FULL PAPER ***Anatomy***

Adaptation of the Muscles of Mastication to the Flat Skull Feature in the Polar Bear (*Ursus maritimus*)

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(Received 22 June 1999/Accepted 26 August 1999)

ABSTRACT. The muscles of mastication of the polar bear (*Ursus maritimus*) and those of the brown bear (*U. arctos*) were examined by anatomical approach. In addition, the examination of the skull was carried out in the polar bear, brown bear and giant panda (*Ailuropoda melanoleuca*). In the polar bear, the rostro-ventral part of the superficial layer of the *M. masseter* possessed the abundant fleshy portion folded in the rostral and lateral directions like an accordion. Moreover, the rostro-medial area of the superficial layer became hollow in the nuchal direction when the mouth was closed. The *M. temporalis* of the polar bear covered up the anterior border of the coronoid process of the mandible and occupied the almost entire area of the cranial surface. The *M. pterygoideus medialis* of the polar bear was inserted on the ventral border of the mandible and on the ventral part of the temporal bone more widely than that of the brown bear. As results of our measurements of the mandible, an effect of the leverage in the polar bear was the smallest in three species. In the polar bear, the skull was flat, and the space between zygomatic arch and ventral border of the mandible, occupied by the *M. masseter* was the narrowest. It is suggested that the muscles of mastication of the polar bear is adapted to the flat skull feature for supplementing the functions.—KEY WORDS: brown bear, giant panda, muscle of mastication, polar bear, skull feature.

J. Vet. Med. Sci. 62(1): 7–14, 2000

It is well-known that the polar bear (*Ursus maritimus*) is the largest bear and characterized by white fur and elongated head and neck. This bear lives around the Arctic and is adapted to aquatic and cool environments [14, 34]. Moreover, it is thought that the polar bear is the most recent Ursidae evolved from a common ancestor of the brown bear during the Pleistocene [33].

Many morphological studies on the head of the bears have been reported [3, 7, 16, 20, 27, 30–32, 35]. The head of the polar bear is elongated, flat and small as compared with the body size [34]. However, in the muscles of mastication of the polar bear, the detailed examination of the muscle insertion has not been carried out.

Generally, it is thought that the large masticatory force is produced by leverage in the animals of foreshortened head, such as the tiger. We think that the muscles of mastication of the polar bear may be adapted to the flat head feature to keep the essential masticatory functions. In the present study, therefore, the muscles of mastication were examined in the polar bear and the brown bear (*U. arctos*). In addition, the skulls of the polar bear, the brown bear and the giant panda (*Ailuropoda melanoleuca*) were examined.

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MATERIALS AND METHODS

We used the carcasses of the adult male polar bear [15] and the adult female brown bear (Table 1). They are respectively donated from the Ritsurin Park Zoo (Kagawa, Japan) and the Ueno Zoological Park (Tokyo, Japan) to the National Science Museum, Tokyo. The head was separated from each carcass trunk. Fixation of the heads was avoided for preparation of the skeletal specimen. The heads were stored at −20°C. Both fresh heads were anatomically examined. Moreover, the skulls are observed in the polar bears, the brown bear and the giant panda. The measurements of mandible were evaluated as described in Fig. 1. The measurement points on mandible followed the methods of Suenaga [30].

RESULTS

The *Musculus masseter* of the polar bear was indicated in Fig. 2. The rostro-ventral part of the superficial layer of the

Table 1. The carcass specimen used in this study

Species	Museum number	Sex	Age (years)	Donor
Ursus maritimus	M31421	M	20*	Ritsurin Park Zoo
U. arctos	M31422	F	17	Ueno Zoological Park

*: Age was estimated by donor.
M: Male. F: Female.

