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MASTICATORY APPARATUS IN THE GIANT  
PANDA AND THE BEARS

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The peculiar feeding habits of the giant panda (*Ailuropoda melanoleuca*) are well known, and the general adaptation of its dentition to its food is obvious. It feeds exclusively on bamboo, which it is said to strip of the hard outer layers by means of the front teeth. Only the pith, which is still a very coarse food, is eaten. Enormous widening of the crowns of the premolars and molars leads to the formation of rectangular masticatory surfaces. The shape and the extensive wear of the teeth strongly suggest a grinding mastication, although the condyle of the mandible and glenoid fossa show all the characteristic features of a carnivore "hinge" joint. The seeming contradiction of a grinding mandibular movement and the shape of the articulating parts has not been investigated. Solution of this problem requires a functional analysis of the masticatory apparatus.

In order to understand the extreme adaptation in the masticatory apparatus of a carnivore to a specialized, coarse herbivorous diet, it was necessary to extend the investigation to the functional anatomy of the temporo-mandibular joint in other carnivores, among which that of the bears proved especially significant.

Without suggesting any phylogenetic relation between the Ursidae and the giant panda and without trying to form a genetic series in the Ursidae, an adaptational series can be established leading from purely carnivorous to omnivorous and to purely herbivorous species. Such a series might contain the following species:

First group (carnivorous): *Thalarcos maritimus*.

Second group (omnivorous): *Ursus horribilis*, *Euarctos americanus*, *Ursus tibetanus*.

Third group (herbivorous): *Tremarctos ornatus*.

Fourth group (specialized herbivorous): *Ailuropoda melanoleuca*.

#### MATERIAL

Skulls of carnivores from the osteological collections of Field Museum of Natural History<sup>1</sup> were examined, including especially the following species: *Panthera leo*, *Hyaena brunnea*, *Thalarcos maritimus*, *Euarctos americanus*, *Ursus tibetanus*, *Tremarctos ornatus*.

Four skulls of *Ailuropoda melanoleuca* were available. The wear of the teeth shows that they range in age from a fairly young to a rather old individual. The head of an adult Himalayan bear, *Ursus* (*Selenarctos*) *tibetanus*, was available for dissection. On one side the muscles of mastication were dissected, while the other half was cut into frontal sections.

Permission was granted by Mr. Edward Bean, Director of the Chicago Zoological Society, to observe the giant panda, Mei-Lan, during feeding.

#### REVIEW OF LITERATURE

Three points are of importance in a functional analysis of the masticatory apparatus: the osteology of mandible, glenoid fossa, and zygomatic arch; the anatomy of the muscles of mastication; and observations on the movement of the mandible. The literature yields the following pertinent data.

In describing the skeleton of the giant panda Lydekker (1901) makes the following remark: "The jaws of both *Aelurus* and *Aeluropus* differ from the Ursine mandible by the very remarkable conformation of the condyle.

"In the condyle of *Ursus* the articular surface forms a regular semicylinder, with its inner margin approximately at right angles to the long axis. On the other hand, in the two genera under special consideration the articular surface is like a riband wound obliquely on a cylinder of which the ends have been cut off along the margin of the riband. Consequently the inner margin of the articular surface forms an angle of about 45° with the axis of the condyle. No marked approximation to this very peculiar type of condyle is exhibited in the Raccoon." Lydekker also mentions that the zygomatic arch is wide and strong.

<sup>1</sup> I am under obligation to the Museum for granting access to its collections and for use of its laboratory facilities. I want to express my thanks to Mr. D. Dwight Davis, Curator, Division of Anatomy, for his assistance, and to Miss Elizabeth Story, Assistant in the Division of Anatomy, for drawing figures 13-15.



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The muscles of mastication of a bear, *Ursus labiatus* (= *Melursus ursinus*), were described by Toldt (1905). The masseter is divided into two portions. The superficial portion takes its origin from the lower border and a narrow strip of the lateral surface of the anterior third of the zygomatic arch. The fibers run downward and posteriorly to insert above the lower mandibular margin to and including the angular process. The most posterior fibers insert into a ligament that joins the auditory meatus to the mandible; fibers of the internal pterygoid muscle are attached to the same ligament.

