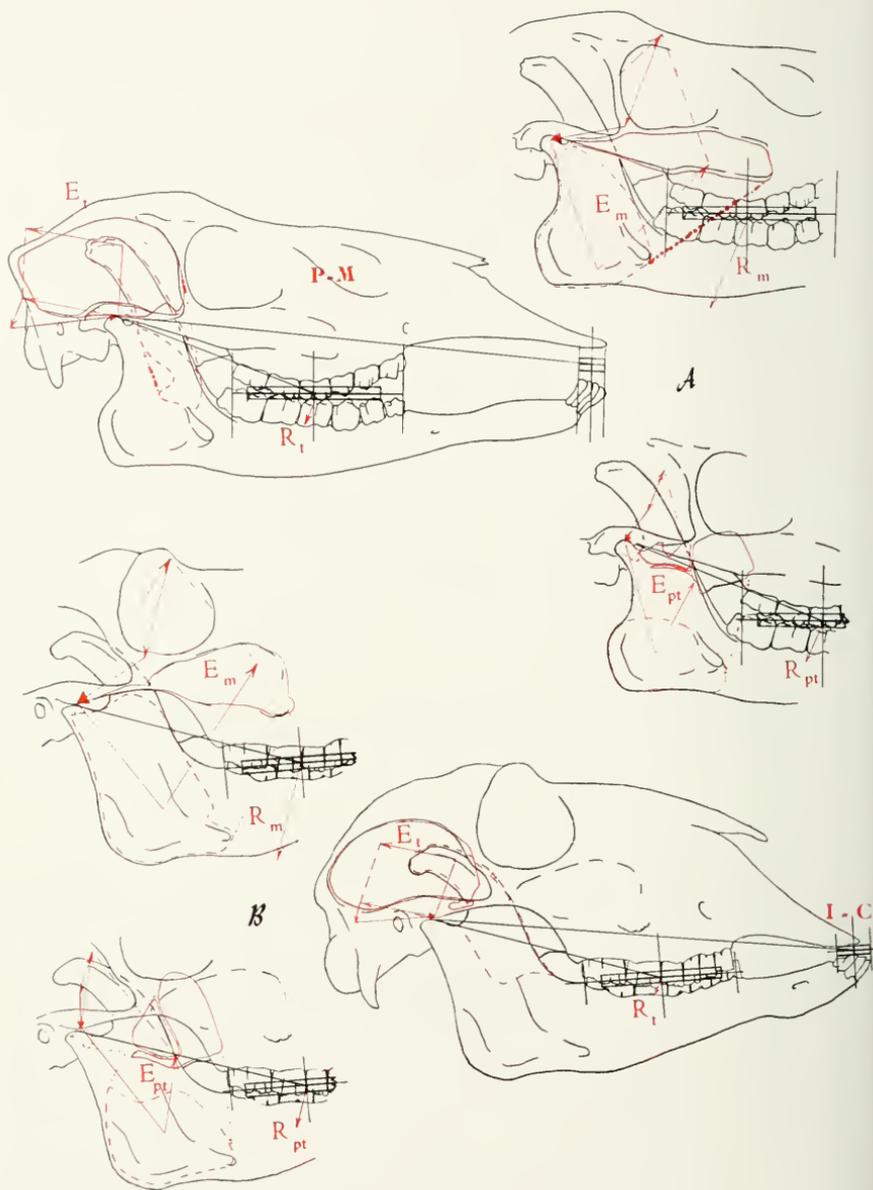


FIG. 45. Outline drawings of skull and jaws of *Odocoileus* (A) and *Orvis* (B) showing all of the other features explained in the caption to Figure 42.

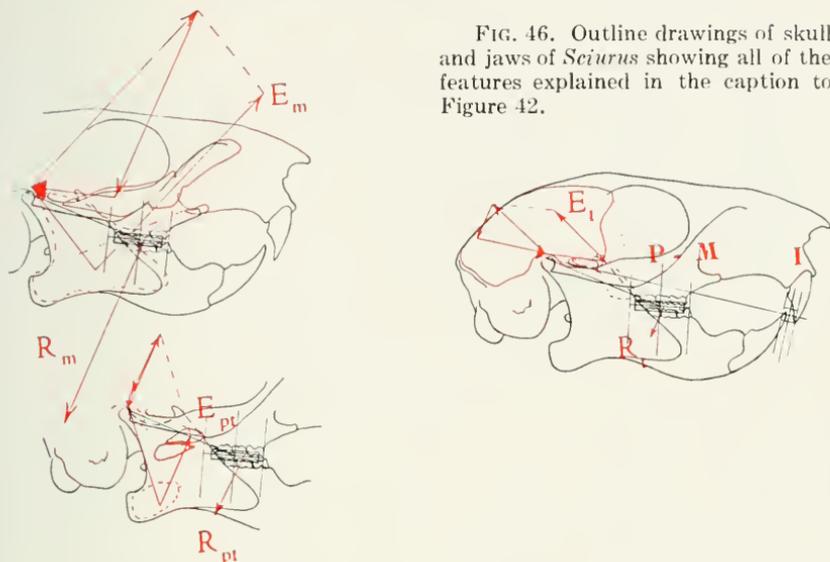


FIG. 46. Outline drawings of skull and jaws of *Sciurus* showing all of the features explained in the caption to Figure 42.

it is a simple matter to determine the values of F_L as described earlier (and see fig. 41). For F_X , sketches (not shown here, but similar to fig. 1, B) are made corresponding to these in Figures 42-47, but in them the projection is onto the idealized vertical cross-section plane. This plane (discussed on pp. 282-284) passes through the jaw musculature. A value for F_X nearly always can be selected according to the extent to which the muscle being considered diverges from the vertical (i.e., from the longitudinal plane) as seen in this idealized cross-section view.¹

The following calculations apply to the P-M region at about level of M_{\perp} . When the same calculations are made for the I-C region, the corresponding values of E are all proportionately smaller because the resultant lever arms are lengthened.

¹ Generally, since the jaw-closing movement lies more or less within the longitudinal plane that part of lever mechanics relating to lever arm lengths as they lie within or projected onto the cross-section plane can be ignored, and only muscle pull directional trends away from the vertical need to be considered. The possible exceptions to this would occur in species with extremely short and, at the same time, broad faces. In such unusual cases, a value for F_X would be more difficult to arrive at. In that instance, since the levers themselves would tend to lie more within the cross-sectional plane than within the longitudinal one, they would have to be considered, too. This could be done by further complicating the sketches by drawing in the jaw condyle, the horizontal ramus, and the dentition, in order that the lever arms could be accurately added. Then, F_X would be determined in the usual ways except that it would be further qualified by an additional factor, i.e., multiplied by the ratio, E/R , of the lengths of the lever arms (in this plane).

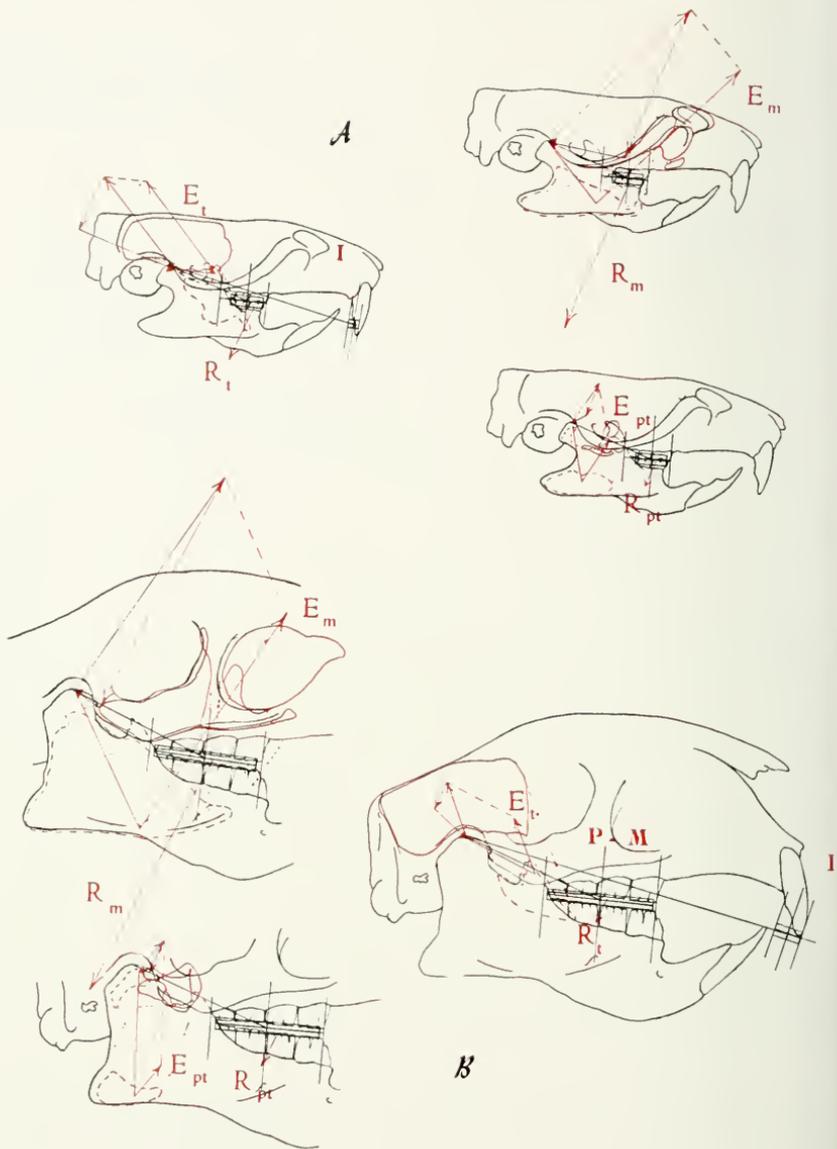


FIG. 47. Outline drawings of skull and jaws of *Rattus* (A) and *Hystrix* (B) showing the jaw-closing muscles' attachment fields and the other features explained in the caption to Figure 42.