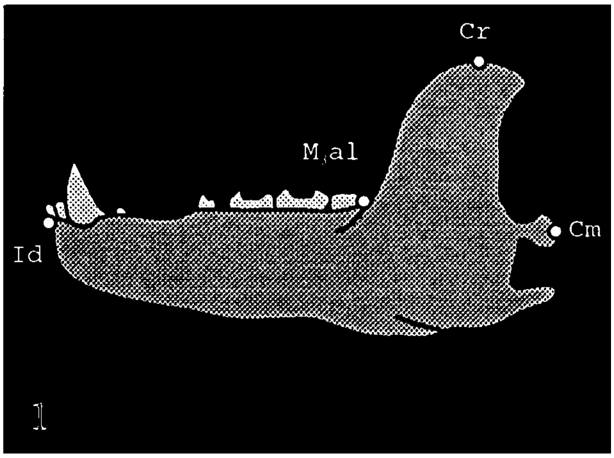

Fig. 1. The measurement points on the mandible of the bear, followed the methods of Suenaga [30]. Cm: condylomediale, the medio-caudal point in condylar process of mandible. Cr: coronion, the highest point of coronoid process. Id: infradentale, the dorsal border of intermandiblar articulation. M_3al: molar-alveolar tertium, the medial point in caudal border of alveolar part of the third lower molar. Total length of mandible (TL): length between Cm and Id. Length of moment arm of temporalis (MAT): length between Cm and Cr. CM: Length between Cm and M_3al.

M. masseter possesses the rich fleshy portion folded in the rostral and lateral directions (Fig. 2A). As the jaws are shut, the part of the *M. masseter* has been folded still more like an accordion. Moreover, the rostro-medial area of the superficial layer becomes hollow in the nuchal direction when the mouth has completely been closed. The superficial layer of the *M. temporalis* is noticed inside the *M. masseter* when the *M. buccinator* has been removed (Fig. 2A). The well-developed *M. temporalis* inserted on the anterior border of the coronoid process of the mandible appears clearly in front of the middle and deep layers of the *M. masseter* (Fig. 2B, C).

The *M. masseter* of the brown bear was shown in Fig. 3. The superficial layer of the *M. masseter* is enlarged in ventro-lateral part of the zygomatic arch, and the folded fleshy portion is not noticed (Fig. 3A). The *M. temporalis* is not found in front of the middle layer of the *M. masseter* when the superficial layer of the *M. masseter* has been removed (Fig. 3B). The *M. temporalis* inserted on the anterior border of the coronoid process of the mandible becomes distinguishable when the middle layer of the *M. masseter* has been removed (Fig. 3C).

The *M. masseter* is completely taken away from the masseteric fossa (Fig. 4A, B). The *M. temporalis* of the polar bear covers up the whole anterior border of the coronoid process (Fig. 4A), but never in the brown bear (Fig. 4B).

In the polar bear, the right and left *M. temporalis* are attached on the midline, and a mid-dorsal sulcus is discerned (Fig. 5A). However, both sides of *M. temporalis* in the brown bear do not meet at the vertex (Fig. 5B).

The *M. pterygoideus medialis* in the polar bear is inserted on the medial and ventral surface of the angular process of the mandible and on the further dorsal part which corresponds to the ventral region of the temporal bone (Fig. 6A). The *M. pterygoideus medialis* in the brown bear is also inserted on the region of the angular process and on the ventral region of the temporal bone (Fig. 6B). However, the insertion area is narrower in the brown bear than in the polar bear from a ventral aspect (Fig. 6). The *M. pterygoideus medialis* in the polar bear is inserted on the near part to the bulla tympanica of the temporal bone (Fig. 6A).

The skulls of the polar bear, the brown bear and the giant panda were indicated in Fig. 7. In the polar bear, the skull is flatter than that in the brown bear (Fig. 7A, B). The skull of the giant panda is the most foreshortened and highest (Fig. 7C). In the polar bear, the space between zygomatic arch and ventral border of the mandible, occupied by the *M. masseter* is narrow (Fig. 7A). On the other hand, the space in the brown bear is wider than that in the polar bear (Fig. 7B). The space in the giant panda is the widest in three species (Fig. 7C).

The measurements of the mandible, the ratios of length of moment arm of temporalis (MAT) to total length of mandible (TL) (MAT/TL) and the ratios of MAT to length between condylomediale (Cm) and molar-alveolar tertium (M_3al) (CM) (MAT/CM) in the polar bear, the brown bear and the giant panda were shown in Table 2. All MAT/TL in the polar bear are smaller than those in the brown bear except M14320 specimen, but MAT/TL in the polar bear does not over that of M14320 specimen. The MAT/TL in the giant panda is the largest. All MAT/CM in the polar bear are the smallest in three species. The MAT/TL and MAT/CM in the giant panda are the largest.