The deep portion of the masseter is divided into two layers that take their origin from the whole length of the inferior border of the zygomatic arch. The fibers descend more vertically than those of the superficial portion and are inserted into the masseteric crest and the outer surface of the mandible between this crest and the lower border of the muscular groove.

The zygomatico-mandibular muscle, according to Toldt, is homologous with the deep layers of the masseter plus the zygomatic part of the temporal muscle in man, and consists of two parts divided by the passage of the masseter nerve. The muscle arises in closest proximity to the temporal muscle from the lower surface of the posterior part of the zygomatic arch and from the medial surface of the anterior half of the zygomatic arch. The fibers insert partly into the tendon of the temporal muscle, partly to the anterior border of the coronoid process and the muscular groove of the mandible.

Toldt stresses the necessity of recognizing the zygomatico-mandibular muscle as a separate muscular unit although it is continuous with the superficial fibers of the temporal muscle. The zygomatico-mandibular muscle is found in all mammals and is characterized by its origin from the inner surface of the zygomatic arch.

The muscles of mastication in the bear were again investigated by Starck (1935), who confirmed Toldt's description. Some of his remarks on the movement of the temporo-mandibular joint are of interest. He writes: "The shape of the articular surfaces of the temporo-mandibular joint and the structure of capsule and discus are the expression of the possible movements in this joint. . . . The articular fossa is fairly shallow. A strong retroglenoid process inhibits any movement posteriorly. Therefore, aside from the simple hinge movement, lateral excursions (grinding movements) are possible. The length of the canines limits to a certain degree the freedom of the joint.

"The articular capsule in its lateral part is extremely slack, and therefore does not inhibit the grinding movements. Observations on living animals in the Cologne Zoo showed me that lateral movements do in fact play an important role in the mastication of the bears. The abrasion facets also prove this unequivocally."

Brodie (1934) was the first to attribute a lateral shifting movement to the mandible of carnivores. "A study of the temporo-mandibular joint in the cats reveals the source of the exact shearing action of the carnassials. The condyles are cylindrical in form and their axes lie in the same transverse line. The fossae embrace them so accurately that disarticulation is extremely difficult. It has been said that these animals possess a true hinged joint but this is not strictly true. When the jaws are closed the upper teeth lie completely buccal to the lowers so that if no lateral movement were possible there would be no contact between upper and lower teeth except at the instant that the jaws came to final rest. All requirements are met by the design of the joint which allows the lower jaw to be dropped and then shifted bodily to one or the other side, the condyles traveling in the line of their axes. A powerful pterygoid, running almost horizontally laterad, provides the power for the shift, and for the maintaining tight contact between the teeth as the masseter closes the jaws."

In a later paper Brodie (1939) mentioned the fact that the masseter, because of its downward and inward course, might also participate in bringing about the lateral shifting movement of the mandible in carnivores.

According to Davis (MS.), the muscles of mastication in the giant panda are in all principal aspects built like those of the bears. The masseter can be divided, though incompletely, into three layers. The temporal muscle is very heavy and divided by a strong tendon into a superficial and a deep stratum. The internal pterygoid is fairly well developed, the external pterygoid rather strong and directed laterad and slightly posteriorly to a groove on the inside of the condyle.

#### OSTEOLOGY AND ANATOMY

*Zygomatico-mandibular muscle.*—Dissection of the masticatory muscles of our Himalayan bear confirmed in most points the descriptions of Toldt and Starck. However, a large part of the zygomatico-mandibular muscle is found to consist of horizontal bundles. This can be seen most clearly on frontal sections (fig. 13).

The horizontal bundles arise from the upper parts of the medial surface of the zygomatic arch and run horizontally inwards and forwards. They insert into the tendon of the temporal muscle and to the uppermost region of the coronoid process.