*Jaw-Closing Useful Power (Efficiency) Calculations—Generalized Group***Didelphis**

$E = M \times F_L \times F_X \times r$	% of total adductor power (comp. w/muscle mass)	Change in C_e from direct muscle proportion C_e	Ratio of muscle group in comparison w/smaller group
$Et = 56.9 \times 1 \times .87 \times 3/8 = 18.6$	62	+5	10.9
$Em = 34.1 \times .87 \times .87 \times 3/8 = 9.7$	32	-2	5.7
$Ept = 9.0 \times .87 \times .71 \times 5/16 = 1.7$	6	-3	1
Total	30.0	100%	

For the I-C regions $Et=11.4$; $Em=5.9$; $Ept=1.1$

Echinosorex

$Et = 61.2 \times .87 \times .71 \times 1/3 = 12.6$	58	-3	5.3
$Em = 27.0 \times .87 \times .87 \times 1/3 = 6.8$	31	+4	2.8
$Ept = 11.8 \times .87 \times .71 \times 1/3 = 2.4$	11	-1	1
Total	21.8	100%	

For the I-C region $Et=7.6$; $Em=4.0$; $Ept=1.4$

Jaw-Closing Useful Power (Efficiency) Calculations—Specialized Groups

GROUP I—"CARNIVORE SHEAR" TYPE

Felis

$Et = 54 \times .87 \times .71 \times 3/7 = 14.4$	49	-5	7.5
$Em = 35 \times 1.0 \times .87 \times 3/7 = 13.1$	45	+10	6.9
$Ept = 11 \times .87 \times .71 \times 2/7 = 1.9$	7	-4	1
Total	29.4	101%	

For the I-C region, $Et=8.4$; $Em=7.6$; and $Ept=1.1$

GROUP II—"UNGULATE-GRINDING" TYPE

Equus

$Et = 14.5 \times 1 \times .87 \times 1/5 = 2.5$	4	-11	1
$Em = 54.5 \times .87 \times 1 \times 4/5 = 37.9$	65	+10	15.2
$Ept = 31.0 \times .71 \times 1 \times 4/5 = 17.6$	30	-1	7.0
Total	58.0	99%	

For the I-C region, $Et=1.4$; $Em=21.7$; and $Ept=10.1$

Odocoileus

$Et = 29.4 \times 1 \times .87 \times 7/20 = 9.0$	22	-7	1
$Em = 46.1 \times .87 \times .87 \times 13/20 = 22.7$	55	+9	2.5
$Ept = 24.5 \times .71 \times 1 \times 11/20 = 9.6$	23	-2	1.1
Total	41.3	100%	

For the I-C region, $Et=4.7$; $Em=11.8$; and $Ept=5.0$

Ovis

$Et = 23.5 \times 1 \times .87 \times 1/4 = 5.1$	12	-12	1
$Em = 52.5 \times .87 \times 1 \times 3/5 = 27.4$	64	+11	5.4
$Ept = 24.0 \times .71 \times 1 \times 3/5 = 10.2$	24	—	2
Total	42.7	100%	

For the I-C region, $Et=2.8$; $Em=15.2$; and $Ept=5.6$

GROUP III—"RODENT-GNAWING" TYPE**Sciurus**

$Et = 19.4 \times .71 \times 1 \times 1/2 = 6.9$	10	- 9	1
$Em = 61.0 \times 1 \times 1 \times 6/7 = 52.3$	74	+13	7.6
$Ept = 19.6 \times .71 \times 1 \times 6/7 = 11.9$	17	- 3	1.7
Total	71.1	100%	

For the I-C region, $Et=3.4$; $Em=26.1$; and $Ept=6.0$

Rattus

$Et = 32.6 \times .71 \times 1 \times 1/2 = 11.6$	21	-12	3.5
$Em = 54.1 \times 1 \times .87 \times 5/6 = 39.2$	73	+19	11.9
$Ept = 13.3 \times .71 \times .71 \times 2/5 = 3.3$	6	- 7	1
Total	54.1	100%	

For the I-C region, $Et=6.6$; $Em=22.5$; and $Ept=2.5$

Hystrix

$Et = 16.6 \times .71 \times 1 \times 1/2 = 5.9$	8	- 9	1
$Em = 71.9 \times .87 \times 1 \times 1/1 = 62.6$	84	+12	12
$Ept = 11.5 \times .71 \times .87 \times 8/9 = 6.3$	8	- 4	1.2
Total	74.8	100%	

For the I-C region, $Et=2.9$; $Em=31.3$; and $Ept=3.2$

Tables B-E (see Appendix) summarize the above relative efficiency information and also provide jaw-closing efficiency (useful power) proportion calculations for all of the other taxa for which the basic prerequisite muscle proportion data have been reported in the literature.¹ The muscle proportions of the latter are also included in the Appendix Tables B - E. The useful power proportions have been calculated with reference to the functional midpoint of the cheek tooth region (i.e., P-M region, at about level of $M\frac{1}{2}$). They were arrived at in the manner indicated above (pp. 281-292).

The confidence that can be put in such calculations of useful power (E) that are based upon data drawn from two or more sources (a

¹ Except the Fabian (1925) and Kuhlhorn (1939) entries (see Tables XI - XIV) which were added in press.

literature source for the muscle proportion data and a muscle attachment and lever map based upon other individual specimens) is naturally lower than it would be were the same specimen to be used throughout. However, when a series of checks on consistency of results was made, using various prepared skulls as the basis for muscle attachment field maps, it was found that only minor variations of a few per cent resulted. Hence, even with my own dissections, I consistently used a prepared skull of another individual to map out the origin and insertion areas and to measure lever arm lengths and figure the angles for the correction factors. (Apparently, the gain from a more exact mapping more than offsets any loss due to individual variation.) The aspect which is perhaps the most subject to error is the locating of the functional midpoint for each muscle group's attachment fields in the absence of a dissection. Location of this point normally reflects a compensation for the form and asymmetries of the mass of the muscle, and, of course, there is no sure way to make a judgment with only a skull and a tabulation of the muscle weights or proportions to go on.

It is of interest to make two kinds of comparison (using Tables B-E) at this point: 1) direct comparison of the calculated relative jaw-closing useful power (percentage) values with the measured (or reported) jaw-closing muscle proportion values themselves, and 2) comparison of the ways any changes in these sets of proportions may affect the manner of characterizing each of the adaptive groups. The first of these comparisons is covered by Tables B-E. It is noteworthy that the proportionate change column shows generally consistent patterns within the adaptive groupings. Furthermore, for closely related forms there is a reasonable consistency as regards the direction of change. Most evident and important is the fact that the mechanical advantages imparted by the various functioning lever systems concerned frequently do indeed produce significant, measurable changes in efficiency proportions from estimates based solely upon muscle proportions.¹ For example, the relatively weakly developed pterygoid musculature of *Didelphis* operates a less efficient lever system (as regards jaw closure) than do either the masseter or

¹ In working with these tables one must be very cautious about 'reading in' a significance where there is an isolated proportionate change of the order of 10-15% or less for, in my opinion, the level of accuracy of the estimates of average angle of muscle pull and average working distances is too crude to permit this. On the other hand, the tables show a good number of instances for which the proportionate change is consistently of a greater order of magnitude (20-25% or more). In these instances there can be little doubt about the fact that such a degree of change does have significance.

the temporalis, and the proportionate change column shows this. It also gives some idea of the extent to which the lever mechanics alters effectiveness of the jaw-closing apparatus. Similarly, the dominant masseter in *Ovis* is seen to make such excellent use of its power through an advantageous leverage mechanics that it shows a significant gain in the proportionate change column.

The second kind of comparison concerns how changes between direct muscle proportions and those incorporating the useful power proportions (summarized in the "proportionate change" column of Tables B-E) may influence characterization of the adaptive groups. For simplicity, in the balance of this chapter the words "gain" and "loss" refer to such changes. First, let us consider the Generalized Group which on the basis of muscle proportions was characterized by the marked dominance of its temporalis musculature, and by the consistency of the ranking order of the jaw-closing muscles which descends from Temporalis, to Masseter, to Pterygoideus (see p. 248). In this group no very striking or consistent changes occur between muscle efficiency proportions based on useful power as compared with direct muscle proportions, and no clearly-marked trends are evident on the basis of the information currently available. The order of ranking never changes. Hence, in no major way does it appear necessary to alter the characterization of the group. However, there is a curious break in the proportionate change column (Table B) for the *M. pterygoideus* muscle group. The gains are exclusively within the section containing the Hominoidea; all of the rest of the forms in the Generalized Group show either no change, or a loss, in this column.¹ This may be significant. Should this pattern continue to

¹ Again, as with other higher primate peculiarities, one is tempted to speculate about the possible significance. This Hominoid exception may be accounted for by considering that super-family to be peripheral in its position in relation to the others within the Generalized Group. It is evident that while the Hominoidea as placental mammals are basically quite generalized in a number of respects (limb and body proportions, morphology, and dental form, etc.), its members show other features that denote a marked degree of specialization (extensive brain development and complexity, great manual dexterity, and ocular co-ordination). We may infer that accompanying these specializations, others related to the manner of use of the dentition and the jaw musculature occurred, too, as indeed the fossil record shows in a general way. In the evolution within the Hominoidea apparently the jaws and teeth became less dominated by selection solely for food gathering and processing, and defensive, or sexual combative functions, and became relatively more dominated by other functions. One such function may have been an increased use of the dentition (and hence of the jaw muscles) as a simple holding device, which action would thus free the hands for other uses. Another, is its use as a delicate manipulating "tool," used either in conjunction with the hands, or largely independent of them. Social grooming is a prime example of such activity. Still another such superimposed function, and this is perhaps the most important development, reached its culmination in *Homo*—use of the jaw musculature to assist the

hold when a broader group coverage becomes available, then a re-characterization of the Generalized Group may well be in order so that this feature (Hominoid peculiarity) may become part of the characterization.

We now turn to the representatives of Specialized Group I ("carnivore-shear" type) in the search for proportion changes between the jaw muscles and the mechanical (useful power) efficiency with which they are used that might cause us to alter the characterization of the group. Again, as with the Generalized Group, no very major change is required. Members of both groups tend to utilize their weak pterygoideus group muscles quite inefficiently. Unlike the Generalized Group where the trend was a weak and erratic one and where there was an exception which called for a rationalization (Hominoidea), in Specialized Group I, a consistent, often pronounced, tendency for inefficient utilization of the pterygoideus is noted. Thus, in addition to a weakly-developed pterygoid muscle group in Specialized Group I (see characterization, p. 251), we find that the leverage considerations cause this weakest of the muscle groups to be inefficiently utilized. Hence this fact is appended as a modification of the means of characterizing the group. There are no consistent or significant changes of this sort for the temporalis or masseter muscle groups.

In the Specialized Group II ("ungulate-grinding" type) forms, the proportionate change column of Table D shows that there is a consistent loss in per cent between muscle mass proportion and muscle useful power proportion at the significant level (by my conservative standard) for the temporalis group. Similarly, although borderline as regards level of significance, there is also a consistent gain for the

tongue in controlling the shape, size, mobility, etc., of the oral cavity for producing the complex vocalizations of communication, be these simple stereotyped calls, or complex speech (language). DuBrul (1958) has discussed this in detail in a fascinating (and generally overlooked) work. He shows how the basic sucking, biting, chewing, and swallowing acts have been taken over, modified, and "chopped up" and incorporated into the mechanisms of speech formation. Many of these speech actions require control that is both subtle and precise, and often this control must be operated over a broad range and be effected with great speed. In the Hominoidea all such speech and pre-speech uses call for a more equally balanced jaw musculature (for sheer power is not necessary) than is the case for the other members of the Anthroipoidea which adhere with far less deviation to the pattern of the majority of forms within the Generalized Group. In general, the evidence of the masticatory apparatus, especially the reduced jaw musculature, with its more nearly equal muscle groups, supports many of the ideas on protohominoid and early hominoid pre-speech developments presented by Hockett and Ascher (1964) who have recently set forth a detailed conceptualization which reconstructs the significant steps of human evolution from the protohominid stage through the pro-hominid stage to a fully hominid stage.

Masseter group. I, therefore, append these facts to the characterization of the group (see p. 255).

In the Specialized Group III ("rodent-gnawing" type) forms the proportionate change column (Table E) indicates that significant changes occur between the direct muscle proportions and the efficiency proportions in all three jaw-closing muscle groups (see p. 259) with regard to each jaw-closing muscle group. Consistently, the dominant masseter group is further enhanced by a more efficient mechanics than the other groups have (for an effective gain of between 15 and 36%). Conversely, with equal consistency, but to a far more variable degree, the weaker muscle groups have a less advantageous mechanics. Hence, they are even less dominant than the direct muscle proportions appear to indicate. The temporalis loss is generally close to 50% (ranging from 36-58%) and that for the pterygoideus is both less pronounced (on the average much less than 50%) and more variable (15 to 63%).