The mandibles of the polar bear, the brown bear and the giant panda were indicated in Fig. 8. The coronoid process of the polar bear is the shortest in the three (Fig. 8). In the giant panda, the breadth of the coronoid process is narrow in upper region (Fig. 8C).

DISCUSSION

The muscles of mastication consist of the *M. masseter, M. temporalis, M. pterygoideus medialis* and *M. pterygoideus lateralis* [8, 9, 18]. The *M. masseter* shows a multipinnate muscle divided by the tendinous sheet [8, 24, 28]. The structure of the *M. masseter* has been examined in many mammals [6, 10–12, 25, 27, 36, 37]. In the Ursidae, Stark [27] divided the *M. masseter* into three portions. However, the division methods have not been reported. Gaspard [10] demonstrated that the *M. masseter* of the Carnivora (*Canis*) is alternately partitioned by the upper and lower aponeuroses and divided into three layers.

In this study, the *M. masseter* of the polar bear and the brown bear was examined according to the definition of Gaspard [10]. We could divide the *M. masseter* of each bear into three layers as shown in the *Canis* [10, 24]. In the

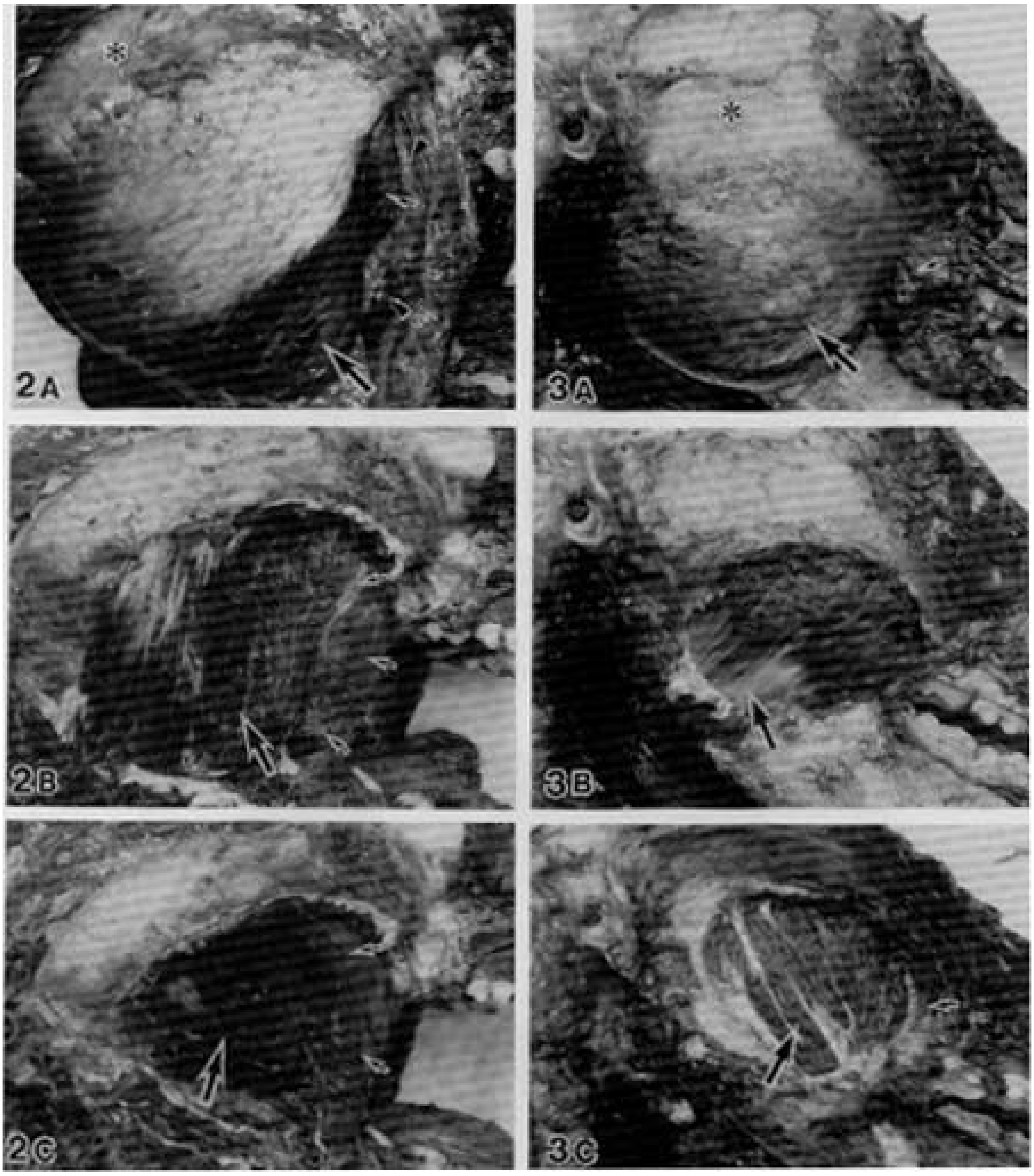

Fig. 2. The right lateral view of the mandibular portion of the polar bear. The right direction is the rostral part. A: The superficial layer of the *M. masseter* possesses the abundant fleshy portion folded in the rostral and lateral directions (large arrow). The *M. temporalis* (small arrow) is noticed inside the *M. masseter*. Asterisk, the zygomatic arch. Arrowheads indicate the *M. buccinator*. B: The middle layer of the *M. masseter* (large arrow) is confirmed behind the well-developed *M. temporalis* (small arrows) inserted on the anterior border of the coronoid process of the mandible. This part of *M. temporalis* originates from the temporal fossa. C: The deep layer of the *M. masseter* is inserted on the masseteric fossa (large arrow). Small arrows indicate the *M. temporalis*.

Fig. 3. The right lateral view of the mandibular portion of the brown bear. The right direction is the rostral part. A: Large arrow and small arrow show respectively the superficial layer of the *M. masseter* and the *M. buccinator*. Asterisk, the zygomatic arch. B: The middle layer of the *M. masseter* is inserted on the ventro-caudal margin of the masseteric fossa by the tendon (arrow). C: The *M. temporalis* (small arrow) inserted on the anterior border of the coronoid process is found in front of the deep layer of the *M. masseter* (large arrow).

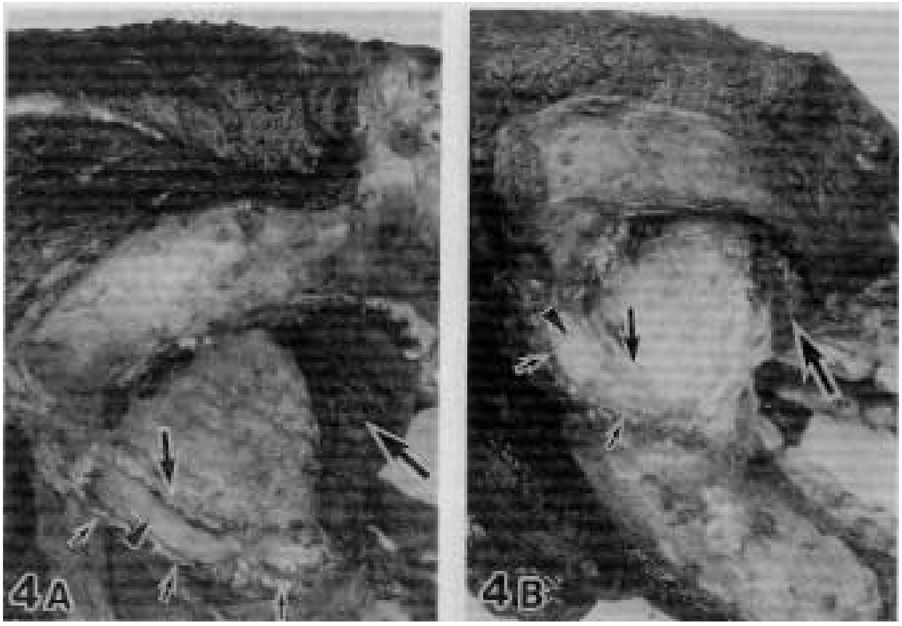

Fig. 4. The right lateral view of the mandibular portion of each bear. The *M. masseter* has completely been removed. The right direction is the rostral part. A: The head of the polar bear. The *M. temporalis* covers up the anterior border of the coronoid process of the mandible (large arrow). B: The head of the brown bear. Large arrow indicates the *M. temporalis*. Small arrows: The insertion of the middle layer of the *M. masseter* by the tendon. Arrowhead: The insertion of the middle layer by the fleshy portion. Intermediate arrow: The insertion of the deep layer by the tendon.