*Glenoid fossa.*—The glenoid fossa is relatively shallow in *Thalartos*, *Ursus*, and *Euarctos*. In *Tremarctos* it is much deeper. This

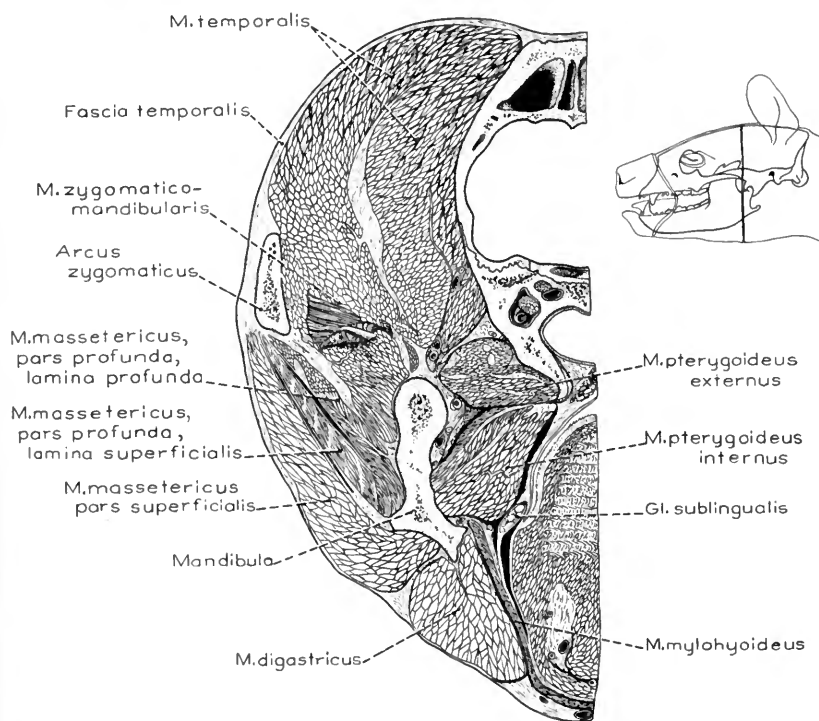


FIG. 13. Frontal section through the head of a Himalayan bear anterior to the mandibular condyle (inset). Posterior surface of anterior half. Bundles of the zygomatico-mandibular muscle are reflected to show the horizontal course of its fibers.

is caused mainly by a downward extension of its anterior edge, especially in the lateral parts. In one specimen of *Tremarctos* the fossa embraces the condyle so far that the mandible cannot be removed from the skull.

The glenoid fossa is also very deep in the giant panda. Medially and posteriorly it extends onto the postglenoid process; laterally and anteriorly it extends in a tongue-like expansion onto the inferior surface of the zygomatic arch. In this way it forms the counterpart

to the "spiral riband" of the condyle. Extreme opening of the jaws, far beyond the movement possible in the living animal, is required to remove the condyle of the mandible from the glenoid fossa.

*Zygomatic arch.*—The root of the zygomatic arch, in the (secondarily) carnivorous polar bear (fig. 14, *a, b*), is a wide horizontal plate of bone that bears the glenoid fossa inferiorly and has a smooth, slightly concave upper surface. The zygomatic arch itself (zygomatic process of the temporal bone) develops from the antero-lateral corner of this root plate rather abruptly, the bone being twisted into a vertical position. The zygomatic arch in its entire length is of uniform and moderate width. The inner surface is entirely smooth.

The following changes can be observed in the omnivorous *Euarctos americanus*, *Ursus tibetanus*, and *Ursus horribilis* (fig. 14, *c, d*): The twist of the zygomatic root plate into the zygomatic process of the temporal bone occurs not on the antero-lateral corner but along the whole lateral edge of the plate. This leads to an elongation of the zygomatic arch posteriorly. At the same time the temporal part of the zygomatic arch, especially in its posterior region, gains in height. Furthermore, the medial surface of the zygomatic arch in its posterior part is not smooth, but shows ridges and grooves for the origin of heavy muscle and tendon bundles.

In the herbivorous *Tremarctos* (fig. 14, *e, f*) the process of widening of the temporal part of the zygomatic arch posteriorly and upwards has made further progress; the upper border of the zygomatic arch is now concave in its anterior, strongly convex in its posterior half. The lower border is slightly concave for its entire length.

In *Ailuropoda*, adapted to coarse herbivorous diet, the expansion of the zygomatic arch is carried to the extreme (fig. 14, *g, h*). The temporal part extends upward as a wide plate heavily ridged on its medial surface. At the same time the lateral curve of the zygomatic arch is increased considerably.