Summary and Conclusions

In the Preface and Introduction the history and nature of studies of the mammalian masticatory apparatus are considered. The fundamental plan and the various basic adaptive arrangements of the masticatory structures are discussed and broadly categorized. Most significantly, 1) in addition to the usually recognized Specialized Groups, a Generalized Group is designated and characterized, and 2) the need to recognize and handle the totality of the Mammalia in such categorizations is set forth. The Generalized Group is considered to occupy a central "core" position, which makes it the most important of all the groups to know, recognize, and understand. It is found to correspond quite well with the generalized metatherian-eutherian grade mammals long since recognized by paleontologists and anatomists mainly on the basis of their dental and skeletal features. This approach provides a focus for the study of mammalian masticatory adaptation and brings further order and significance to the field.

In the second section of the work, detailed descriptions of dissections of the jaw musculature of a representative assortment of the recognized adaptive types are given. These follow a set, standard, consistent plan which provides a fundamental basis for direct comparisons, and for an elementary comparative mechanics. This procedure is a basic requisite of any work that is to serve these comparative ends. The other results from this section follow in order of their importance: 1) new descriptive information on *Echinosorex* is given, the jaw musculature of which has not previously been reported; 2) significant additional details and descriptive information on *Didelphis*, *Felis*, *Odocoileus*, *Sciurus*, and *Hystrix* are set forth; 3) a broadened comparative base is provided by the other forms dissected (*Equus*, *Ovis*, *Rattus*) and, finally, 4) scattered descriptions are brought together and some are translated as a service of convenience.

The third section of this work treats the adaptive groups in detail, and deals with the nature of a number of problems related to the

comparisons, especially to a comparative mechanics. Included are discussions of some of the limitations of such comparisons and methods as they are used, both here and by others. At the end of Section III, each adaptive group is characterized anew on the basis of both inter- and intra-group comparisons of jaw muscle proportions. A set of graphic comparisons has been devised for this purpose. The characterizations are conservatively drawn. In general, for the three Specialized Groups they constitute refinements and elaborations of earlier characterizations.

In the fourth section, mechanics in relation to functions are considered. Fundamentally, the relative degree of muscle development and lever mechanics are treated as the principal elements in jaw mechanics, and a simple formula for extending jaw muscle comparisons up to a static mechanical useful power level is proposed and utilized. The results of this treatment are discussed.

Application of the formula for calculating an estimate of relative jaw-closing power efficiency for the major muscle groups is presented. This includes its application, not only to the forms dissected for this study, but also to all others from the literature for which the necessary muscle proportion data were available. Thus, the broadest possible mechanical comparison is gained, which in turn leads to further refinement of the characterizations for some adaptive groups.

Characteristics of the Generalized Group are as follows: There is a strong tendency for the dentition to be of the primitive, metatherian-eutherian type with a full, or nearly full, dental formula, and with the teeth having the primitive cusp arrangements little modified. Jaw closure is snapping, and the movement which is restricted laterally is of the hinge type. The temporalis musculature is always dominant; the order of dominance consistently descends from the temporalis group to masseter group to pterygoideus group; and most variations in the temporalis musculature are offset by reciprocal changes in the masseter musculature. No clear-cut trends are observed as a result of application of the formula for jaw-closing efficiency, though there seems to be a tendency for the forms of the Generalized Group to utilize the pterygoideus complex less efficiently than the other jaw muscle groups. This tendency is reversed, however, in one segment of the group, the Hominoidea.

An important additional comment not noted by earlier workers emerges at this point. The large size of the temporal fossa in Mesozoic and in very many early Tertiary mammals, and even in some mid-Tertiary ones, especially those of South America, provides evidence that the pattern of jaw muscle proportions characteristic of the Generalized Group is extremely versatile in its functional capabilities. Without major alterations, in addition to serving the primitive mammals and those with a generalized mammalian dentition (i.e., forms of Generalized Group), this muscle pattern appears to be quite capable of serving some mammals that have achieved an advanced dental specialization. In the carnivorous direction, the forms of Specialized Group I all have their masticatory musculature proportioned, essentially as do the forms in the Generalized Group. In the herbivorous, ungulate-like direction, many forms that closely approach Specialized Group II dentally, nevertheless still have (or apparently had) a jaw musculature with the proportions typical of members of the Generalized Group. Taeniodonts, Homalodotheres, Toxodonts, Astrapotheres, Uintatheres, and Proboscideans all retain the primitive condition of a dominant Temporalis muscle, or at least a very highly developed one, in spite of their very advanced and specialized dentitions. Even within the more modern groups of ungulates, many of the early forms show a tendency for this same kind of generalized jaw muscle pattern; to judge by the temporal fossa, the temporalis in condylarths, titanotheres, early rhinos, and chalicotheres was relatively much more massive a muscle than it is in any of the more advanced perissodaetyls. I conclude, therefore, that this great versatility of the generalized musculature, which enables it to serve not only a generalized dentition and generalized masticatory functions, but also to serve some very advanced, specialized ones as well, is of great importance. Apparently, only with very drastic modification of the dentition and/or other parts of the masticatory apparatus (such as exists in Specialized Groups II and III) does it become necessary for the musculature to become distinctly altered.

Specialized Group I is characterized by adaptations for predation: a long, tapered snout, a fast-acting, powerful, but generalized jaw musculature capable of straight hinge closure, and a dentition equipped for grasping, piercing, slashing, and shearing. Jaw muscle proportions are basically similar to those present in forms of the Gen-

eralized Group. The tendency for the masseter muscle group to offset the extensive temporalis dominance by itself (i.e., without the pterygoideus group sharing this reciprocation) is even more marked in Specialized Group I than in the Generalized Group. Calculations of jaw-closing useful power indicate that these forms consistently tend toward a poor level of utilization of the pterygoideus musculature, the weakest of its jaw-closing muscle components. Thus, we see that Specialized Group I is, in fact, specialized mostly only dentally, particularly for shearing in the premolar-molar region. Other features of the masticatory apparatus show close similarity to those of the Generalized Group, for the musculature and lever mechanics are much the same. These results therefore reinforce the concept discussed above of primitiveness and broad versatility of the Generalized Group's jaw muscle proportion pattern. Specialized Group I is, in this sense, the least specialized of the three adaptively specialized groups although the animals included in this group possess complex dentitions.

In contrast to these rather broad, comparative aspects, two items of a more particular nature relating to carnivores require some discussion. The first relates to work by Becht (1953, p. 512, figs. 3, 4) that treats glenoid and condylar shapes and function: Becht states that when viewed from behind the condylar heads of the jaws of a tiger present laterally tapering, cone-shaped articular surfaces. He makes much of this as a device that functions as a precise securing mechanism, which prohibits an excessive transverse (lateral) movement while still allowing lateral pressure, and thus is a means of insuring a good scissor-closing action. It is true that the condyles of most felids show this lateral taper in caudal view, but this is not the case when they are viewed from the top. In that aspect they present a more nearly straight, parallel-sided outline, or, in some instances, they even taper slightly in the medial direction. In addition, the glenoid itself shows very little if any taper. Thus, I do not find in the glenoid-condyle articulation the very neat mechanism for insuring good shearing action or preventing an excess of lateral movement that Becht has reported. As I see it, the tapered appearance of the posterior face of the condyle simply reflects the hyperdevelopment of a surface for articulation with the equally hyperdeveloped post-glenoid process. The reason for the hyperdevelopment of the latter has been analyzed by Davis (1955) and has been further discussed above. It is sufficient to note that this hyperdevelopment is in response to the strong, posteriorly directed resultant pressures at the joint. It is conceivable that such a post-glenoid expansion could form a cone-shaped glenoid cavity in which a conformably cone-shaped condyle could articulate, and thereby function as Becht sug-

gested, but, in fact, it does not do so to any marked degree, as far as I can see, either in the tiger or in other felids. However, Becht's notion that some apparatus must perform such a securing function in order to guarantee an effective shear is one with which I am in entire agreement. Worthmann (1922) and Baum and Zeitschmann (1936) completely overlooked the necessity for such a device, although Brodie (1934b), Starek (1935), Sicher (1944), and Davis (1955) all recognized it clearly. Every (personal communication), on the other hand, minimizes the need for this. He claims that the escapement clefts between the valleys along vertical shearing surfaces and the "hollow ground" nature of the blades eliminates much of this need for strong lateral pressures. This, too, seems to be an overlooked point. However, at the beginning of each bite before the bolus has "locked" the shear surfaces into place relative to one another, a very precise and definite lateral pressure requirement exists. Scapino (1965) provides the most recent significant advance in understanding within this area. His study disclosed happenings at the jaw joints of dogs during 1) centric jaw opening, 2) lateral shifting for carnassial alignment, and 3) the subsequent forceful closure of the jaws.

The second item is related to the former in that it may provide the securing or checking device necessary for achieving the precise alignment needed for an effective shear function. It was noted above that in *Felis*, *M. pterygoideus externus* has a most peculiar twisted form (fig. 12C), at least when compared with a broad suite of mammals. It is this twisting of several strands into a strong, taut cord that provides a checking cable or stop mechanism. This self-tightening, taut-cord feature could function in several ways: 1) On the active side of the jaw, at the onset of jaw closure, it could prevent excessive lateral shifting of the open jaws so as to prevent them from overshooting at any stage of the rapid closure stroke. Thus, it could prevent an inappropriate dental contact and the probable traumatic results of such contact. Also, as the very end of the shearing stroke is approached, a final tightening would serve to counteract the pull of the still tightly tensed masseter, and thereby allow enough movement toward the centric position to let the jaws close fully without any jamming of the lower carnassial blade against the protocone of the upper tooth. 2) On the side opposite the active side, it would provide some lateral pressures (slight because of their transference across a flexible symphysis). Combined lateral pressures would result, as Becht indicated, from the synergistic action of the *M. zygomaticomandibularis* of the active side and the *Mm. pterygoideus internus* and *externus* of the opposite side; these muscles are the only ones with strong laterally directed components. Whether or not a similar condition of *M. pterygoideus externus* applies in other felids, or in any of the rest of the carnivores is a matter for further investigation.

Specialized Group II is characterized by both jaw musculature and by dental specialization. There is a strong tendency for development of an incisor cropping device in the incisor-canine region of the dentition, accompanied by variably developed canines. The markedly modified, usually crested or lophed premolar-molar dentition, which has evolved for the complex grinding movements necessary to break down fibrous plant foods, dominates the group characterization. The musculature for operating this dental battery with its more pronounced lateral and medial movements is, to judge by the living forms, strikingly distinctive in its proportions from that of the other groups. Consistent temporalis group dominance has been supplanted by masseter group dominance. For about half the forms reported, the temporalis musculature shows the least development among the jaw muscle groups. No consistent pattern of reciprocal development to offset the dominant muscle group is found. From the standpoint of relative jaw-closing useful power, it is observed that the temporalis group lost and the masseter group gained, relative to the proportions assumed from direct comparisons of the muscles themselves. These facts I interpret as indicating that Specialized Group II marks a more extreme level of specialization away from the Generalized Group than does Specialized Group I. The generalized muscle proportion pattern (and to some extent its leverages) is no longer adequate for the demands of the dentition and accordingly it has been drastically altered. The ways in which this has been accomplished show variation and at present no consistent order is recognizable.

