Three-Dimensional CT Examination of the Mastication System in the Giant Anteater

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The gross anatomy of the mastication system of the giant anteater (*Myrmecophaga tridactyla*) was examined by means of three-dimensional image analysis. The anteater rotates the mandibles medially and laterally to control its tongue when it is elongated and to house it when it is relaxed. Three-dimensional CT image analysis demonstrated that the shape and size of the oral cavity changes drastically when the mandibles are rotated. The oral cavity expands bilaterally when the dorsal part of the mandibles bend medially. Macroscopic observations and muscle-weight data supported the observation that the superficial temporal and medial pterygoid muscles act as the main medial and lateral rotators of the mandible, respectively. The low height of the mandibular ramus and the incomplete zygomatic arch in this species represent adaptations for the rotational movement of the mandibles, since they both contribute to the medially oriented transmission of force from the temporal muscles and to preventing collision between the mandibles and the cranium during the rotational movement.

Key words: computed tomography, giant anteater, pterygoid muscle, temporal muscle, three-dimensional image analysis

INTRODUCTION

The elongated splanchnocranium, including the mandibles (dentary) of the giant anteater (*Myrmecophaga tridactyla*) are morphologically adapted for feeding on ants and termites. The giant anteater uses its extraordinarily long tongue to transfer food to the esophagus, and the elongated oral cavity provides the space where the long tongue is housed. It is well known that the well-developed salivary glands of the anteater serve in a highly-specialized manner to pre-digest insects. In spite of these clearly adaptive mechanisms, the functional significance of the size and position of the mastication muscles has remained unclear in this species. Fine anatomical descriptions have been published (Owen, 1854; Macalister, 1875; Parker, 1885: Edgeworth, 1935; Reeve, 1940; Naples, 1982, 1985a, 1985b, 1986), and the homology and character polarity of the masticatory muscles of anteaters have been examined (Reiss, 1997). Motion analysis of live individuals was also undertaken to suggest likely mandible movements from observations of feeding behavior (Naples, 1999). However, since the actual movement of the mandibles has not been clarified in three-dimensional space, the real function of the specialized, elongated toothless mandibles during opening and closing movements has remained unclear in the giant anteater. In this study, therefore, we attempted to elucidate the movement of the mandible and the functions of the mastication muscles by applying CT (computed tomography) scanning and three-dimensional image analysis to the body of a dead giant anteater.

MATERIALS AND METHODS

The carcass of a giant anteater (*Myrmecophaga tridactyla*) donated to the National Science Museum, Tokyo, by Ueno Zoological Gardens was used for the analysis. After pathological checks, the head region was serially sectioned by CT (Aquilion 16; Toshiba Medical Systems, Tokyo, Japan) from the rostral to the caudal planes in parallel sections 0.5 mm thick, without gaps.

The mandible was artificially positioned on the CT-scanning

Table 1. Biological data for the specimens used in this study.

specimen number	sex	body weight (kg)	head and body length (mm)	age	cause of death	date of death	origin
NSMT-M34333*	male	27.1	1140	adult	hepatocirrhosis	2006.1.14	Ueno Zoological Gardens
NSMT-M5901	male	unrecorded	1227	adult	unrecorded	1959.3.27	Ueno Zoological Gardens
NSMT-M10336	female	unrecorded	1278	adult	unrecorded	1964.5.5	Izu Shaboten Park
NSMT-M19540	unrecorded	unrecorded	unrecorded	adult	unrecorded	1976	Ueno Zoological Gardens

* The carcass was used for CT analysis in this individual.

machine in both normal and rotated states. Three-dimensional images of bone movements were reconstructed from the series of CT sections to elucidate muscle actions. We applied voxel transmission (volume rendering) techniques to visualize bone movements using a three-dimensional image analyzing system (AZE Virtual Place; AZE Corporation, Tokyo, Japan). The rotational range of the mandible was also quantitatively examined with the same software using three landmarks from the upper jaw (the most rostral point of the incisive bone and the most caudal point of the zygomatic bone on each side) and also the three landmarks from left mandible (the most caudal point of the condylar process, the most caudal point of the angular process, and the most rostral point of the dorsal horizontal plane of the mandibular ramus region). In the three-dimensional digitalized space created with the software, the two planes representing the upper jaw and the mandible were made using the two sets of three landmarks. The rotational angle was calculated from the normal vectors of the two planes, including the three landmarks each on the upper jaw and the mandible.

