How Mammalian Molar Teeth Work

by A. W. Crompton and Karen Hiiemäe

"You are old," said the youth, "and your jaws are too weak
For anything tougher than suet;
Yet you eat all the goose, with the bones and the beak —
Pray, how did you manage to do it?"

"In my youth," said the old man, "I took to the law,
And argued each case with my wife,
And the muscular strength, which it gave to my jaw,
Has lasted the rest of my life."

Lewis Carroll

Father William is not alone in his capacity to chew his food powerfully; almost all mammals prepare their food for swallowing by chewing. To do this they have evolved a wide range of tooth types capable of coping with diets as diverse as mollusks, ants, leaves and fruit. The mammalian dentition has other functions besides chewing food; it, or parts of it, are used for food-gathering, as weapons of offense and defense, for grooming fur and for social activities. Not all these varied functions are performed by all the teeth, and a characteristic of the mammals is that they have evolved a differentiated tooth row with four types of teeth, each specialized for particular activities. The anterior teeth, incisors and canines, are used predominantly for food-gathering, as weapons of offense and defense and for grooming. In carnivores, the canines are used as weapons in the bringing down of the prey. Food is actually cut, ground or crushed by the cheek teeth, the premolars and molars, and it is these teeth that are specialized and adapted to various kinds of diet.

Mammalian teeth are formed from the two hardest of biological tissues, enamel and dentine, which have a low organic content. This is the reason why they have a better chance of becoming petrified than the remainder of the skeleton and why the evolutionary history of mammals is to a large extent based on teeth. Many of the early mammals, in fact entire families in a few cases, are known only from a few teeth. To a large extent, therefore, documentation of the fossil record of mammals over the last 135 million years (from the Jurassic to the Recent) has been based on the study of molar forms. The pattern of cusps, ridges and fossae which characterize the molar crown is ideally suited for classifying mammals, and its progressive alteration is valuable in tracing evolutionary change.

Characteristic features of the dentition are therefore used to determine such

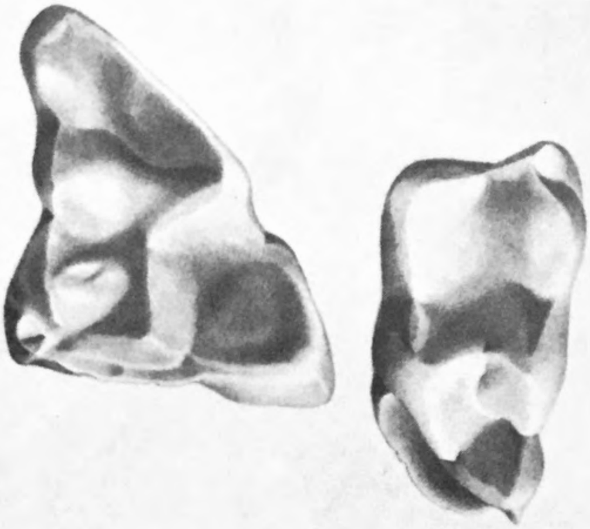


Fig. 1. A lower and upper molar from the opossum showing the basic tribosphenic pattern.

things as relationships, evolutionary history and rates of evolutionary change, and little attention has been paid to the adaptive significance of the changes in molar form or accompanying changes in the architecture of the skull. Almost nothing of the functional advantages these changes conferred on the mammals developing them was known until recently. This is not surprising as mastication is not fully understood in man, let alone the remaining mammals. The position has essentially been one where the "what" of evolutionary change in mammalian dentitions was known from the available fossils, but not the "how" or "why". (The same is to a large extent true of the remainder of the skeleton.)

The lack of functional studies on mastication can be partly explained by the absence of suitable techniques for examining the feeding process in living animals. Although attempts were made to use photography and cinephotography shortly after their invention, they failed because tissues of the cheeks hid the movements of the jaws, teeth and tongue. However, the invention and development of the image intensifier in the last two decades has made it possible to use cinefluoroscopy and cinefluorography to record masticatory behavior. The techniques were described in the Spring 1968 issue of *Discovery* (3 (2): 50) and provide a method by which movements of both soft and hard tissues can be observed and recorded on video tape or film. By analyzing successive frames of a cinefilm, we can plot the movements of the various parts of the jaws during all the stages of feeding activity. At present we are examining the movements of mastication in several modern mammals and have practically completed a study on the American opossum, *Didelphis marsupialis.*

One of the major achievements of paleontological research during the latter part of the nineteenth and beginning of the present century was the discovery that the various types of molars found in recent and modern mammals evolved from a primitive molar with a relatively simple shape and crown pattern. This archetypal or "tribosphenic" molar characterizes all the primitive pouched and placental mammals and is also found in several living groups. We argued that if we could show what was involved in mastication in mammals which have primitive tribosphenic molars and determine the relationship between the shape of the tooth and the movements of mastication, this would provide a basis for understanding the function of early mammalian molars. Moreover, if similar studies were carried out on animals with more specialized dentitions such as carnivores, herbivores and primates, then the results, together with those from the first investigation, would help explain the factors involved in the evolution of the different types of mammalian molars. The opossum which is virtually a "living fossil" was the ideal animal for the first part of the study. The skull and jaws have remained almost unchanged for the last 70 million years, whilst its dentition and particularly the tribosphenic molars are almost identical to those of the earliest pouched and placental mammals.