An interesting particular noted in the equids deserves notice here; the mammalian masseter group musculature *usually* is arranged according to a more or less uniformly layered plan: sheets, or divisions of sheets, are superimposed conformably one upon the other. In my dissection of *Equus*, immediately beneath the superficial masseter (and incorporated into it) there appeared a distinctly different sort of pattern. A stout tendon interrupted the familiar layering and intersected the mass so as to insert upon the angular process in a rugose line running at right angles to those made by the insertion of the tendon sheets within the layers of masseter muscle (figs. 14B; 15A). Clearly, an explanation for such an exceptional condition should be sought. An almost diagrammatic picture of the origin and evolution of this peculiarity is to be found in certain Miocene and Pliocene fossil horse genera (fig. 47). It is correlated with all of those other features that indicate the shift in habitus from browsing to grazing, and is fully understandable in the light of increased mechanical requirements accompanying this shift; the need was obviously for an

expanded jaw musculature located so as to afford greater mechanical advantage. This need was satisfied by adding new muscle anterior to the usual front edge of the masseter to both superficial and deep layers, thereby gaining a much improved leverage advantage. The tendon bar situated transverse to the layering of the masseter thus appears to be a further development of what was once (in the Oligocene and earlier) the anterior edge of the masseter and its superficial, anteriorly enveloping tendon sheet. The beginnings of this change can be seen in *Parahippus* and *Merychippus*, and it is seen to be coming into progressively full development in *Neohippiarion*, *Pliohippus*, *Hippotigris*, and *Equus* (fig. 48A-E). In fact, once focused upon, this development can even be seen incipiently in *Mesohippus*. This is a shorter range development concurrent with the later phases of the general reduction of importance of the temporalis muscle and gain of the masseter. Temporalis reduction is inferred from the decrease in proportionate size and degree of cresting of the temporal fossa, which correlates with advances in the equid lineage.

Specialized Group III is characterized by a distinctive jaw musculature and by a dentition sharply divided into two distinct functional regions. The anterior part of the incisor-canine region has become drastically altered for gnawing by a reduction in number of teeth to a few fully hypsodont, chisel-shaped ones. Hypsodonty in the premolar-molar region is more variable, and the number of teeth in this region is also considerably reduced. The distinctive diastema between these dental regions in both upper and lower jaws and the shortened span in the lower jaw between the functional incisor surfaces and the jaw joint imposes two requirements. One of these, anterior shifting, allows the incisors to function and the cheek teeth to disengage; equally important is the other, posterior shifting, back to the normal grinding position, which brings the cheek teeth into function and disengages the incisors. The generalized jaw muscle arrangement was evidently unable to cope with these modifications—at least this is true for the advanced stage of development represented by the living forms. During the evolution of this Specialized Group III, the masseter complex became by far the dominant jaw muscle group and grew to operate with the greatest efficiency due to advantageous lever mechanics. The once dominant temporalis, in the living group III forms usually accounts for only 10–20% of the total jaw-closing musculature—a percentage comparable to that of the pterygoid group. Masseter dominance is consistent and appears to have been so in most fossil forms, too, perhaps even in the earliest rodents (Wood, 1965). So great has been the need for in-

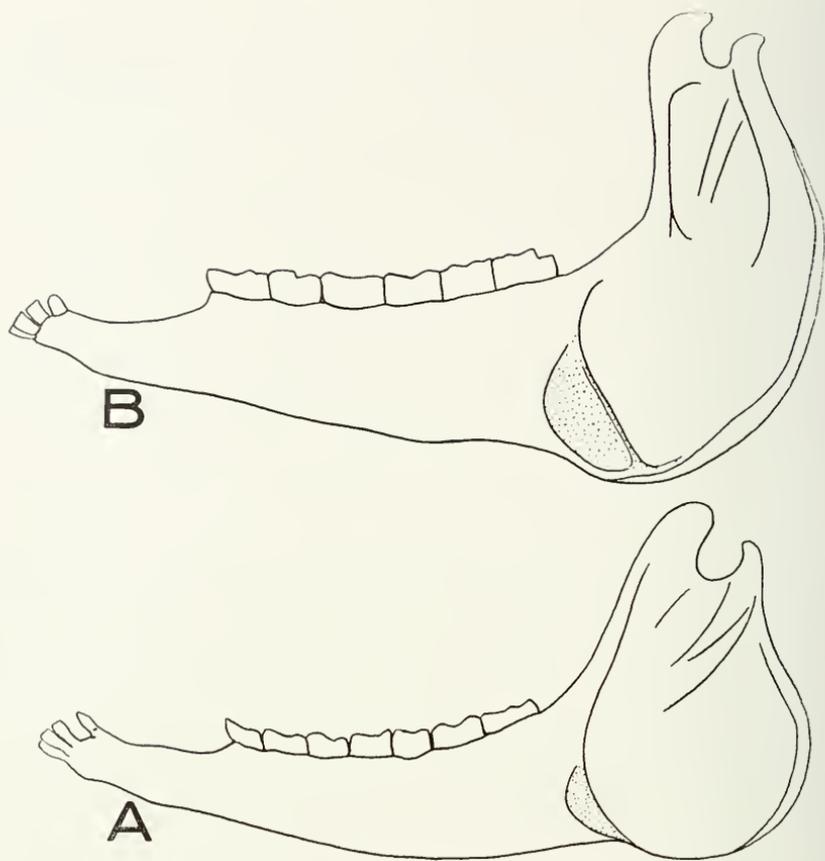
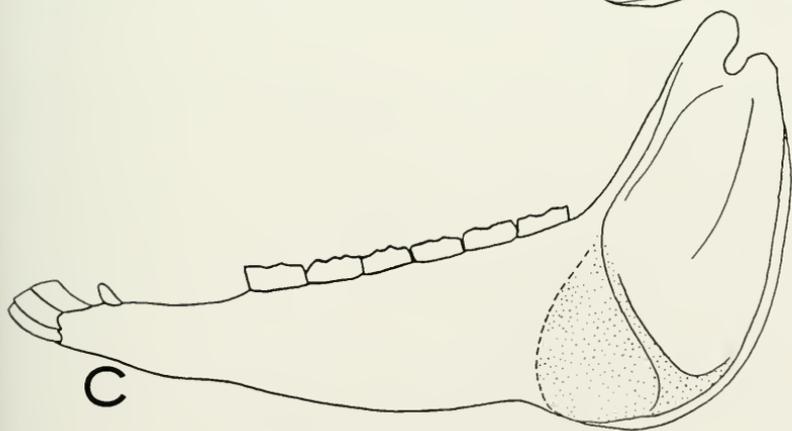
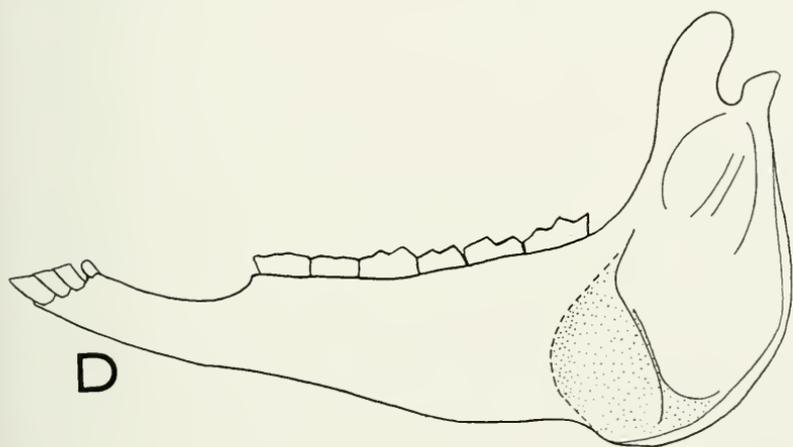


FIG. 48. Evolution of the peculiar insertion tendon bar of the deep masseter in *Equus*. A, FMNH P 25144, *Mesohippus*. B, FMNH UM 530, *Meryhippus*. C, FMNH P 27113, *Pliohippus*. D, FMNH P 26926, *Neohipparion*. E, FMNH 41095, *Equus*.

Stippled area=anterior attachment of the original tendinous covering of the masseter, and in the more recent forms the subsequently added anteriormost mass of the masseter. This area is seen to increase both absolutely and in relative proportion in the sequence from the *Mesohippus* to *Equus*. Note, too, that the more anteriorly situated insertion in the terminal members of the series places the muscle in a position of greater mechanical advantage, i.e., further from the jaw joint (fulcrum).



creased masseter apparatus that apparently in some the zygomatico-mandibularis has given rise to a new muscle unique in this group—the maxillomandibularis. This new muscle acts to position the lower jaws (and hence the opposing cheek teeth) with great precision because of the unique manner by which its pull direction is concentrated on tendon strands and is bent pulley fashion around a rigid bony structure before inserting upon the jaws. The muscle passes through the infraorbital foramen, the lower rim of which acts as the pulley. It has an expanded area of origin attachment in front of the foramen. Such a precision positioning device compensates for the less restrictive glenoid which is more open in its construction, permitting anterior-posterior slipping to occur. In *Hystrix*, even the temporalis muscle functions somewhat around a "pulley," the posterior buttress of the zygomatic arch, apparently for the same reason.

The effectiveness of the gnawing incisors and other features peculiar to Specialized Group III may occasionally become so complete that in several rodent lineages (i.e., some Cricetines, Hershkovitz, 1962) the incisors assume the entire dental function. They make contact with the food initially, and efficiently perform not only the gnawing but also the masticatory function. When this happens, the cheek teeth apparently are left with little or no function to serve. Hershkovitz reported species for which this trend has been carried to the limit: the cheek teeth have atrophied to the point of extreme degeneracy, and are nearly functionless (although still hypsodont), simple cylindrical pegs. Such repeated occurrences demonstrate the remarkable degree of modification of Specialized Group III from the Generalized Group. Clearly, it is the most specialized of the successful Specialized Groups.

Consideration of the very few aberrant extinct groups for which a serious attempt to understand the masticatory apparatus (including the musculature) has been made, supports the conclusion arrived at here that in most instances evolution of the masticatory musculature lagged behind that of the dentition. These are: 1) Flerov's (1957) report that the Dinocerata had a Specialized Group I type of musculature¹ to serve a dentition that apparently belonged in Specialized Group II (the ungulate-mill type); 2) Owen's (1859, 1865,

¹ Flerov either confused Specialized Group I and Generalized Group patterns, or else he did not recognize the latter category at all. Whichever is the case, the muscle patterns of the two are essentially the same and his point is understandable—a generalized musculature serves a specialized dentition.

and 1870) and subsequent reports by other authors giving different interpretations (Gill, 1954; Woods, 1956), clearly shows that in spite of its remarkable shearing cheek teeth, *Thylacoleo*, the marsupial lion, had a temporal fossa indicating that it, too, operated with either a Generalized or Specialized Group I type of musculature; 3) Simpson's (1933b) analysis of the cranial features (giving muscle restorations) and dentition of a triconodont, which he concluded had the ultimate in dental shearing adaptations; 4) Simpson's (1933a) treatment of the multituberculates showed that dentally they had achieved the Specialized Group III level, although the evidence indicates the pattern of the temporalis musculature appears to have had a more generalized cast to it.

The need now is for similar fresh interpretations of some of the generalized (stem line) mammals. Difficult as they are to interpret, the patterns of wear-facets in the specialized groups are usually relatively easily understood compared with those in the generalized group.