Comparison of the zygomatic arch in the carnivorous lion and the carrion-feeding hyena shows a striking parallel to the findings in the polar bear and the omnivorous Ursidae. The zygomatic arch of a lion is of moderate and uniform width throughout its entire length. The arch of a hyena is strongly convex laterad; the posterior (temporal) part is considerably widened.

#### DISCUSSION

*Observations on living panda.*—While the panda was feeding on carrots and dog biscuits, the lateral movement of the mandible could

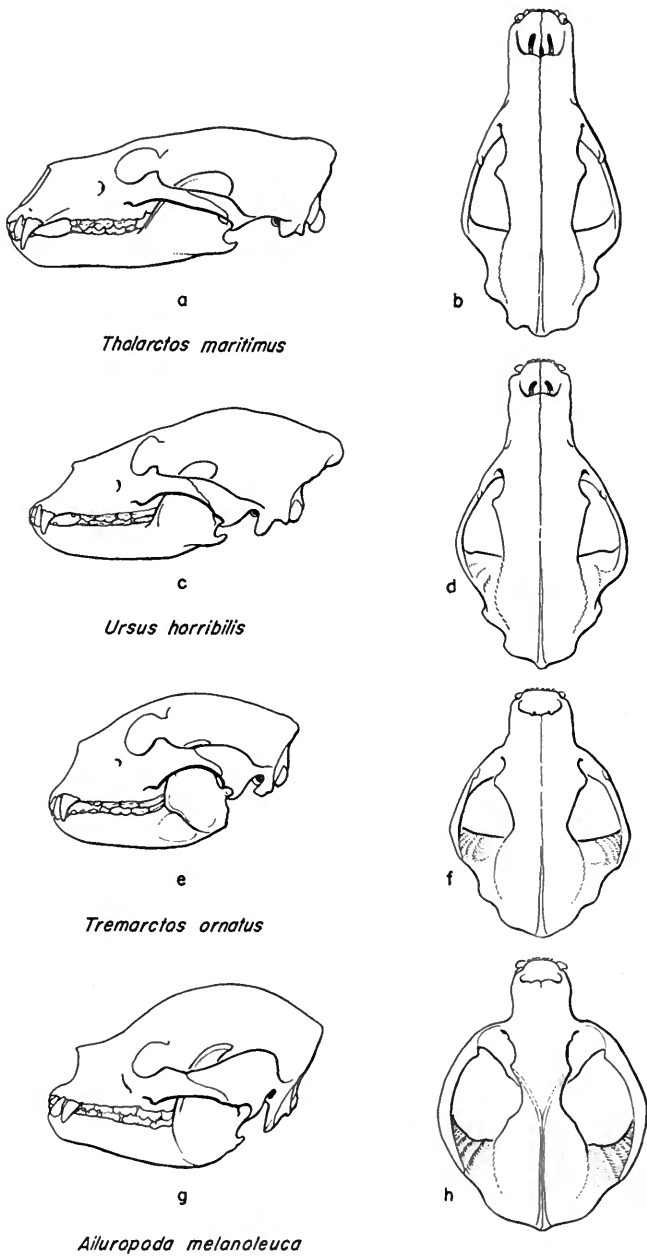


FIG. 14. Adaptational series in the development of the zygomatic arch.

readily be seen and determined by palpation of the mandibular angle during mastication; but in the living animal it is impossible to decide whether the lateral movement is one of rotation or of shifting.

*Movement of temporo-mandibular joint in carnivores.*—Brodie's assertion of a lateral shifting movement of the mandible in carnivores (cats) can be confirmed. The formation of the mandibular condyles and the glenoid fossae and the arrangement of the musculature make such a movement entirely possible. Proof of the actual occurrence of this movement can be found on the teeth of old specimens of any of the great cats. The carnassials of such an animal (e.g. lion) show characteristic wear. Facets are seen on the inner (lingual) surface of the upper and the outer (buccal) surface of the lower carnassial. These surfaces do not come into contact at all during simple hinge movements of the jaw. A lateral shift is the only possible means of accomplishing a gliding of these surfaces on one another to perfect the shearing action, as Brodie has emphasized.