The masticatory muscles were observed with the naked eye, described, then excised. Wet muscle weights were recorded to the nearest 10^{-3}g using an electronic balance. In addition to the whole specimen, three skulls in the National Science Museum, Tokyo, were macroscopically examined in this study (Table 1).

RESULTS

Macroscopic observations

The superficial masseter muscle mainly consists of one layer connecting the ventral area of the temporal process of the zygomatic bone to the ventro-lateral area of the mandible. The muscle envelops the lateral area of the angular process of the mandible. The profound masseter muscle lies in a deep layer in the most rostral region of the main bundle (Fig. 1). The direction of the two muscles appears rostrocaudal and horizontal. The digastric muscle comprises a single, thin bundle.

The zygomatic bone posteriorly does not reach the zygomatic process of the temporal bone, and the zygomatic arch lacks the ventro-lateral area of the orbit (Fig. 2). The temporal muscles consist of three bundles. The bundle of the superficial temporal muscle is largest, and runs superficially from the dorsal region of the temporal fossa to the dorsal horizontal surface of the mandible (Fig. 2). The thick zygomatic part of the superficial temporal muscle arises from the caudal region of the temporal fossa and from the medio-caudal area of the zygomatic process of the temporal bone to the dorsal horizontal surface of the mandible. The two bundles are wedge-shaped (Fig. 3). The thinner profound temporal muscle runs from the most ventral point of the temporal fossa to the dorso-medial area of the mandible, and its bundle is triangular from a dorso-lateral aspect (Fig.3). The direction of the bundle is dorso-ventral.
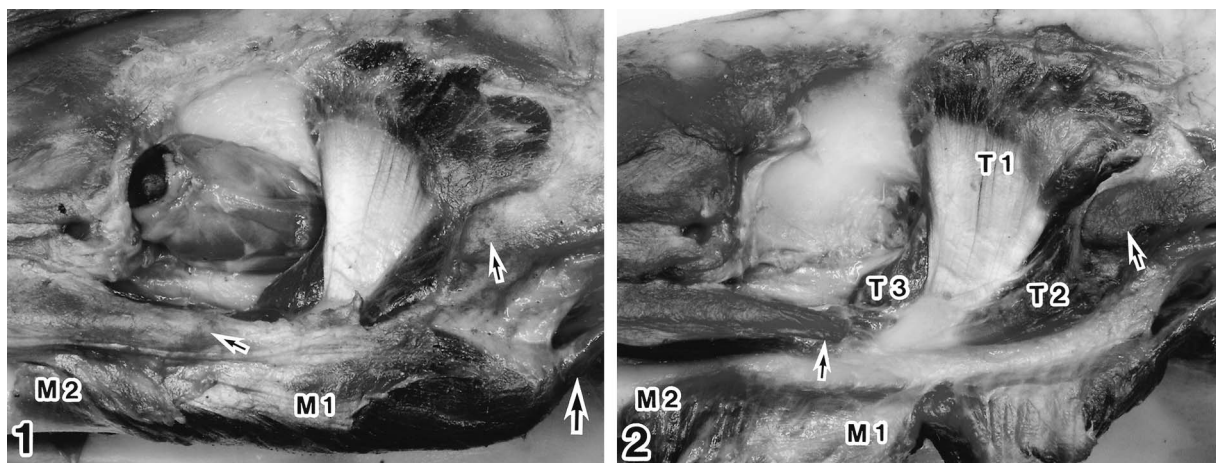
The medial pterygoid muscle is flat and enlarged in the

Fig. 1. Left lateral aspect of the head. Rostral direction is to the left. After removal of the lacrimal gland, the main single bundle of the superficial masseter muscle is seen (M1). The thin layer of the profound masseter muscle (M2) can be observed in the cranial region of the main bundle. The small bundle of the digastric muscle (large arrow) runs from the ventral area of the occipital bone to the ventro-caudal area of the mandible. The incomplete zygomatic arch (small arrows) is seen.