Butler (1952, 1961, and subsequently) has done more to interpret dental-wear facets than any other worker.¹ Mills (1955, 1966), too, has done work along these same lines, but unfortunately he has employed another set of designations for the sets of dental wear-facets. These works and those of Every (1960, 1965, and personal communication, 1966) who has dealt mainly with primates and insectivores, reflect, as do the recent works of MacIntyre (1966), Van Valen (1966), Welsch (1967), and Mills and Kermack (in Pederson *et al.*, 1967), a growing interest in the potential of such approaches.

In the symmetrodonts and pantotheres, and in the generalized marsupials and insectivores —, i.e., those groups near the metatherian-eutherian stem — there are often many small restricted wear-facets occurring on individual cusps. These facets are situated at various angles of inclination, and often lie in several planes. These are caused by "micro-shearing" and grinding actions (operating in addition to

¹ His first study on this subject (Butler, 1952) was appended to a more narrowly restricted subject, and I feel has been somewhat overlooked because of this. In it he made a most significant contribution to our understanding of the meaning and the formation of dental wear facets. Working with a series of Perissodactyls, by identifying each facet of the molar teeth by correlating those that oppose one another in upper and lower dentitions, and by assigning a precisely defined set of numerals to each set of facets he has given us an orderly means of referring to them. Subsequently (Butler, 1961), he has reviewed the nature, origin, and evolution of these facets in many specialized groups including some of the very aberrant mammal lineages. He has arrived at a general explanation of the facets. More recently he had added one further refinement to the method: he now records the direction of movement that is scored into facets as minute wear striae. These he now indicates (approximately) schematically (pers. comm., 1966).

the major piercing-crushing actions) of cusp against food against cusp, not entire tooth against food against tooth. Presumably, these small facets on individual cusps should be interpretable in terms of jaw movements just as are the grosser facets in the specialized groups. In practice, however, such interpretations are often uncertain and difficult.¹ Also, in some instances attrition facets may form in another way, namely, from the abrasive action of food against cusp (or tooth) alone. In these cases, it is appressed there either by some soft structure, or by an adjacent though not directly occluding area of the opposing teeth. An example of this is to be found in *Solenodon* (I plan to describe this in detail in a future paper) in which the extensive faceting of the styler cusps can only be caused by the food itself as there is no possible way for this region of the upper teeth to occlude with any part of the lower teeth. Furthermore, the interlocking of the anterior teeth and the limitations of the jawjoint also prohibit such occlusion. Thus, I suspect that this sort of wear faceting may well prove to be more commonplace in the Generalized Group than is now recognized. Specifically, such examples must be kept in mind in interpreting facets on such teeth as those of the mammals of the Trinity formation, and other Mesozoic therians.

In the light of these many observations, it becomes apparent that the masticatory musculature in the generalized metatherian-eutherian grade mammals (Generalized adaptive Group) is an extremely facile structure. It is capable of serving a wide variety of dentitions (which may themselves be adapted for a variety of diets), from the most generalized to some that are quite specialized, before there is any need for it to become significantly altered in its own morphology and mechanics. Thus, it works well for the shear type (Specialized Group I), which requires little change in the leverages involved and which is still operable within the confines of the same basic muscle proportions and arrangements. Hence, the close similarity between this group and the Generalized Group.

The situation is markedly different, however, in Specialized Groups II and III. They are far removed from the generalized pattern and the specializations are evident in the alteration of the primitive generalized masticatory musculature. Typical of both the mill

¹ Every (personal communication) is also making important strides in tooth-wear facet interpretation. He distinguishes two main sorts of facets caused by food processing, abrasion, and attrition facets—the latter being the true facet of mastication. In addition, he recognizes another sort of attrition facet which is caused by tooth grinding—an innate tooth-sharpening response related to combative stress in Primates and some other mammalian orders.

type (Specialized Group II) and the gnawing type (Specialized Group III) is a great development of the masseter at the expense of the temporalis. There the similarity stops. In Group II, in addition to this change which affords a more powerful closing force, there is a considerable development of the pterygoid which provides (along with the zygomaticomandibularis) the force suited for the lateral shifting movements. However, there is evidence that the generalized muscle pattern is able, to a limited extent at least, to operate in forms with dentitions already quite specialized in the Group II direction—a fact that indicates Group II is perhaps not quite as far removed from the generalized condition as is Group III. In the latter, it appears that the masticatory musculature and the dentition made their remarkable evolutionary changes quickly and almost simultaneously. Apparently, the generalized pattern cannot meet adequately the additional requirements imposed by advanced gnawing incisor functions and the accompanying needs to shift the jaws forward to perform these operations. Hence, it is unlikely that the transition stages involving a generalized jaw muscle pattern operating a well-developed "rodent" dentition will be found.

Annotated Bibliography and Reference List

This extensive listing, and that given by Schumacher (1961a), together provide a reasonable coverage of the pertinent literature. It does have one particular deficiency: no attempt was made to thoroughly cover the German veterinary literature, especially that of the period from about 1890 to 1930 which is extensive, and is not readily available to me. The list is keyed by a few symbols to indicate the nature of the subject matter and its pertinence as follows:

General Works (G). These are usually comparative and/or descriptive studies treating more than one mammalian order. (Many of the standard comparative anatomies are omitted to save undue duplication in this area.)

Some works place emphasis on function or mechanical aspects and analysis (F).

Those in which the major emphasis is on the same subject matter as this study are designated by an asterisk (*).

Works that are more narrowly restricted taxonomically than the above are also included and designated by (R). The more useful ones for my purpose are further denoted by a (+).

Two other symbols are used, (P) and (N). The former indicates a work which deals with paleontological materials to a considerable degree. The latter indicates works frequently referred to by other authors but that are not easily available to me and hence were not seen.

Finally, works added while this was in press are designated by (A), and the many taxonomically restricted works (R) are tabulated (author's name, date) by order at the end of the bibliography.

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APPENDIX TABLE A

Listing of all mammalian orders with an assessment of our level of knowledge of the masticatory apparatus for each order.

Key to symbols:

[In the order and adaptive type of masticatory apparatus category] †=Extinct Group; G=Generalized Group; S I=Specialized Group I (carnivore-shearing type); S-II=Specialized Group II (herbivore-grinding type); S-III=Specialized Group III (rodent-gnawing type); N=None of the standard groups.

[In the Extent of Knowledge categories] E=Extensive; A=Adequate; B=Barely adequate; I=Inadequate.

[In the Number-letter scale of evaluation of the relative reliability of our information relating to jaw musculature] 1=Known through detailed, illustrated descriptions of dissections that give individual muscle (or muscle group) weights, proportions or percentages for a sample of the group, and a basic functional analysis that is at least as sophisticated as the one deemed usable for this work. 1A=In the case of fossil forms, those known through detailed, illustrated restorations of muscle masses based upon muscle attachment scar maps, and done in close comparison with living representatives, or at least with extant forms showing parallel adaptive features of the masticatory apparatus so that a reasonable assessment of function could be made. 2=Known through illustrations or descriptions of dissections, but lacking in enough detail to prevent making a comparative functional analysis without extensive restudy. Hence, those potentially capable of upgrading on the scale. 2A=For the fossil forms, those known through adequate materials which could have (but which have not) been studied adequately, nor had muscle restorations made. These, too, are capable of upgrading on this scale. 3=Known only through skeletal and dental features, there being no reasonably adequate descriptions of dissections available. Hence, these are potentially capable of upgrading to the number 1 position on this scale. 3A=Fossil forms known through less than adequate materials, so that it is not possible presently to restore skull and jaws adequately enough to permit reliable muscle restorations. Often these are known only from teeth. The potential for upgrading this group is dependent upon the discovery of further and more complete materials.

The orders are mainly those of Simpson, 1945, with slight modifications; Patterson, 1956, for Mesozoic mammals, and Ride, 1965, for marsupial orders.

TABLE A.—Level of our knowledge of masticatory apparatus for all mammalian orders.

Order and group classification	Extent of knowledge of —				Comments	
	Dental anatomy	Cranial anatomy	Jaw musculature	Functional mechanics		
NON-THERIA Monotremata N	(See comments)	A	B	I	2	All living forms have completely degenerate dentitions. Also the few known fossils. Very aberrant. Highly specialized for aquatic life and feeding, or for ant eating and digging.
†Multituberculata N or S-III	A	A	B	B to I	mostly 2A or 3A (1A for one)	A varied group. Most are specialized with procumbent incisors that were apparently used for piercing and grasping, and in many for gnawing; premolars for holding and shearing; molars for grinding. Muscle scars fit this interpretation.
†Triconodonta S-I (or possibly N or G)	B (A for one)	B	B	B to I	3A for most (1A for one)	Premolars and molars are highly efficient shearing structures, being elongated, serrate, and aligned. Virtually no ectental movement possible, but ectental force necessary to make the shear operate. Hence masticatory apparatus one of the most highly specialized of the carnivorous types.
†Docodonta N	B	I	I	I	3A	Molars with emphasis on opposition for crushing and grinding, hence presumably herbivorous in diet, possibly fructivorous and omnivorous, too.
THERIA †Symmetrodonta N, but with affinities to S-I and G (see text)	B	I to B	I to B	I to B	3A	Molars triangular with embrasure shear surfaces along oblique anterior and posterior facing sides. Crest on crest action evident, too, as indicated by minute wear facets on individual cusps. This is evidence for ectental movement (not just force). This is a key group for which understanding is needed as it is the earliest and most generally accepted ancestral group for all of the Theria.

Order and group classification	Extent of knowledge of—					Comments
	Dental anatomy	Cranial anatomy	Jaw musculature	Functional mechanics	Jaw musculature evaluation scale	
†Pantotheria G and S-I (see text)	B to A	B	B to I	I	3A	Molars basically triangular with embrasure shear surfaces as in Symmetrodonts. Here there is a notable additional development of protocone and talonid which provides the first good opportunity within the Theria for direct opposition for crushing and grinding. Therefore, in this group all three major functional dental components are present (shearing, alternation and opposition). Hence, for the rest of the orders this is the starting point, and, in this sense as well as in others (see text), it constitutes the basic or generalized kind of dentition for all Methatherian-Eutherian mammals.
Marsupialia. Here divided into: (1) Marsupicarnivora Most G, many S-I	A or E	A	B to A	B to I for most A to E for one	mostly 2A or 3, 1 for one case	Largely omnivorous-carnivorous or insectivorous in diet. Usually rather generalized in other ways. The S-I group shows a marked tendency toward strictly carnivorous or insectivorous diet as the scale of specialization ascends.
(2) Paucituberculata G to S-I	A to (B for †)	A to (I for †)	B to I	I (B by inference)	2	Insectivorous to insectivorous-carnivorous and possibly somewhat omnivorous. Molars have well developed labial, in-line shear surfaces, but cusps are high and well suited for piercing. They are directly opposed and also crush to some extent.
(3) Peramelina G	A or E	A	I	I	3	Insectivorous-omnivorous, but basically insectivorous.
(4) Diprotodonta S-II or S-III	A or E	A	B to I	B to I	some 2, most 2A, 3, 3A	Specialized omnivorous-herbivorous, but with strong tendency in most groups for herbivorous feeding.

TABLE A.—Level of our knowledge of masticatory apparatus for all mammalian orders (Continued).