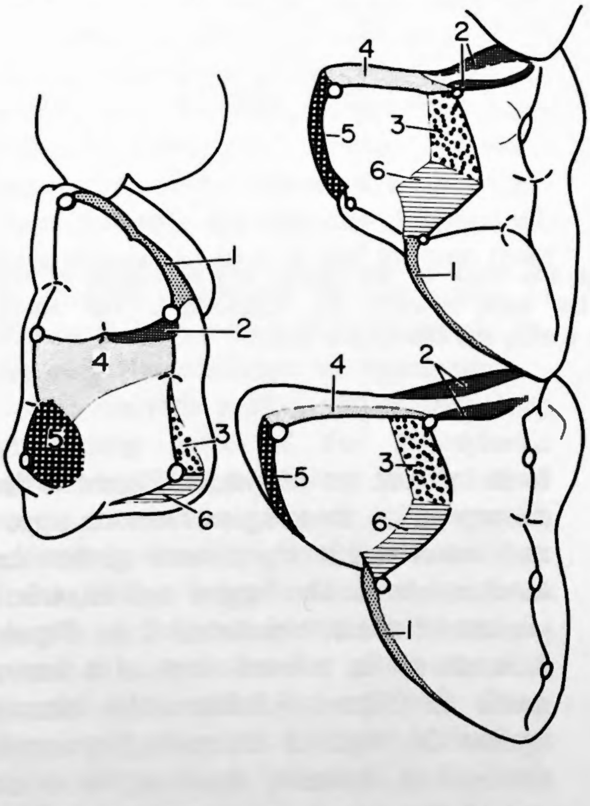


Fig. 2. Occlusal views of the upper and lower molars in the opossum showing the matching shearing planes used in cutting the food.

The occlusal surface of the upper molars of *Didelphis* is basically triangular in shape (Fig. 1) with the base of the triangle external. Successive upper molars are separated by a wide V-shaped embrasure (Fig. 2). The crowns of the teeth have several prominent cusps which are arranged so that when the teeth come completely into occlusion the high cusps of the lower teeth form a triangle which fits into the embrasure between the upper molars. By using the x-ray apparatus and studying the dentition, we have been able to show that the opossum uses its molar teeth in two ways. When food is first chewed, the upper and lower teeth do not come into contact but act like a meat tenderizer, puncturing and crushing the food. Only after it has been thoroughly pulped is it cut up into smaller pieces by the teeth working like scissors. Both these types of activity are possible because the sharply pointed high cusps act to puncture and pulp the food, while their slopes form the shearing planes used to cut it. In fact, the arrangement of the cusps forms a series of six matching shearing surfaces on upper and lower teeth. These are shown in Figure 2. As the jaws close and the teeth come into occlusion, the shearing surfaces on the