Tooth wear like that of the lion is still more pronounced in the hyenas in which the abrasions occupy almost the entire opposing surfaces of the carnassials. This seems to be in accordance with the bone-breaking habit of these animals, in which the carnassials act under much stronger force.

Use is being made of shearing action during the closing phase of the movement. The mandible is moved in a combination of hinge and shifting movement, which must be termed a screw movement. The temporo-mandibular joint of the carnivores must, therefore, be classified as a hinge and screw joint. The extent of the lateral component is small compared with the rotating component in the cats and hyenas. The height of the sectorial teeth is responsible for this fact. The curve of the canines fits perfectly into this screw movement.

*Muscles concerned with screw movement of temporo-mandibular joint.*—Most descriptions of the muscles of mastication in carnivores point out the fact that the external pterygoid has an almost frontal course. This muscle is, as Brodie remarks, capable of shifting the mandible to one side parallel to itself. The external pterygoid, however, is relatively weak, especially in cats. Its function is probably the shifting of the mandible during the opening phase of the movement, which is done without great force.

In the closing phase great force is required. This force is added to that of the external pterygoid by the synergistic action of the zygomatico-mandibular muscle of the contralateral side.

Most authors describe the different layers of the masseter and temporal muscles as in a two-dimensional plane only. Careful dissection and, most of all, frontal sections reveal that the deeper layers of the masseter deviate more and more from a sagittal plane. They course not only down and back or vertically downward, but have also a course down and medially. A large amount of the fibers of the zygomatico-mandibular muscle runs an entirely horizontal course and at the same time medially and anteriorly. These parts of the muscle therefore exert a strong pull laterally. They aid quite evidently in producing the lateral component of the screw movement.

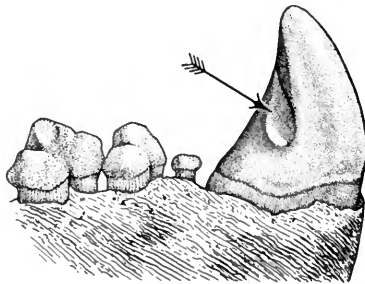


FIG. 15. Attrition facet on the lower canine of *Ailuropoda*.

The right external pterygoid pulls the mandible to the left side, the left zygomatico-mandibular being its synergist.

*Movement of mandible in bears and giant panda.*—In the adaptation to omnivorous and later herbivorous diet, the high sectorial teeth of the carnivores are changed to seco-bunodont teeth in the bears and to bunodont teeth in *Ailuropoda*. That these teeth function in a grinding and not merely in a crushing action can be proved by observation of the living animals. Lateral movement has been seen in bears (Starck) and in the panda (my own observation). The extreme wear of the side teeth in bears as well as in the panda has long been known and correlated with a grinding action.

This lateral movement is a further development of the lateral shifting component of the screw movement characteristic for all carnivores. The flatness of the glenoid fossa in some bears caused Starck to assume a lateral movement similar to that in ungulates and primates in which the mandible *rotates* laterally. This is quite obviously wrong. Even in *Ursus* and *Euarctos* such a movement would entail a separation of the articulating surfaces from each other and from the very thin and practically immovable discus. Further-

more, it can be shown that just those bears that are entirely herbivorous, like *Tremarctos* and the panda, have a glenoid fossa so deep that the mandible cannot be removed or can hardly be removed on the dry skull. Some proof for the screw movement can be obtained by leading the mandible of an old specimen along the trituration facets of the molars. Then, quite automatically, the mandible shifts bodily, parallel to itself, to one side.



FIG. 16. Skull of the giant panda in lateral position of the mandible. Upper canine fitting the attrition facet on lower canine.

Absolute proof is given by the observation of a peculiar facet on the lower canines in the giant panda (fig. 15). This facet is already visible in young animals as a nick on the postero-lateral, concave surface of the canine. The upper canine does not come into contact with this point of the lower one in any position of the lower jaw but after a screw movement of the mandible. Or—in other words—if one tries to fit the tip of the upper canine into this facet, the mandible automatically assumes a laterally shifted position (fig. 16). In this position the molars and premolars of this side meet head on (fig. 17); if the mandible is brought back into rest position the side teeth glide on each other along their trituration marks.