Order and group classification	Extent of knowledge of—					Comments
	Dental anatomy	Cranial anatomy	Jaw musculature	Functional mechanics	Jaw musculature evaluation scale	
(5) Marsupialia, indet. as to order: †Thylacoleonidae N or S-I	A	A	B to I	I	2A	Highly specialized for shearing, thought to be carnivorous by some, herbivorous by others.
Notoryctidae N or G	A	A	B	I	3	Degenerate, generalized dentition. Insectivorous, possibly somewhat omnivorous feeders with extra teeth.
Insectivora. Here divided into: (1) Menotyphla G or N	E	E	A	A for one, B most	2	Generalized with insectivorous diet. Dentition with shearing, piercing predominant, but with crushing and crest-on-crest action evident, too.
(2) Lipotyphla G, but some tending toward S-I or S-II, or S-III. Some N	E	E	A	A to B	2	Insectivorous diet. Dentition with piercing and shearing predominant, but with crushing and grinding important in many, especially those tending toward S-II and S-III. Some specialized by loss of zygomatic arch, and/or by development of additional jaw articulation joints.
Dermoptera N or S-II	A (I for the † forms	A	I	I	3	Diet frugivorous and herbivorous. Dentition departed from typical generalized pierce-shear type in the direction of S-II for molars. Incisors highly modified "comb-like."
Chiroptera Many G, some approach S-I, others S-II, others N	E	E	B to I	I	3 for most, 2 for a few	Many bats have a generalized dentition with piercing and shearing components well developed. The group is very diverse, and crushing components are often added to the basically insectivorous or insectivorous-omnivorous dentitions. Crushing and grinding dominates in those that are frugivorous to herbivorous. Others are carnivorous, still others highly specialized blood-suckers.

TABLE A.—Level of our knowledge of masticatory apparatus for all mammalian orders (Continued).

Order and group classification	Extent of knowledge of—				Comments
	Dental anatomy	Cranial anatomy	Jaw musculature	Functional mechanics	
Primates G basically, some tendency toward S-II or S-III pronounced for many	E	E	A	A for some lesser values for most	Dentition has elements of shearing, crest-on-crest, grinding, piercing, and crushing action all present. Emphasis on grinding and crushing in those specialized toward the herbivorous diets. Most are omnivorous, but with a tendency toward one or more specializations for herbivorous, carnivorous, insectivorous, or frugivorous diets.
††Tillodontia G basically, but with tendency toward S-II	A	B	I	I	Dentition generalized, but with crushing and opposition well developed which appears to have been suitable for an omnivorous to herbivorous diet.
††Taeniodonta G for some, N for others	A	A to B	I	I	Earliest forms with distinctly more generalized dentition, but one with well-developed crushing-grinding opposition surfaces. Advanced later forms, specialized in peculiar ways quite removed from most other mammals, with canines enlarged and incisiform and cheek teeth hypsodont, cylindrical opposing crushing-grinding devices. Diet unknown, probably becoming more herbivorous at first, and probably becoming more herbivorous in the advanced forms, possibly root or tuber feeders.
Edentata †Paleanodontia N	B	B	I	I	Dentition degenerate, often suggesting specialization for insect feeding, especially ant or termite feeding. Diet may have been omnivorous-insectivorous.

TABLE A.—Level of our knowledge of masticatory apparatus for all mammalian orders (*Continued*).

Order and group classification	Extent of knowledge of —					Comments
	Dental anatomy	Cranial anatomy	Jaw musculature	Functional mechanics	Jaw musculature evaluation scale	
Xenarthra N	E	E	A for two, B or I for rest	B or I	2 for few, 3 or 3A for rest	Cheek dentition usually quite degenerate. Total masticatory apparatus specialized and modified. Marked tendency for unusual development of M. Masseter and sometimes M. digastricus. Diet varied, some herbivorous, some insectivorous, some omnivorous. Some of the insectivorous forms are highly adapted for ant or termite feeding. Some with dentition gone.
Pholidota N	A (edentulus)	A	I	I	3	Dentition gone in living forms, and dentary reduced, tongue specialized for ant-eating, hence these very specialized insectivore feeders.
Lagomorpha S-III	E	E	A	A	I	Incisors modified for gnawing and nipping. Diet herbivorous. One of the few forms for which cinematographic studies of chewing and swallowing have been made.
Rodentia S-III Sciuromorpha	E	E	A	A	I	Incisors for gnawing procumbent and so arranged that at least a moderate shifting is necessary for occlusion. Diet from omnivorous and insectivorous-omnivorous to frugivorous and herbivorous, mainly the latter two. M. masseter complex quite standard.
Myomorpha	E	E	A	A	I	Incisors as in Sciuromorpha. Diet also. M. masseter complex modified so that a M. maxillomandibularis is developed and passes through the infraorbital foramen.
Hystriomorpha	E	E	A	A	I	Incisors as in all Rodentia. Diet mainly herbivorous, some possibly omnivorous. M. masseter complex modified with M. maxillomandibularis hyperdeveloped and passing through the greatly enlarged infraorbital foramen.

Extent of knowledge of—

Jaw musculature evaluation scale

Order and group classification	Dental anatomy	Cranial anatomy	Jaw musculature	Functional mechanics	Jaw musculature evaluation scale	Comments
Cetacea N †Archaeoceti	A	A to B	I	I	2A	All with masticatory specialization involving dental degeneration. All basically carnivorous (fish or invertebrate feeders)—few exceptions reported. The most primitive whales. They have a near-normal placental dental formula with differentiation into distinct series. Cheek teeth alternating, with some cusp-on-cusp and shearing occlusion.
Odontoceti	E	E	B	I	3	All with dentition degenerated, individual teeth usually are simple cones. In some there is a considerable increase in number of teeth over the normal placental number.
Mysticeti	E	E	I	I	3	Complete degeneration of normal dentition and replacement by another structure—whalebone. Accordingly, there is a great reduction or degeneration of the masticatory muscles.
Carnivora S-I	E	E	E	A	I	Although this order typifies the S-I of shearing masticatory apparatus, it also contains members which have departed from this condition somewhat.
†Creodonta	A	A	B	I	2A	Tendency for the shearing-crushing modification.
Fissipeda	E	E	E	A	I	Most with predominantly piercing and shearing dentitions, some with additional departures toward crushing. Nearly all are carnivorous, insectivorous, piscivorous, invertebrate feeders, or carrion feeders. Few omnivorous or even herbivorous.
Pinnipeda	E	E	B	B	2 or 3	Tend to be modified toward reduced, simple alternating, often conical teeth.

TABLE A.—Level of our knowledge of masticatory apparatus for all mammalian orders (*Continued*).

Order and group classification	Extent of knowledge of—					Comments
	Dental anatomy	Cranial anatomy	Jaw musculature	Functional mechanics	Jaw musculature evaluation scale	
†Condylarthra G to S-II	E	A to E	B	I	2A	This close to, if not the basic, primitive ungulate stock and most features of the masticatory apparatus agree with this view. The dentition and jaw musculature were generalized, the dentition showing some tendency for cusp-on-cusp, crushing, shearing and grinding specializations which in their extreme approach those of the S-II group.
†Liptopterna S-II	E	A	B	I	2A	A condylarthran offshoot that has carried on the trend toward S-II type of specialization for mill action involving grinding as well as shearing-crushing movements.
†Notoungulata S-II						Presumably another condylarthran offshoot. Like the Litopterns they possess the S-II type of masticatory apparatus, with perhaps more emphasis upon grinding. Often with I-C specializations.
†Notioprogonia	A	A	B	I	2A	The most generalized of the suborders.
†Toxodonta	E	E	B	I	2A	
†Hegetotheria	A	A	B	I	2A	
†Tyopotheria	E	E	B	I	2A	
†Astrapotheria S-II	A	A	B	I	2A	One suborder has more generalized masticatory structures, especially dentition (<i>Trigonostylopidae</i>), while the other (<i>Astrapotherioidea</i>) has an advanced S-II kind of grinding dentition.
Tubulidentata N	A	A	A	I	1 or 2	Generally considered to be dentally degenerate. Cheek teeth presumably as simple opposing crushing tools. Show a unique histological specialization

TABLE A.—Level of our knowledge of masticatory apparatus for all mammalian orders (Continued).

Order and group classification	Extent of knowledge of—					Comments
	Dental anatomy	Cranial anatomy	Jaw musculature	Functional mechanics	Jaw musculature evaluation scale	
†Pantodonta ? N, possibly S-II or G	E	A	B to I	I	2A	Aberrant group for which the jaw muscle attachment areas suggest the generalized pattern to have prevailed, but with the dentition progressively tending toward the S-II type.
†Xenungulata	B	B to I	I	I	3A	Dentition suggests an approach toward S-II type.
†Dinocerata ? N, possibly G, S-I, or S-II	E	A	A for one	B to I	1A for one	Dentition alone would suggest a masticatory apparatus type N with a strong tendency toward type S-II. Jaw muscle scars indicate, as Flerov has pointed out, that the musculature was of the S-I type. Actually, the G type may be the best placement (see p. 306).
†Pyrotheria ? N or S-II	E	A	I	I	2A	Apparently lat. excursion was primary grinding movement of jaws.
Proboscidea N, possibly some G, some S-II	A	A	I	I	2A	The most generalized suborder. Teeth suggest tendency toward the S-II type, but M. temporalis appears to be the dominant masticatory muscle as in the G type.
†Mastodontoida	E	E	B	I	2A	Dentition suggests that grinding was done, but again the temporalis muscle scars indicate that this was the primary masticatory muscle. Peculiar tusk development also a further complication.

TABLE A.—Level of our knowledge of masticatory apparatus for all mammalian orders (*Continued*).

Order and group classification	Extent of knowledge of—					Comments
	Dental anatomy	Cranial anatomy	Jaw musculature	Functional mechanics	Jaw musculature evaluation scale	
Elephantoidae	E	E	A	A	I	Specialized grinding cheek dentition, but again M. temporalis is by far the dominant muscle of mastication.
†Deinotherioidea	A	A or B	I	I	2A or 3A	Aberrant group. Cheek teeth with transverse lophs used for grinding. Again M. temporalis appears to be dominant.
†Barytherioidea ? N, or perhaps G or S-II	B	I	I	I	3A	A very poorly known order that is often included as a Proboscidean suborder. Cheek teeth tend to wear as if by extensive grinding and ascending ramus of jaw suggests conditions similar to Proboscideans, too.
†Embrithopoda ? N, or possibly G or S-II	A	A	I	I	2A	Another aberrant, specialized group. Jaw muscle scars indicate rather generalized proportions. Teeth suggest the S-II type of specialization.
Hyracoidea S-II	E	E	B	I	2A	Both dentition and jaw musculature suggest the S-II or mill type of grinding masticatory adaptation. The muscle scars for the M. pterygoideus complex are tremendously developed as are those for the M. masseter complex. Although, to judge from its insertion scars, the M. temporalis appears reduced, its origin scars do not indicate a very drastic reduction in its mass, merely a relative one.

TABLE A.—Level of our knowledge of masticatory apparatus for all mammalian orders (*Continued*).

Order and group classification	Extent of knowledge of—				Comments
	Dental anatomy	Cranial anatomy	Jaw musculature	Functional mechanics	
Sirenia N	A	A	I	I	Some have dentition which exceeds the standard eutherian cheek tooth count. Occlusion is cusp-on-cusp in some, and approaches an oblique shear between opposing cusps in others. Masticatory muscle scars indicate a number of peculiarities of <i>M. temporalis</i> and <i>M. Pt. externus</i> , but they do not appear to be as radical as the dental peculiarities.
†Desmostyilia N	A	B to I	I	I	Possibly an early offshoot of the prior order, they show cusp-on-cusp abrasion in the cheek teeth. Too poorly known for any sort of speculation.
Perissodactyla S-II	E	E	A	A for one, B or I, for others	One of the "classic" S-II mill types. Lateral movements extensive and accomplished by synergistic actions of <i>Mm. masseter</i> and <i>pterygoideus groups</i> . <i>Temporallis</i> reduced. Cheek teeth become extensively abraded by grinding.
Artiodactyla S-II	E	E	A	A	Same as above.