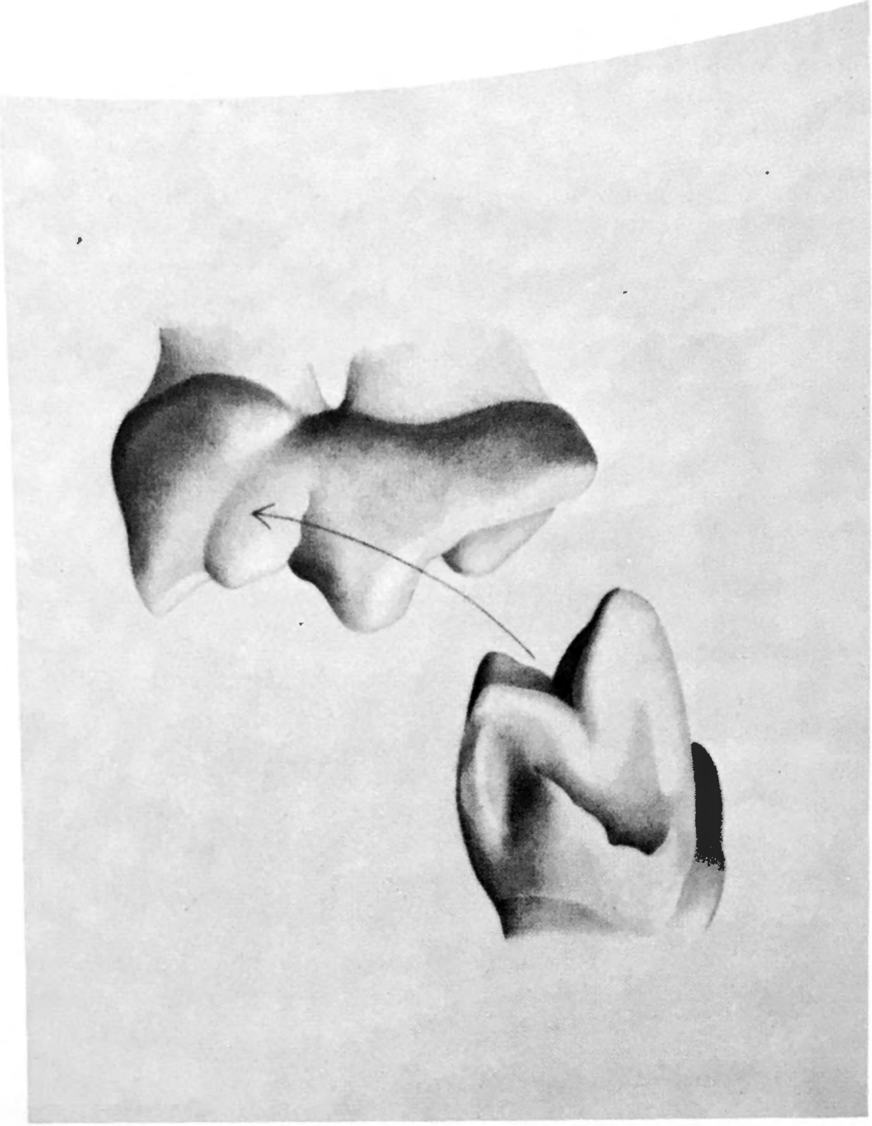


Fig. 3. **The main matching shearing surfaces on the back of the upper and the front of the lower molars of the opossum. The upper molar has been reversed for comparison. The arrow indicates the path the lower surface would take during the chewing stroke.**

back molars slice past each other first and then those of the other teeth in succession. This explains why the food always ends up at the front of the molar series after each cutting stroke, necessitating an elaborate series of tongue movements to carry it back ready for the next.

The arrangement of these shearing surfaces on the crown of the tooth can best be seen from above, the occlusal view, whilst their size and extent are shown in views of individual molars from in front or behind. In Figure 2 the corresponding shearing surfaces on upper and lower teeth have been given the same numbers. The largest and most important of these, numbered 1 in Figure 2, is shown in a front view of a lower molar in Figure 3. Since this shears against the back of the preceding upper molar, it is obviously necessary to rotate one of these teeth in order to show the two surfaces simultaneously, but this makes it difficult to illustrate how the two surfaces cut against each other. To overcome this problem the the upper tooth has been reversed in Figure 3. The upper border of the shearing surface on the lower tooth is V-shaped and the lower border of the matching surface on the upper is crescentic. This makes a perfect shearing mechanism because as the lower surface passes across the upper during a shearing movement, so the opposing "V" and "crescent" trap and steady the food particles as they are cut. All the other shearing surfaces function in a similar way.

In addition to the discovery that the opossum molars are used to pulp rather than cut the food for up to 60 percent of the time spent in mastication, the cinefluorographic recordings have brought some very interesting facts to light. Chewing does not occur on both sides of the jaw simultaneously; repeated chewing strokes on one side are followed by a long series of strokes on the other, so when one side of the mouth is active, the other is passive and vice versa. During chewing the lower jaw does not simply move straight up and down; when the teeth come into contact, the entire lower jaw moves sideways a short distance towards the midline of the skull. This movement as it would be seen from in front is illustrated by the arrow in Figure 3. It has the effect of greatly increasing the efficiency of mastication.

The multiple cutting planes and sharp puncturing cusps of the tribosphenic molars in the opossum are ideally suited to an omnivorous diet of insects, small animals and soft plant foods such as fruits. Many living insectivores such as shrews, moles, treeshrews, etc., have retained this type of molar which was also present in the small but relatively abundant early placental and pouched mammals which lived between 70 and 80 million years ago.

As has been stated above, it is possible to derive the more specialized molars of other mammals from the primitive tribosphenic type. Most mammals, living and extinct, other than those that have retained the primitive molar pattern, are clearly either carnivores or herbivores. To illustrate how molar, jaw and skull architecture are changed to cope with these different types of food, a typical herbivore, the goat, and a typical carnivore, the lynx, are compared below with a primitive omnivorous mammal, the opossum.