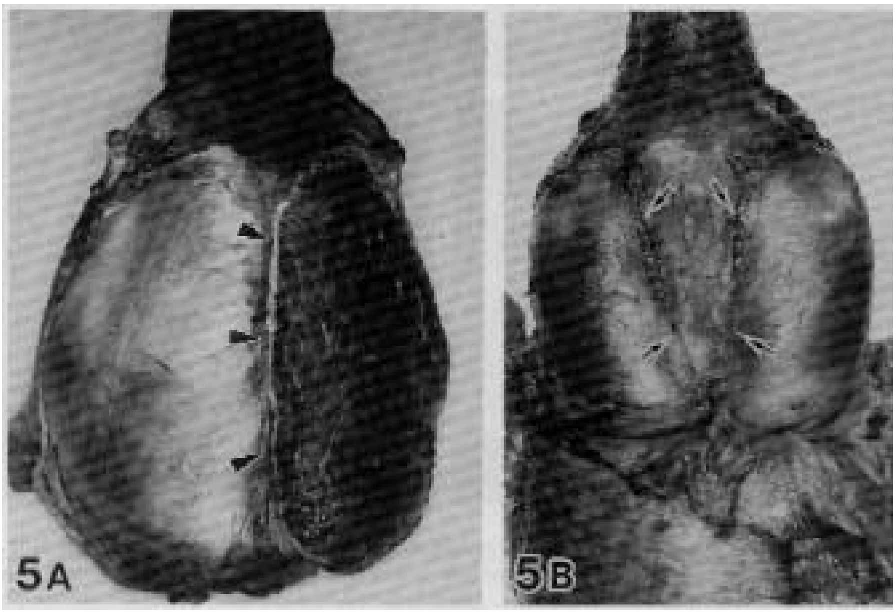

Fig. 5. A: The dorsal view of the head of the polar bear. The mid-dorsal sulcus is formed by the attachment of the right and left *M. temporalis* on the midline (arrowheads). The right fascia of the *M. temporalis* has been removed. B: The dorsal view of the brown bear. The right and left *M. temporalis* are not attached on the midline of the skull. Arrows indicate the part of temporal line.

polar bear, the rostro-ventral part of the superficial layer of the *M. masseter* possessed the abundant fleshy portion folded in the rostral and lateral directions. Moreover, the space between the zygomatic arch and the ventral border of