TABLE B-1.—Comparison of Measured Muscle Mass (%) with the Calculated Useful Power Values (c_c) for each jaw-closing muscle group. Forms of the Generalized Group. See p. 282 for explanation of abbreviations.

MARSUPIALIA: DIDELPHIDAE

Form (& source)	Muscle mass (c_c)	Calculated useful power (c_c)	Change (in c_c points)	Proportionate change
<i>Didelphis virginiana</i> (fr. Turnbull)	Mt 56.9	Et 62.0	+5.1	9% gain
	Mm 34.1	Em 32.3	-1.8	6% loss
	Mpt 9.0	Ept 5.7	-3.3	37% loss
<i>Didelphis</i> (fr. Klatt)	Mt 54.5	Et 59.8	+5.3	10% gain
	Mm 35.1	Em 33.4	-1.7	5% loss
	Mpt 10.4	Ept 6.8	-3.6	35% loss

INSECTIVORA: ERINACEIDAE

<i>Echinorex gymnurus</i> (fr. Turnbull)	Mt 61.2	Et 57.7	-3.5	6% loss
	Mm 27.0	Em 31.2	+4.2	16% gain
	Mpt 11.8	Ept 11.0	-0.8	7% loss

PRIMATES: ANTHROPOIDEA: CEBOIDEA: CEBIDAE

<i>Cebus variiegatus</i> (fr. Schumacher)	Mt 53.7	Et 53.4	-0.3	1% loss
	Mm 28.4	Em 30.6	+2.2	8% gain
	Mpt 18.0	Ept 16.0	-2.0	11% loss
<i>Cebus apella</i> (fr. Schumacher)	Mt 54.7	Et 54.5	-0.2	—
	Mm 27.8	Em 30.0	+2.2	8% gain
	Mpt 17.5	Ept 15.6	-1.9	11% loss
<i>Saimiri sciurus</i> (fr. Schumacher)	Mt 54.2	Et 54.4	+0.2	—
	Mm 31.2	Em 29.7	-1.6	5% loss
	Mpt 14.3	Ept 15.8	+1.5	10% gain

PRIMATES: ANTHROPOIDEA: CERCOPITHECOIDEA:
CERCOPITHECINAE and COLOBINAE

<i>Macaca mulatta</i> (fr. Schumacher)	Mt 57.4	Et 55.2	-2.2	4% loss
	Mm 26.6	Em 33.2	+6.6	25% gain
	Mpt 16.1	Ept 11.6	-4.5	28% loss
<i>Macaca sinica</i> (fr. Schumacher)	Mt 59.5	Et 57.1	-2.4	4% loss
	Mm 26.0	Em 32.4	+6.4	25% gain
	Mpt 14.6	Ept 10.5	-4.1	28% loss
<i>Papio cynocephalus</i> (juv.) (fr. Schumacher)	Mt 58.2	Et 59.4	+1.2	2% gain
	Mm 23.2	Em 24.7	+1.5	6% gain
	Mpt 18.6	Ept 16.0	-2.6	14% loss
<i>Papio sphinx</i> (fr. Schumacher)	Mt 63.6	Et 71.8	+8.2	13% gain
	Mm 22.7	Em 18.5	-4.2	19% loss
	Mpt 13.8	Ept 9.7	-4.1	30% loss
<i>Colobus polykomos</i> (juv.) (fr. Schumacher)	Mt 47.7	Et 43.2	-4.5	9% loss
	Mm 31.2	Em 40.8	+9.6	31% gain
	Mpt 21.1	Ept 16.0	-5.1	24% loss

TABLE B-1.—Comparison of Measured Muscle Mass (C_c) with the Calculated Useful Power Values (C_c) for each jaw-closing muscle group. Forms of the Generalized Group (*Continued*).

PRIMATES: ANTHROPOIDEA: HOMINOIDEA:
PONGIDAE and HOMINIDAE

Form (& source)	Muscle mass (C_c)	Calculated useful power (C_c)	Change (in C_c points)	Proportionate change
<i>Pongo</i> <i>pygmaeus</i> (fr. Schumacher)	Mt 50.7	Et 49.1	-1.6	3 C_c loss
	Mm 30.1	Em 29.2	-0.9	3 C_c loss
	Mpt 19.3	Ept 21.7	+2.4	12 C_c gain
<i>Pongo</i> (fr. Bluntschli)	Mt 55.4	Et 53.9	-1.7	3 C_c loss
	Mm 27.0	Em 26.4	-0.5	2 C_c loss
	Mpt 17.5	Ept 19.8	+2.2	13 C_c gain
<i>Homo sapiens</i> (fr. Theile)	Mt 47.1	Et 47.3	+0.2	—
	Mm 30.7	Em 27.6	-3.1	10 C_c loss
	Mpt 22.3	Ept 25.1	+2.8	13 C_c gain
<i>Homo sapiens</i> (fr. Schumacher)	Mt 45.3	Et 45.4	+0.1	—
	Mm 29.0	Em 26.2	-2.8	10 C_c loss
	Mpt 25.8	Ept 28.5	+2.7	10 C_c gain

TABLE B-2.—Comparison of Measured Muscle Mass (C_c) with the Calculated Useful Power Values (C_c) for each jaw-closing muscle group. Forms of Miscellaneous group.

TUBULIDENTATA: ORYCTEROPODIDAE

Form (& source)	Muscle mass (C_c)	Calculated useful power (C_c)	Change (in C_c points)	Proportionate change
<i>Orycteropus</i> <i>aethiopicus</i> (fr. Frick)	Mt 38.1	Et 19.2	-18.9	50 C_c loss
	Mm 40.3	Em 57.2	+16.9	42 C_c gain
	Mpt 21.6	Ept 23.6	+ 2.0	9 C_c gain

PROBOSCIDEA: ELEPHANTIDAE

<i>Elephas</i> <i>maximus</i> (fr. Stocker)	Mt 69.9	Et 74.5	+4.6	7 C_c gain
	Mm 22.1	Em 22.5	+0.4	2 C_c gain
	Mpt 8.0	Ept 3.1	-4.9	61 C_c loss

TABLE C.—Comparison of Measured Muscle Mass (%) with the Calculated Useful Power Values (%) for each jaw-closing muscle group. Forms of Specialized Group I (shear type). See p. 282 for explanation of abbreviations.

FISSIPEDA: CANOIDEA: CANIDAE

Form (& source)	Muscle mass (%)	Calculated useful power (%)	Change (in % points)	Proportionate change
<i>Canis familiaris</i> (fr. Becht)	Mt 67.0	Et 65.6	-1.4	2% loss
	Mm 23.0	Em 26.0	+3.0	13% gain
	Mpt 10.0	Ept 8.4	-1.6	16% loss
<i>Canis familiaris</i> (fr. Davis)	Mt 64.0	Et 62.6	-1.8	3% loss
	Mm 27.0	Em 30.3	+3.3	12% gain
	Mpt 9.0	Ept 7.5	-1.5	17% loss
<i>Canis lupus</i> (fr. Schumacher)	Mt 68.2	Et 69.0	+0.8	1% gain
	Mm 24.1	Em 24.6	+0.5	2% gain
	Mpt 7.6	Ept 6.4	-1.2	16% loss
<i>Canis dingo</i> (fr. Schumacher)	Mt 67.6	Et 72.1	+4.5	7% gain
	Mm 24.5	Em 21.1	-3.4	14% loss
	Mpt 7.9	Ept 6.8	-1.1	14% loss
<i>Alopecx</i> (fr. Klatt)	Mt 65.1	Et 67.3	+2.2	3% gain
	Mm 25.9	Em 24.3	-1.6	6% loss
	Mpt 9.0	Ept 8.4	-0.6	7% loss
<i>Urocyon</i> (fr. Klatt)	Mt 57.0	Et 56.8	-0.2	—
	Mm 32.9	Em 33.1	+0.2	1% gain
	Mpt 10.1	Ept 10.2	+0.1	1% gain
<i>Dusicyon</i> (<i>Pseudalopex</i>) (fr. Klatt)	Mt 64.0	Et 60.4	-3.6	6% loss
	Mm 25.0	Em 27.5	+2.5	10% gain
	Mpt 11.0	Ept 12.1	+1.1	10% gain
<i>Dusicyon</i> (<i>Cerdocyon</i>) (fr. Klatt)	Mt 57.4	Et 59.3	+1.9	3% gain
	Mm 31.7	Em 32.7	+1.0	3% gain
	Mpt 10.9	Ept 8.0	-2.9	27% loss
<i>Cuon javanicus</i> (fr. Klatt)	Mt 59.8	Et 65.4	+5.6	9% gain
	Mm 30.7	Em 27.7	-3.0	10% loss
	Mpt 9.5	Ept 6.9	-2.6	27% loss
<i>Otocyon</i> sp. (fr. Klatt)	Mt 65.7	Et 67.8	+2.1	3% gain
	Mm 28.0	Em 27.2	-0.8	3% loss
	Mpt 6.2	Ept 4.9	-1.3	21% loss
<i>Tremarctos</i> <i>ornatus</i> (fr. Davis)	Mt 65.0	Et 72.5	+7.5	12% gain
	Mm 27.0	Em 24.1	-2.9	11% loss
	Mpt 8.0	Ept 3.4	-4.6	58% loss
<i>Ursus</i> <i>americanus</i> (fr. Starck)	Mt 65.6	Et 72.4	+6.9	11% gain
	Mm 28.6	Em 25.3	-3.3	12% loss
	Mpt 6.0	Ept 2.3	-3.7	62% loss
<i>Ursus</i> <i>arctos</i> (fr. Becht)	Mt 64.0	Et 68.1	+4.1	6% gain
	Mm 30.0	Em 26.6	-3.4	11% loss
	Mpt 6.0	Ept 5.3	-0.7	12% loss

TABLE C.—Comparison of Measured Muscle Mass (C_c) with the Calculated Useful Power Values (C_c) for each jaw-closing muscle group. Forms of Specialized Group I (shear type) (Continued).