If flesh can be cut into pieces of suitable size for swallowing, it needs no further mastication. The carnivores have therefore modified the shearing system of the tribosphenic molar. Instead of having several small shearing surfaces on several teeth as do mammals with tribosphenic molars, they have developed a few large shearing surfaces concentrated on one or two teeth. Usually the last upper premolar and the first lower molar have the most exaggerated development and are called the "carnassials". In Figure 4 the transition from a tribosphenic molar to a carnassial is illustrated. In the upper figure the entire premolar-molar dentition is shown and in the lower figure individual teeth are illustrated to show the shearing surfaces more clearly. The large blades of the carnassials are ideally suited to cutting large lumps of flesh or cracking bones as they work on the principle of concentrating all the power of the bite on a small area with very deep shearing surfaces so large pieces can be cut with one stroke. These shearing planes are aligned along, rather than across the jaw as in tribosphenic molars. For this reason little transverse movement of the lower jaw is required in biting, so it moves almost entirely up and down (see Fig. 5).

An herbivorous diet poses a completely different problem. Tough, fibrous plant foods have to be completely broken down in preparation for digestion. Carnassials are useless for this purpose and the

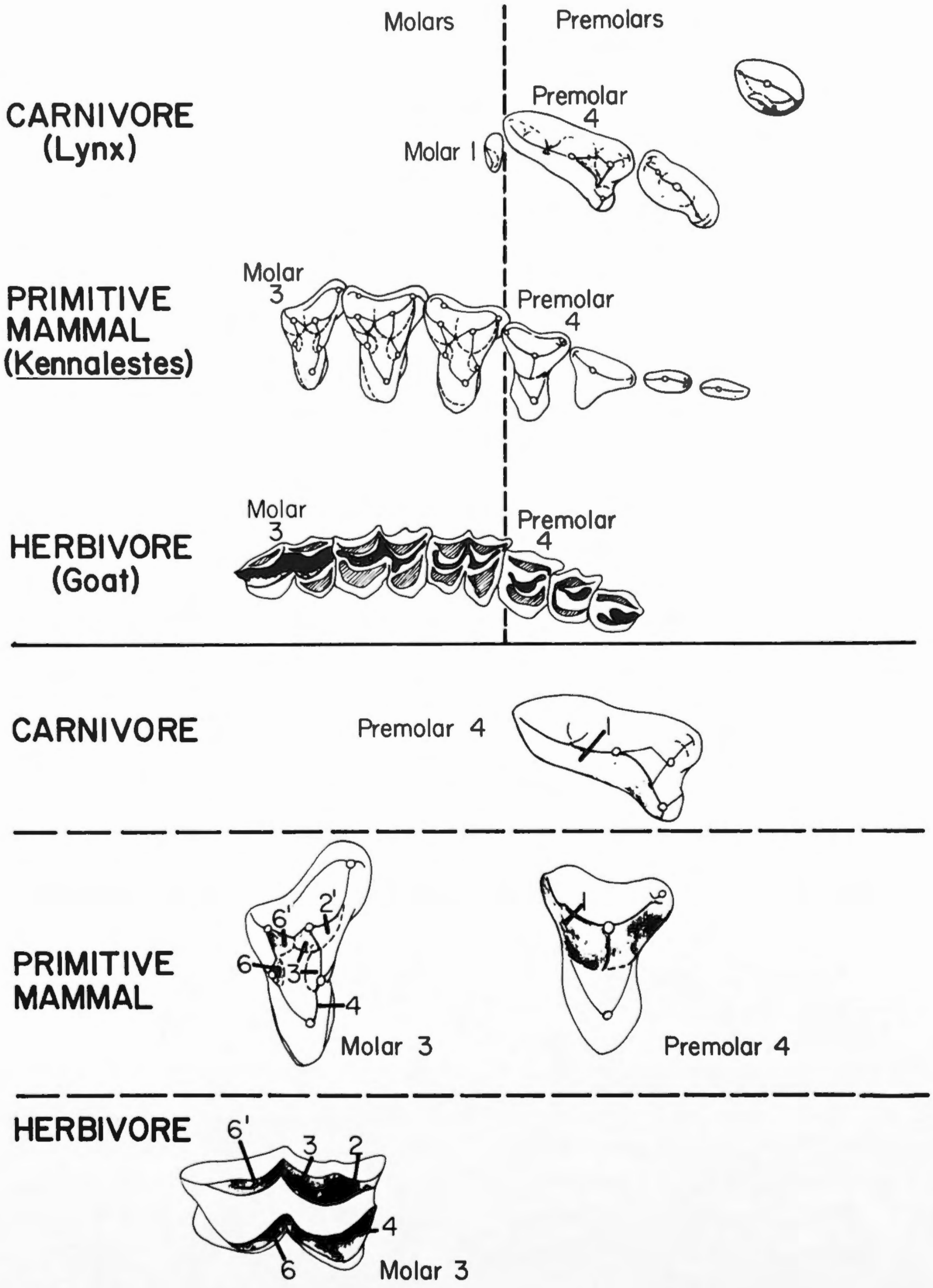
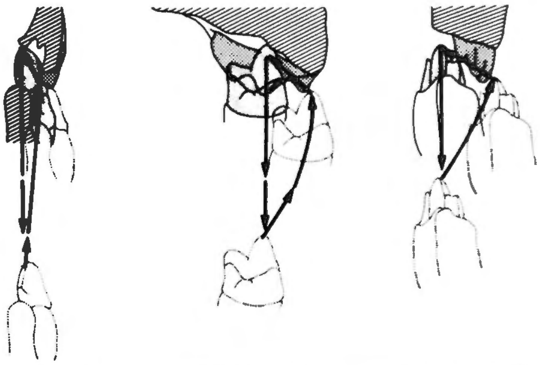