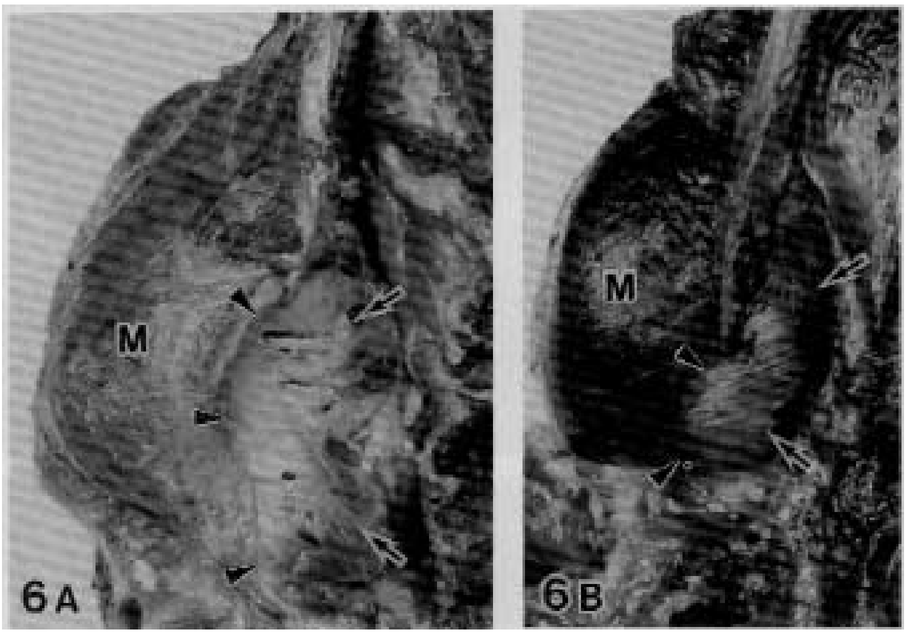

Fig. 6. A: The ventral view of the head of the polar bear. B: The ventral view of the head of the brown bear. Arrows: The *M. pterygoideus medialis*. Arrowheads: The insertion of the *M. pterygoideus medialis* on ventral surface of the mandible and skull. M: The superficial layer of the *M. masseter*.

Table 2. Measurement values and the measurement ratios in the mandible

Museum number	Species	Sex	TL (mm)	MAT (mm)	CM (mm)	MAT/TL	MAT/CM
M05624	*Ursus maritimus*	NR	229.3	62.5	93.7	0.27	0.68
M31460	*U. maritimus*	NR	217.4	56.8	83.3	0.26	0.68
M00867	*U. arctos*	NR	204.5	58.6	75.5	0.29	0.78
M01848	*U. arctos*	NR	282.0	83.4	103.9	0.30	0.80
M01911	*U. arctos*	NR	254.8	83.3	101.6	0.32	0.82
M09523	*U. arctos*	M	209.1	61.1	66.0	0.29	0.93
M12305	*U. arctos*	NR	233.3	71.3	85.5	0.31	0.83
M14408	*U. arctos*	NR	196.8	56.9	68.2	0.29	0.83
M14410	*U. arctos*	NR	222.5	63.8	81.8	0.29	0.78
M14320	*U. arctos*	F	217.1	59.7	78.9	0.27	0.76
M14535	*U. arctos*	F	207.5	60.7	75.4	0.29	0.81
M21010	*U. arctos*	M	276.8	81.3	108.2	0.29	0.75
M28266	*U. arctos*	NR	186.7	54.4	64.9	0.29	0.84
M31458	*Ailuropoda melanoleuca*	F	211.7	77.5	64.2	0.37	1.21

All biological data have been recorded with specimens.
NR: Not recorded. M: Male. F: Female.
TL: Total length of mandible, length between Cm and Id.
MAT: Length of moment arm of temporalis, length between Cm and Cr.
CM: Length between Cm and M_3al.
MAT/TL: The ratio of MAT to TL.
MAT/CM: The ratio of MAT to CM.

the mandible, occupied by the *M. masseter* was narrower than that in the brown bear. So, the fiber of the most rostral *M. masseter* in the polar bear, connects between zygomatic arch and ventral border of the mandible is shortened as compared with that in the brown bear. It is suggested that the rostro-ventral part of the superficial layer of the *M. masseter* has been folded in the rostral and lateral directions like an accordion to keep a long distance between the upper