Form (& source)	Muscle mass (C_c)	Calculated useful power (C_c)	Change (in C_c points)	Proportionate change
<i>Ursus arctos</i> (fr. Starck)	Mt 64.0	Et 68.1	+4.1	6 C_c gain
	Mm 31.0	Em 27.5	-3.5	11 C_c loss
	Mpt 5.0	Ept 4.4	-0.6	12 C_c loss
<i>Thalarcos maritimus</i> (fr. Schumacher)	Mt 76.7	Et 75.7	-1.0	1 C_c loss
	Mm 17.9	Em 20.4	+2.5	14 C_c gain
	Mpt 5.4	Ept 3.9	-1.5	28 C_c loss
<i>Thalarcos maritimus</i> (fr. Davis)	Mt 73.3	Et 72.1	-1.2	2 C_c loss
	Mm 21.1	Em 23.9	+2.8	13 C_c gain
	Mpt 5.5	Ept 4.0	-1.5	27 C_c loss
<i>Aluopoda melanoleuca</i> (fr. Davis)	Mt 59.8	Et 63.1	+3.3	6 C_c gain
	Mm 36.5	Em 34.9	-1.6	4 C_c loss
	Mpt 3.6	Ept 2.0	-1.6	44 C_c loss
FISSIPEDA: PROCYONIDAE and MUSTELIDAE				
<i>Procyon (Euprocyon)</i> (fr. Klatt)	Mt 60.3	Et 61.3	+1.0	2 C_c gain
	Mm 29.3	Em 29.8	+0.5	2 C_c gain
	Mpt 10.4	Ept 8.9	-1.5	14 C_c loss
<i>Procyon lotor</i> (fr. Davis)	Mt 69.2	Et 59.7	-9.5	14 C_c loss
	Mm 23.1	Em 34.5	+11.4	49 C_c gain
	Mpt 7.7	Ept 5.7	-2.0	26 C_c loss
<i>Nasua</i> sp. (fr. Klatt)	Mt 67.2	Et 71.5	+4.3	6 C_c gain
	Mm 22.4	Em 22.5	+0.1	—
	Mpt 10.4	Ept 6.1	-4.3	41 C_c loss
<i>Ailurus</i> sp. (fr. Klatt)	Mt 74.8	Et 71.2	-3.6	5 C_c loss
	Mm 16.8	Em 19.2	+2.4	14 C_c gain
	Mpt 8.4	Ept 9.6	+1.2	14 C_c gain
<i>Lutra lutra</i> (fr. Schumacher)	Mt 78.9	Et 81.0	+2.1	3 C_c gain
	Mm 17.0	Em 16.9	-0.1	1 C_c loss
	Mpt 4.2	Ept 2.1	-2.1	50 C_c loss
FISSIPEDA: FELOIDEA: HYAENIDAE and FELIDAE PINNIPEDIA: PHOCIDAE				
<i>Proteles</i> sp. (fr. Klatt)	Mt 65.7	Et 73.3	+7.6	12 C_c gain
	Mm 22.5	Em 24.8	+2.3	10 C_c gain
	Mpt 11.7	Ept 1.9	-9.8	84 C_c loss
<i>Felis f. domestica</i> (fr. Turnbull)	Mt 54.3	Et 48.9	-5.4	10 C_c loss
	Mm 35.2	Em 44.6	+9.4	27 C_c gain
	Mpt 10.5	Ept 6.5	-4.0	38 C_c loss
<i>Felis puma concolor</i> (fr. Schumacher)	Mt 53.0	Et 59.7	+6.7	13 C_c gain
	Mm 38.2	Em 34.8	-3.4	9 C_c loss
	Mpt 8.7	Ept 5.6	-3.1	36 C_c loss

TABLE C.—Comparison of Measured Muscle Mass (%) with the Calculated Useful Power Values (%) for each jaw-closing muscle group. Forms of Specialized Group I (shear type) (Continued).

Form (& source)	Muscle mass (%)	Calculated useful power (%)	Change (in % points)	Proportionate change
<i>Panthera leo</i> (fr. Schumacher)	Mt 59.1	Et 55.7	-3.4	6% loss
	Mm 33.6	Em 39.8	+6.2	18% gain
	Mpt 7.3	Ept 4.5	-2.8	38% loss
<i>Panthera leo</i> (juv.) (fr. Schumacher)	Mt 60.1	Et 62.6	+2.5	4% gain
	Mm 31.0	Em 31.1	+0.1	—
	Mpt 8.9	Ept 6.4	-2.5	28% loss
<i>Panthera tigris</i> (fr. Becht)	Mt 48.0	Et 45.4	-2.6	5% loss
	Mm 45.0	Em 52.1	+7.1	15% gain
	Mpt 7.0	Ept 2.5	-4.5	64% loss
<i>Panthera onca</i> (fr. Davis)	Mt 64.0	Et 60.6	-3.4	5% loss
	Mm 28.0	Em 33.3	+5.3	19% gain
	Mpt 8.0	Ept 6.1	-1.9	24% loss
<i>Halichoerus gryphus</i> (juv.) (fr. Schumacher)	Mt 62.8	Et 63.7	+0.9	1% gain
	Mm 28.2	Em 29.7	+1.5	5% gain
	Mpt 9.0	Ept 6.5	-2.5	28% loss

TABLE D.—Comparison of Measured Muscle Mass ($\%$) with the Calculated Useful Power Values ($\%$) for each jaw-closing muscle group. Forms of Specialized Group II (mill type). See p. 282 for explanation of abbreviations.

PERISSODACTYLA: EQUOIDEA: EQUIDAE

Form (& source)	Muscle mass ($\%$)	Calculated useful power ($\%$)	Change (in $\%$ points)	Proportionate change
<i>Equus caballus</i> (fr. Turnbull)	Mt 14.5	Et 4.3	-10.2	70 $\%$ loss
	Mm 54.5	Em 65.3	+10.8	20 $\%$ gain
	Mpt 31.0	Ept 30.3	- 0.7	2 $\%$ loss
<i>Equus caballus</i> (fr. Becht)	Mt 11.1	Et 4.3	-6.8	61 $\%$ loss
	Mm 57.5	Em 66.2	+8.7	15 $\%$ gain
	Mpt 31.4	Ept 29.5	-1.9	6 $\%$ loss

ARTIODACTYLA: SUIFORMES: SUIDAE

<i>Sus scrofa</i> (fr. Schumacher)	Mt 27.5	Et 17.5	-10.0	36 $\%$ loss
	Mm 49.9	Em 56.7	+ 6.8	14 $\%$ gain
	Mpt 22.7	Ept 25.8	+ 3.1	14 $\%$ gain

ARTIODACTYLA: TYLOPODA: CAMELIDAE

<i>Camelus dromedarius</i> (fr. Schumacher)	Mt 43.4	Et 26.4	-17.0	39 $\%$ loss
	Mm 30.4	Em 37.2	+ 6.8	22 $\%$ gain
	Mpt 26.3	Ept 36.4	+10.1	38 $\%$ gain

ARTIODACTYLA: RUMINANTIA: CERVIDAE and
BOVINAE and CAPRINAE

<i>Odocoileus virginianus</i> (fr. Turnbull)	Mt 29.4	Et 21.9	-7.5	26 $\%$ loss
	Mm 46.1	Em 54.7	+8.6	19 $\%$ gain
	Mpt 24.5	Ept 23.3	-1.2	5 $\%$ loss
<i>Capreolus capreolus</i> (fr. Schumacher)	Mt 32.1	Et 18.2	-13.9	43 $\%$ loss
	Mm 38.8	Em 50.7	+11.9	31 $\%$ gain
	Mpt 29.1	Ept 31.1	+ 2.0	7 $\%$ gain
<i>Bos indicus</i> (fr. Becht)	Mt 11.0	Et		
	Mm 49.0	Em		
	Mpt 40.0	Ept		
<i>Bison bonasus</i> (fr. Becht)	Mt 10.6	Et	(Potentially available but un-	
	Mm 60.0	Em	certainty about limit attach-	
	Mpt 29.4	Ept	ments prevents calculations.)	
<i>Oris aries</i> (fr. Turnbull)	Mt 23.5	Et 11.9	-11.6	49 $\%$ loss
	Mm 52.5	Em 64.2	+11.7	22 $\%$ gain
	Mpt 24.0	Ept 23.9	- 0.1	—
<i>Oris aries</i> (fr. Zey)	Mt 25.7	Et 13.4	+12.3	48 $\%$ loss
	Mm 46.2	Em 57.9	+11.7	25 $\%$ gain
	Mpt 28.1	Ept 28.7	+ 0.6	2 $\%$ gain
<i>Oris aries</i> (juv.) (fr. Schumacher)	Mt 29.6	Et 15.9	-13.7	46 $\%$ loss
	Mm 40.9	Em 52.8	+11.9	29 $\%$ gain
	Mpt 29.6	Ept 31.2	+ 1.6	5 $\%$ gain
<i>Oris musimon</i> (fr. Schumacher)	Mt 25.1	Et 13.0	-12.1	48 $\%$ loss
	Mm 48.3	Em 60.0	+11.7	24 $\%$ gain
	Mpt 26.7	Ept 27.1	+ 0.4	1 $\%$ gain

TABLE E.—Comparison of Measured Muscle Mass (%) with the Calculated Useful Power Values (%) for each jaw-closing muscle group Forms of Specialized Group III (gnawing type). See p. 282 for explanation of abbreviations.

LAGOMORPHA and RODENTIA: SCIUROMORPHA

Form (& source)	Muscle mass (%)	Calculated useful power (%)	Change (in % points)	Proportionate change
<i>Oryctolagus</i> (fr. Schumacher)	Mt 12.4	Et 6.1	- 6.3	51% loss
	Mm 62.9	Em 81.6	+18.7	30% gain
	Mpt 24.8	Ept 12.3	-12.5	50% loss
<i>Lepus</i> (fr. Schumacher)	Mt 15.0	Et 7.8	- 7.2	48% loss
	Mm 56.9	Em 77.6	+20.7	36% gain
	Mpt 28.1	Ept 14.6	-13.5	48% loss
<i>Sciurus niger</i> (fr. Turnbull)	Mt 19.4	Et 9.7	- 9.7	50% loss
	Mm 61.0	Em 73.6	+12.6	21% gain
	Mpt 19.6	Ept 16.7	- 2.9	15% loss
<i>Sciurus niger</i> (fr. Miller)	Mt 16.5	Et 8.0	- 8.5	52% loss
	Mm 64.8	Em 76.4	+11.6	18% gain
	Mpt 18.7	Ept 15.6	- 3.1	17% loss
<i>Marmota marmota</i> (fr. Starek and Wehrli)	Mt 18.7	Et 9.6	- 9.1	49% loss
	Mm 65.7	Em 82.0	+16.3	25% gain
	Mpt 15.5	Ept 8.4	- 7.1	46% loss

RODENTIA: MYOMORPHA, HYSTRICOMORPHA

<i>Rattus norvegicus</i> (fr. Turnbull)	Mt 32.6	Et 21.4	-11.2	36% loss
	Mm 54.1	Em 72.5	+18.4	31% gain
	Mpt 13.3	Ept 6.1	- 7.2	54% loss
<i>Rattus norvegicus</i> (fr. Schumacher)	Mt 25.6	Et 11.0	-11.6	57% loss
	Mm 63.4	Em 83.2	+19.8	31% gain
	Mpt 11.1	Ept 5.9	- 5.2	47% loss
<i>Hystrix mulleri</i> (fr. Becht)	Mt 13.0	Et 5.4	- 7.6	58% loss
	Mm 74.0	Em 85.0	+11.0	15% gain
	Mpt 13.0	Ept 9.5	- 3.5	27% loss
<i>Hystrix</i> sp. (fr. Turnbull)	Mt 16.6	Et 7.9	- 8.7	52% loss
	Mm 71.9	Em 83.7	+11.8	16% gain
	Mpt 11.5	Ept 8.4	- 3.1	27% loss
<i>Cavia porcellus</i> (fr. Schumacher)	Mt 17.6	Et 8.6	- 9.0	51% loss
	Mm 66.4	Em 84.2	+17.8	27% gain
	Mpt 16.0	Ept 7.2	- 8.8	55% loss
<i>Hydrochoerus</i> <i>capybara</i> (fr. Muller)	Mt 6.8	Et 3.1	- 3.7	54% loss
	Mm 77.1	Em 91.0	+14.1	18% gain
	Mpt 16.1	Ept 5.9	-10.2	63% loss





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