Fig. 4. A comparison of premolar and molar teeth from a primitive mammal, *Kennalestes,* that lived sometime between 80 and 100 million years ago in Central Asia with a modern carnivore (the lynx) and an herbivore (the goat). In the lower half of the figure individual teeth are compared to illustrate how the shearing planes (2, 3, 4 and 6) of a primitive mammalian tooth have been modified for vertical masticatory movements in the carnivore and horizontal movements in the herbivore.

difficulty which a dog has trying to bite a few blades of grass illustrates this point. In general, the herbivores have evolved square molar teeth whose occlusal surfaces are covered by a series of low ridges or lophs which work like a wood file, thoroughly grinding the food. The characteristic lophs of herbivore molars have evolved from the tribosphenic molar by a gradual process of suppression of the height of individual cusps and an exaggeration of the ridges connecting them. This is shown in Figure 4. In common herbivores such as goats, cows, camels and horses, the lophs run across the teeth from back to front, more or less parallel with the tooth row, giving a large area of almost horizontally oriented shearing surfaces. The vegetation is rasped and ground between the lophs on the upper and lower molars as the latter are dragged sideways across the uppers. To do this the slight sideways movement of the jaw seen in the cutting action of the opossum molar has become greatly exaggerated (Fig. 5) and is the most important movement in the chewing stroke. Rodents, which are also herbivores, chew their food in much the same way. The lophs on the rodent molar are arranged transversely across the molars at right angles to the long axis of the tooth row so a forwards as well as slightly sideways movement is involved in the chewing stroke. Not only is vegetation tough and difficult to masticate but it also has, by comparison with flesh, a low nutritive value, necessitating the consumption of very large quantities. This explains the other major modification of the tooth row seen in herbivores, a progressive molarization of the premolars, to form a long row of very similar teeth maximizing the surface area available for horizontal shearing. In carnivores on the other hand the premolars and molars are highly diverse and the tooth number reduced.



CARNIVORE **OPOSSUM** **HERBIVORE**

Fig. 5. The movement of a lower molar relative to the corresponding upper during a chewing cycle as viewed from behind. The exaggeration of the horizontal movement in the herbivore and of the vertical movement in the carnivore during the final phase of the chewing stroke as compared with the opossum can be seen.

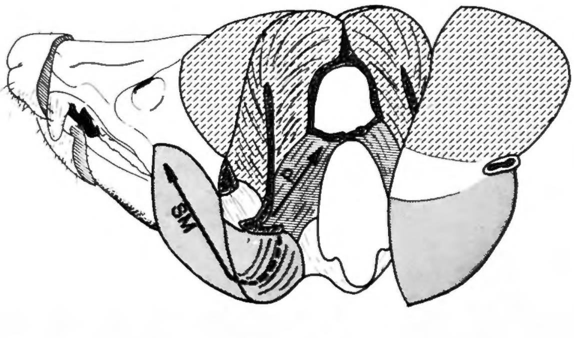


Fig. 6. The muscles of mastication in the opossum viewed from the side and behind (in section) to show the arrangement of the "slings" moving the lower jaw.

All three types of mammal, omnivore, herbivore and carnivore, "chew" their food. Regardless of whether the food is actually pounded and then cut, sliced or ground, all ways in which food is chewed, the mechanism involved is the same. "Chewing" movements depend on the passage of a shearing surface on a lower tooth across its corresponding surface on the upper. The differences between these groups of mammals lie in the position and height of the shearing surfaces and hence the jaw movements required to utilize them. In the opossum the main shearing surface is orientated at about 40 degrees to the long axis of the tooth row and is of limited height and extent. The movement of the jaw in chewing is therefore a combination of upwards, forwards and sideways movement (Fig. 5). The carnivores have selectively elongated one of these shearing surfaces and increased its height to form the carnassial. In addition, by rotating the long axis of the shearing plane parallel with that of the tooth row, a simple vertical movement (Fig. 5) produces an effective slicing action. The shearing surfaces in the herbivores have been greatly reduced in height and have become orientated almost horizontally on the slopes of low ridges. To carry the occlusal surface of the lower molar across the upper in a shearing movement, the jaw moves sideways (Fig. 5).