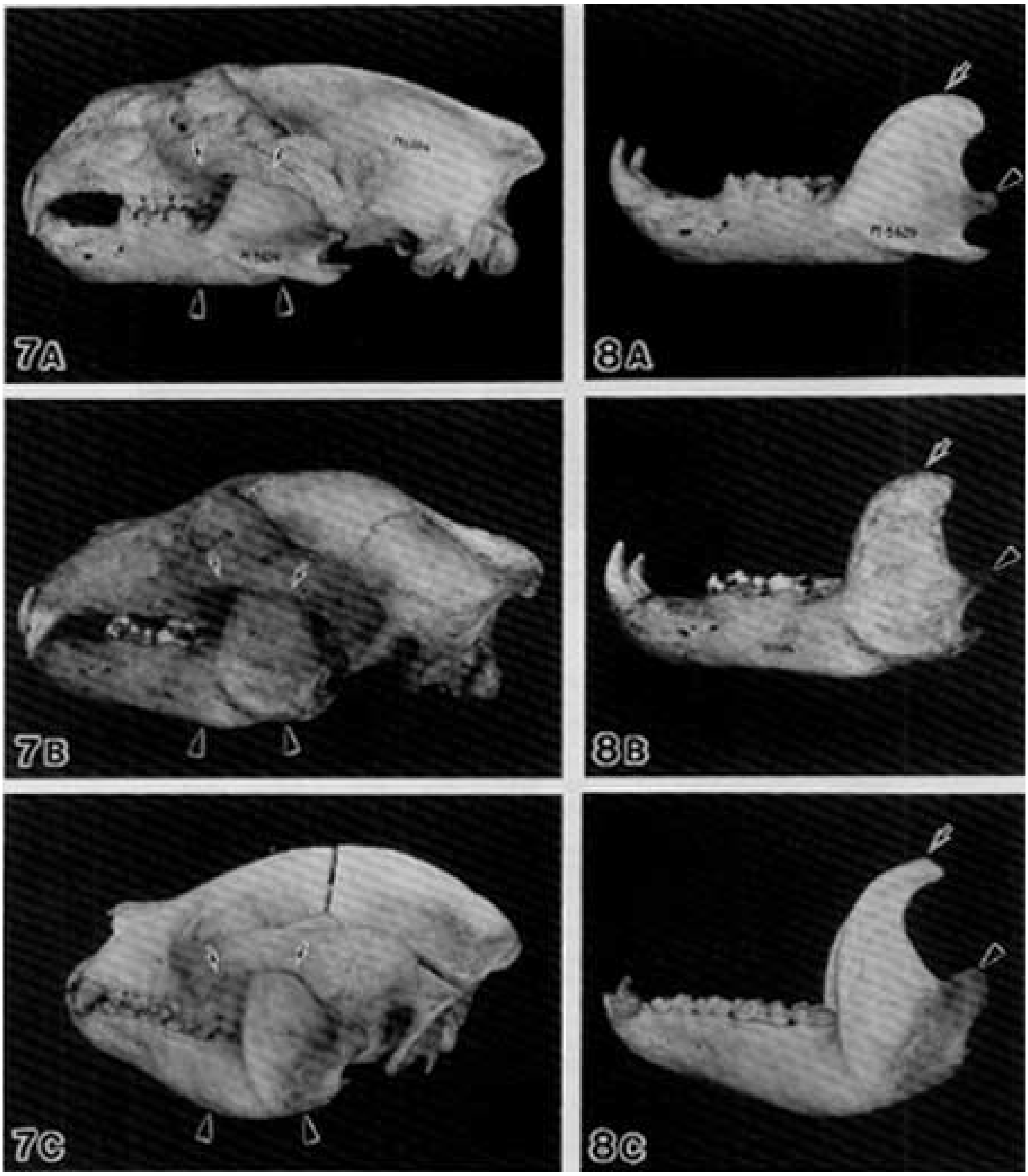

Fig. 7. The left lateral view of the skull in the polar bear, brown bear and giant panda. Three photographs are in the same reduced scales. A: The skull of the polar bear (M05624). The skull is the flattest, and the space between zygomatic arch and ventral border of the mandible, occupied by the *M. masseter* is the narrowest in three species. B: The skull of the brown bear (M12305). The space is wider than that of the polar bear. C: The skull of the giant panda (M31458). The skull is the highest, and the space is the widest. Arrows: Zygomatic arch. Arrowheads: Ventral border of the mandible.

Fig. 8. The left lateral view of the mandible in the polar bear, brown bear and giant panda. Three photographs are in the same reduced scales. A: The mandible of the polar bear (M05624). The coronoid process is the shortest. B: The mandible of the brown bear (M12305). C: The mandible of the giant panda (M31458). The coronoid process is the longest. Arrow: Coronoid process. Arrowhead: Condylar process.

and lower jaws when the mouth is largely opened. And it may be a reason why the rostro-ventral part of the superficial layer possesses the abundant fleshy portion. When the *M. masseter* is folded in the shutting jaw condition, it is thought that the *M. masseter* produces smaller bite force for crushing than the *M. masseter* not folded in the same condition.

The *M. masseter* of the polar bear was not enlarged as compared with the head size. On the other hand, the *M. masseter* of the brown bear was enlarged in the ventro-lateral part of the zygomatic arch and not folded when the mouth was closed. The *M. masseter* occupied the wide space between the zygomatic arch and the ventral border. It is thought that the brown bear may produce larger masseteric force than the polar bear of the same head size. We suggest that the role of the *M. masseter* is important for the brown bear in the mastication.