The wear on the side teeth in the panda is considerable in older individuals. The continuous wear of the lower canine may weaken it to such a degree that it is mutilated by breaking.

To recapitulate, in cats the shifting component is small compared to the rotating component of the screw movement. In bears



and more so in the panda the shifting component assumes greater proportions. This is due to the decrease in the height of the cusps of the side teeth. In the panda the reduction of the canines allows extensive shift (4-5 mm.) during a relatively slight opening movement.

*Changes in zygomatic arch and zygomatico-mandibular muscle.*—The zygomatico-mandibular muscle is well developed in all carni-



FIG. 17. Basal view of skull shown in figure 16. The mandible is shifted to the right side of the animal.

vores. But there is a striking increase in its volume correlated with the increasing importance of the lateral shifting movement of the mandible. On one side such an emphasis on the lateral movement can be shown in the hyenas as against the cats; on the other side development of omnivorous and later herbivorous habits in the bears and in the panda leads in the same direction. The enlargement of the zygomatico-mandibular muscle can easily be envisaged on the skeleton by observing the increase in its area of origin on the medial surface of the zygomatic arch.

It has been noted that the zygomatic arch undergoes a progressive change in the animals arranged in an adaptational series. The arch is rather slender and of equal width throughout in *Thalarchos*. In *Ursus* and *Euarctos* its posterior (temporal) part widens out superiorly and exhibits muscular ridges on its inner surface. In *Tremarctos* this process is still farther advanced, and is carried to an extreme in the panda.

These changes in the zygomatic arch are correlated with changes of the zygomatico-mandibular muscle. This muscle, especially its horizontal part, originating from the superior area of the medial surface of the zygomatic arch, is weakest in the polar bear and gains in volume in *Ursus* and *Euarctos*. It is strongly developed in *Tremarctos* and of excessive strength in the panda.

The changes of the zygomatic arch and the zygomatico-mandibular muscle are parallel to the adaptation to carnivorous, omnivorous, herbivorous, and specialized herbivorous diet. It is obvious that the grinding movement of the mandible due to the lateral shift gains in importance in adaptation to herbivorous diet. The increase in the extent and force of this movement is parallel to the increase in volume and power of the zygomatico-mandibular muscle.

In the panda the increase in height of the coronoid process of the mandible moves the insertion area of the zygomatico-mandibular muscle upward. This in turn acts to increase further the cross section of the horizontal fibers of the zygomatico-mandibular muscle.

The striking length of the mandibular condyle and the development of its articulating surface into a "spiral riband" can be understood as an adaptation to the extent and force of the screw movement of the mandible.

#### SUMMARY

(1) The existence of a lateral shifting movement during the shearing action of the carnassials in cats (Brodie) is confirmed and is proved by the observation of abrasion facets. The same movement exists in the other carnivores.

(2) The temporo-mandibular joint in carnivores is not purely a hinge joint, but is also capable of screw movements. It must be designated as a "hinge and screw" joint.

(3) The weak external pterygoid and the strong zygomatico-mandibular muscles—both horizontal and nearly frontal in direction—perform the lateral shifting component of the screw movement.

(4) The screw movement of the mandible assures the shearing action in the Felidae and the Hyaenidae. The same screw movement allows a grinding action in bears and in the giant panda.

(5) In cats the rotating component is more prominent than the lateral component of the screw movement. The reverse is true in bears and especially in the giant panda.

(6) In a functional series represented by *Thalarcos*, *Ursus*, *Tremarctos*, and *Ailuropoda*, carnivorous diet changes to omnivorous, then to herbivorous, and finally to specialized coarse herbivorous diet. The grinding action increases in importance in this series.

(7) This same series shows a gradual widening and strengthening of the zygomatic arch, especially in its posterior part.

(8) The increase in surface area of the zygomatic arch increases the area of origin of the zygomatico-mandibular muscle.

(9) The increase of the zygomatico-mandibular muscle increases the power of the lateral shifting component of the screw movement of the mandible.

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