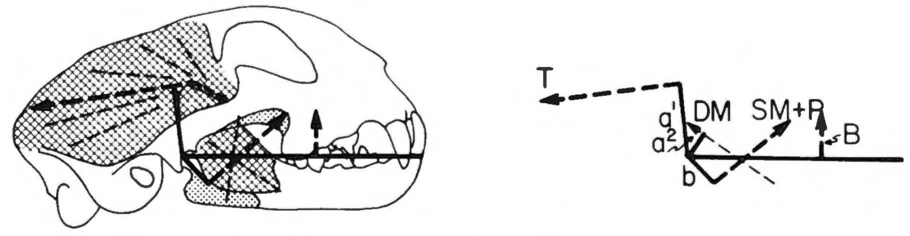
As these changes in orientation of the shearing surfaces on the molars gradually evolved, corresponding changes occurred in the anatomy of the jaw muscles and in the architecture of the skull.

The lower jaw of mammals is moved by the synchronized contraction and relaxation of three main muscle masses. These muscle masses may be divided into two blocks. In a primitive mammal such as the opossum, the larger is the block suspending the lower jaw from the skull and enveloping it externally and internally in a vertically arranged sling. The inner part of this block is formed by the temporalis muscle which passes downwards and outwards from the side of the skull and is attached to the inner surface of the jaw (Fig. 6). Balancing this is the outer mass of the first block, the deep masseter muscle, which runs downwards and inwards from the cheekbone to insert on the outer surface of the jaw. These two muscles act together to move the jaw upwards and to provide much of the "power" required for cutting the food. As they almost always function together, they will be considered as one basic unit when the mechanics of the muscles are discussed. The second block consists of two muscle masses which form a sling whose fibers have a forwards and upwards orientation. The inner mass is formed by the pterygoid muscle which runs upwards and forwards to the base of the skull from the lower edge of the inside of the jaw, and matching it on the outer surface the superficial masseter which passes up from the external surface of the angle of the jaw to insert on the front of the cheekbone (Fig. 6). The pterygoid muscle and superficial masseter muscle are thought to form a "push-pull" sling around the lower jaw and are capable of moving it upwards and sideways.

A reasonable generalization is that the temporalis and deep masseter are primarily responsible for the upward movement of the jaw, whereas the superficial masseter and the pterygoid muscle produce and control a combination of upwards, forwards and sideways movement. Therefore, it would be expected that in carnivores with simple up and down jaw movements, the temporalis and deep masseter will be the larger of the two muscle blocks, whereas in herbivores, where sideways movements are important, the second block consisting of the pterygoid and superficial masseter muscles will be the larger of the two muscle blocks. The different methods of chewing in the various types of mammals can therefore be explained by variation in the arrangement of the muscles and in their relative masses.

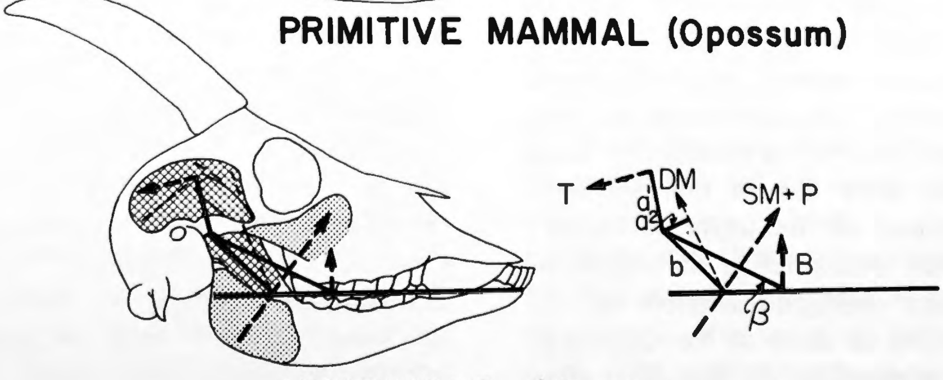
In Figure 7 the positions of the muscle masses and the shape of the skull and lower jaw in a primitive omnivorous mammal (the opossum), an herbivore (the goat) and a carnivore (the lynx) are shown. All the skulls have been drawn vertically aligned on the jaw joint to make comparison easier. Superimposed on these drawings is a simplified representation of the mechanics of the jaw in each case. This system of lever arms (moment arms) is shown separately on the right to illustrate the basic differences in the three types of masticatory mechanisms.