The *M. temporalis* of the polar bear covered up the anterior border of the coronoid process of the mandible, but that of the brown bear did not. The *M. temporalis* of the polar bear occupied the almost entire area of the cranial surface, although the *M. temporalis* of the brown bear was not inserted on the vertex. All MAT/TL and MAT/CM in the polar bear were smaller than those in the brown bear except one specimen. It is suggested that the larger the MAT /TL and MAT/CM are, the larger the force at the each point, Id and M_3al is by leverage when same force is acted on coronion (Cr). We think that the same effect of leverage is applied at the correspondence points between infradentale (Id) and M_3al. It may be assumed that the *M. temporalis* of the polar bear supplements functions by covering up the anterior border of the coronoid process and the almost entire area of the cranial surface.

In the present study, we observed the head of the female brown bear. It has been reported that the skull feature represented by temporal line, extra sagittal crest and so on is different between both sexes [30, 31]. These differences indicate that the male bear develops the muscles of mastication more than the female. However, in most brown bears of both sexes, the right and left temporal lines have been separated on the frontal bone. On the other hand, the temporal lines of the polar bear meet on the frontal bone. So, the brown bear is broad forehead as compared with the polar bear. In the brown bear of both sexes, the space between the zygomatic arch and the ventral border of the mandible occupied by the *M. masseter* is wide, the coronoid process is long, and the skull feature is not flat. We think that the feature of the muscles of mastication basically resembles between both sexes, and that there are differences of masticatory function such as bite force and mouth opening system between the polar bear and the brown bear.

In the polar bear, the *M. pterygoideus medialis* was inserted on the medial and ventral surface of the angular process of the mandible and on the further dorsal part. The *M. pterygoideus medialis* was inserted on the ventral border of the mandible and on the ventral part of the temporal bone more widely than that in the brown bear. It is thought that the insertion of the *M. pterygoideus medialis* in the polar bear is adapted to elongated and flat head.

The skull of the giant panda was the most foreshortened and highest in three species. The space between zygomatic arch and ventral border of the mandible was the widest. Davis [7] stated that the giant panda possesses the strong jaws for biting. We also think that the giant panda may produce the large masseteric force. The MAT/TL and MAT/CM were the largest in three species. Theoretically, the giant panda is expected to produce the large bite force by the leverage. However, the upper region of the coronoid process may be slender for the *M. temporalis* to be inserted on. Thus the bite force by the *M. temporalis* may be below our expectations.

The polar bear is the largest carnivorous animal and at the top of the arctic marine food chain [2, 21]. It is well-known that the polar bear mainly feeds on the seals [14, 29, 34]. The brown bear is an omnivorous animal and feeds on plants, fruits and a few animals [1, 4, 5, 13, 17, 19]. On the other hand, the giant panda mainly feeds on bamboo. It has been shown that the *M. temporalis* is the largest muscle among the muscles of mastication of the Carnivora, and that the *M. masseter* is the largest among those of the Herbivora for grinding plants [8, 9, 26]. In the Carnivora, Radinsky [22] separated the families by the characters of cranial feature which reflects the bite strength and diet. However, the Ursidae was not distinguished by his analysis [23].

As results of examinations in the muscles of mastication and the skull, we suppose that morphological differences reflect the eating habits of bears. The brown bear possesses the more suitable feature of the *M. masseter* for feeding plants than the polar bear. In addition, it is thought that the polar bear has morphologically adapted the muscles of mastication to the flat skull feature for supplementing the functions.

ACKNOWLEDGMENTS. We thank Dr. Mitsuko Masui, Dr. Masaru Saito and Dr. Yoshitaka Abe and the staff of the Ueno Zoological Park for providing the materials of the brown bear and the giant panda. We wish to express our gratitude to Dr. Kazumi Kagawa (Ritsurin Park Zoo) for the donation of the carcass of the polar bear. We are also grateful to Miss Tomoko Ogoh and Miss Tomoko Yoshida (Department of Zoology, National Science Museum, Tokyo) and to Miss Norika Yakuou (Department of Ichthyology, Tokyo University of Fisheries) for their support.

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