All movements of the lower jaw occur about the jaw joint. In chewing, the force exerted by the muscles is used both to move the jaw and to cut the food between the teeth. This bite force (B in Fig. 7) is shown at an arbitrarily selected point where the most powerful chewing is presumed to take place. The bite force is transmitted to the facial bones and then to the skull, and the point of maximum bite is closely related to the facial root of the cheekbone which, because it forms a thick bony buttress, absorbs much of the bite force. Each of the muscle blocks forms a lever arm acting about the joint. The lengths of the arms shown as a_1 for the temporalis, a_2 for the deep masseter and b for the superficial masseter and pterygoid (Fig. 7) depend on the distance between the insertion of the muscles on the jawbone and the jaw joint. The direction of pull of a



CARNIVORE (Lynx)

PRIMITIVE MAMMAL (Opossum)



HERBIVORE (Goat)

Fig. 7. Lateral views of the skull, lower jaw and jaw muscles in a primitive mammal, a carnivore and an herbivore. The attachment areas of the *temporalis and deep masseter* are cross-hatched and those of the *pterygoid and superficial masseter* muscles are stippled. The fine dotted lines indicate the directions of their constituent fibers, the thick dotted line the "average" direction of pull for each muscle, and the thick solid lines the lever arms from the point of application of muscle pull on the jaw to the jaw joint. The lever arm for the bite force B and the plane of the teeth are also shown as solid lines. The mechanics of the system are shown separately on the right.

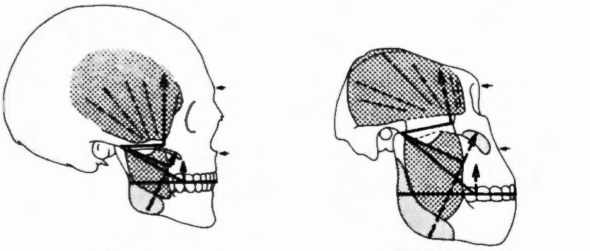
muscle is governed by the orientation of its fibers. As this is slightly different for the temporalis and deep masseter, although they work together, the two are shown separately in the mechanical diagrams. These three muscle levers produce the force of the bite (B) which is connected to the jaw joint by a fourth lever arm. The angle β of this lever arm to the plane of the teeth, which is also shown as a thick horizontal line in Figure 7, depends on the height of the jaw joint above the teeth.

In the opossum the leverage on the jaw represented by the lever arms a_1 and a_2 from the temporalis (T) and the deep masseter (DM) is much greater than that provided by the pterygoid (P) and the superficial masseter (SM), although the arm b is almost as long as a_1. This is because of the relatively much greater bulk of the temporalis and deep masseter. In a primitive mammal the greater part of the chewing force B is therefore provided by the temporalis and deep masseter whereas the superficial masseter and pterygoid muscles, while they obviously add to the bite force, are also responsible for the sideways movement of the lower jaw as well.

The differences between herbivores and primitive mammals shown in the diagram all follow from one major change. As the herbivores have evolved, they have gradually moved the jaw joint above the level of the tooth row, so increasing the angle between the lever arm of the bite force and the plane of the teeth. Associated with this, the lever arms of the superficial masseter and pterygoid muscles are enlarged relative to those of the deep masseter and temporalis. At the same time, the mass of the superficial masseter and pterygoid have been increased. Consequently, in herbivores these two muscles produce the greater part of the vertical bite force, but as they are responsible for lateral movements as well, the net result is that these mammals are capable of moving the jaws sideways when the lower teeth are firmly forced against the uppers. The characteristic shape of the herbivore jaw with its large square angle is explained by the large areas of attachment needed for the bulky superficial masseter and pterygoid. An additional effect of raising the jaw joint above the tooth row, and the wide areas of attachment of the superficial masseter and pterygoid muscles, is a more even distribution of the bite force along the tooth row; this in turn is related to the molarization of the premolars. Therefore, the changes in relative proportions and areas of attachment of the muscles of mastication in herbivores is intimately related to the structure and function of the molars.

Carnivores, on the other hand, must be able to use their canines in bringing down their prey by snapping the jaws shut, and they must then be able to cut the flesh efficiently. These are two separate but related problems, both of which have involved changes in the jaw as compared with a primitive mammal. An opossum can open its mouth as much as 53 degrees, a very wide gape, as all the muscles lie behind the tooth row. In the carnivores the muscles are even further back, compressing the superficial masseter and reducing the length of its lever arm. This greatly limits its capacity to produce lateral movement (which is unimportant in the carnivores) but at the same time increases the speed with which the jaws can be closed. Carnivores rely on an extremely powerful bite across the carnassials for cutting flesh. This is produced almost entirely by the action of the temporalis and deep masseter which are comparatively very large. In these animals the jaw joint has been lowered and brought virtually into line with the tooth row, so the lever arm of the bite force runs along the line of the teeth.

To increase the available mass of the temporalis and the leverage it can exert, the muscle attachment spreads far back on the skull so that the major force component of this muscle is nearly horizontal and its powerful backwards pull could dislocate the jaw. Because the superficial masseter inserts near the jaw joint, the major component of this muscle is horizontal rather than vertical and its powerful contraction could also dislocate the joint by pulling the jaw forwards. Dislocation is however prevented by thick bony flanges which lie in front of and behind the condyle on the lower jaw and convert the joint into a hinge which practically limits jaw movements to vertical opening and closing. But a tightly locked jaw joint would be catastrophic to herbivores as it would prevent the sideways jaw movements shown above to be essential to break down tough fibrous foods. But because the principal muscles of mastication in herbivores are the superficial masseter and pterygoid muscles and because the major components of these are vertical rather than horizontal, powerful contractions of these muscles do not tend to dislocate the jaw joint, and therefore bony flanges which would restrict jaw movement do not develop.



MAN
Homo sapiens

NEAR-MAN
Australopithecus boisei

Fig. 8 **Lateral views of the skull, jaw and muscles in man (*Homo sapiens*) and an ancestral hominid or near-man, *Australopithecus boisei*. The lever arms illustrated are the same as for Figure 7.**

The changes in the skull, jaw and muscles involved in the evolution of the chewing mechanisms of herbivores and carnivores can be explained by the need to increase lateral movement in the former and reduce it in the latter. In fact, the position of the jaw joint is itself virtually diagnostic of an animal's diet. Where the joint lies on the level of the teeth, the animal is readily recognized as one which is either actively carnivorous or has been so during its history. Conversely one where the joint is found to lie well above the tooth row is, or has been, herbivorous. On that criterion alone, man is a herbivore! Figure 9 shows the position, relative size and simplified mechanics for the jaw muscles of modern man and an ancestral hominid or near-man, *Australopithecus boisei.* In modern man, a jaw joint lies well above the tooth row with the muscles forming a vertically arranged mass about the back of the mandible. Comparison of the mechanics of this system with that of the goat (Fig. 9) shows the only real difference to be the orientation of the lever arm for the temporalis (a_1), which is almost horizontal in man. For a given degree of pull by the muscle the net effect on the mandible is the same in both positions of a_1. The greater height of the jaw joint above the tooth row in man and therefore the greater angle the lever arm of the bite makes with the plane of the teeth as compared with the goat, suggests that man is capable of forcing the lower jaw sideways despite an exceptionally powerful vertical bite force. In these terms

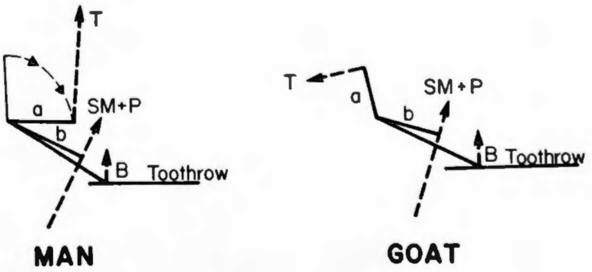


Fig. 9. **The similarity between the mechanics of the jaw muscles in the goat and in man shows that man, in this context at least, is thoroughly herbivorous!**

man is a better herbivore than the goat! The same remark applies to *Australopithecus boisei* (Leakey's nutcracker man) where the vertical height of the jaw, the depth of the face, the mass of jaw musculature and the size of the premolars and molars are even greater than in man. This and the excessive wear of the molars suggests that this hominid was specialized for dealing with tough foods, but more important, it shows that the masticatory mechanism of higher primates closely parallels that of conventional herbivores. A study of mastication in a series of primates would help to explain in functional terms the significance of many of the characteristic features which are so often cited in the descriptions of skulls of man and his antecedents.

Although this account of the functional relationships between the shape of the teeth in mammals and the jaw mechanics associated with their optimal use in chewing is somewhat simplified, it does perhaps illustrate that a clear correlation exists between diet, molar structure and skull architecture in examples of a primitive omnivore, herbivore, carnivore, as well as in man.

From a fairly simple beginning where the jaw moves forwards, upwards and sideways in chewing, using small shearing surfaces on simple tribosphenic teeth, specialization has resulted in the typical carnivorous "carnassial" tooth and the rasping molars of the herbivores. With these changes, the jaw muscles have been modified in their position and proportions and the jaw joint moved relative to the tooth row. Even in man, the form of the jaws can still be correlated with the pattern of movement and fundamental diet despite the great changes in the shape and size of the brain and the shortening of the face.