Fig. 2. Left lateral aspect of the head. Rostral direction is to the left. The superficial (M1) and profound (M2) masseter muscle bundles have been cut and ventrally turned to show the incomplete zygomatic arch (arrows) and the mandible. The superficial temporal muscle (T1), zygomatic part of the superficial temporal muscle (T2), and profound temporal muscle (T3) are observed in the temporal region.
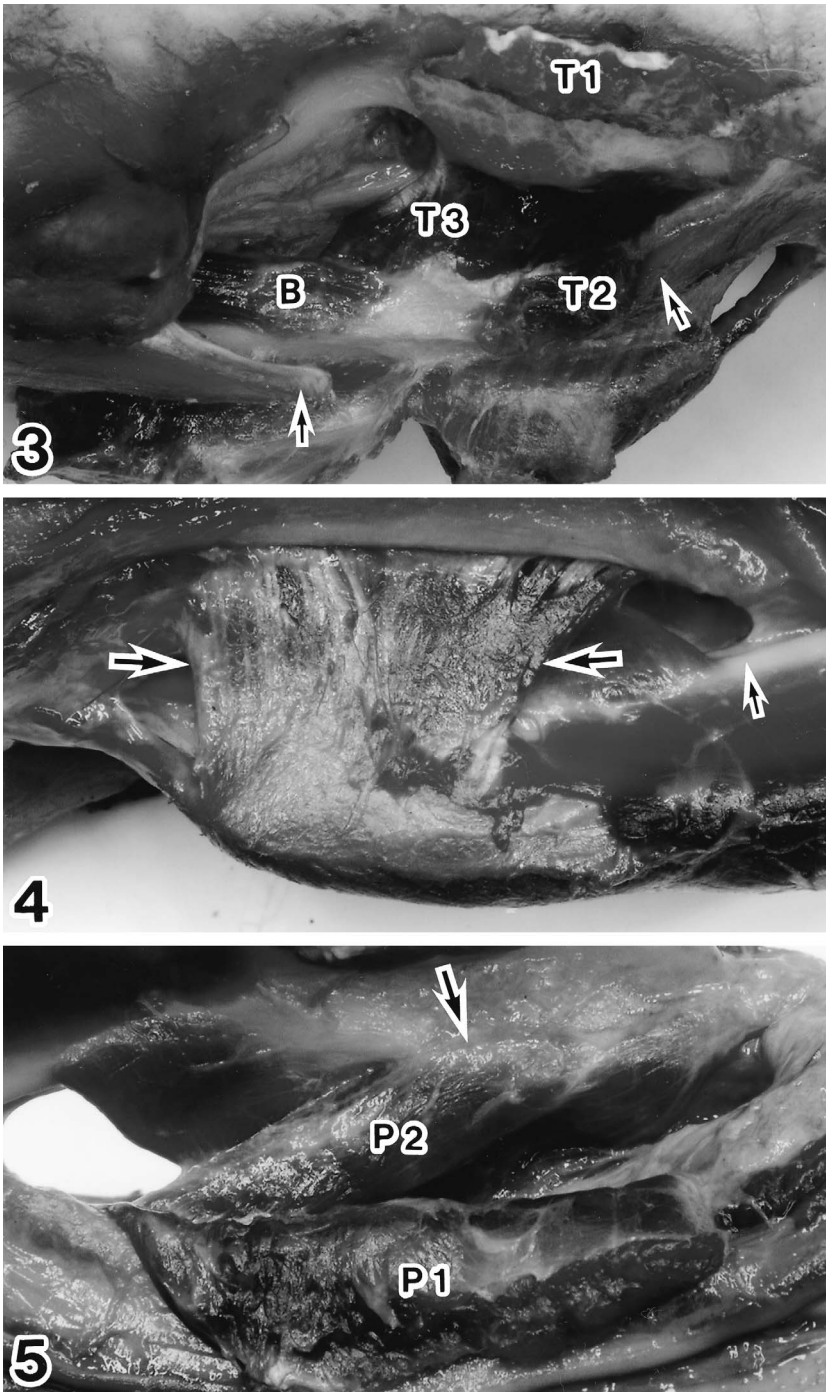
Fig. 3. Left dorso-lateral aspect of the orbital region. Rostral direction is to the left. The bundle of the superficial temporal muscles (T1) has been dorsally removed from the temporal fossa. The zygomatic part of the superficial temporal muscle (T2) reaches the horizontal surface of the mandibular ramus. The internal part of the buccinator muscle (B) insets to the cranial area of the ramus. T3, profound temporal muscle. The incomplete zygomatic arch (arrows) is seen.

Fig. 4. Ventro-medial aspect of the head. Left side. Rostral direction is to the right. The enlarged bundle of the medial pterygoid muscle is revealed (large arrows). The dorso-medial margin of the mandible is seen (small arrow).

Fig. 5. Ventro-medial aspect of the head. Left side. Rostral direction is to the left. After removal of the medial pterygoid muscle, the inferior (P1) and superior (P2) parts of the lateral pterygoid muscle are confirmed. The superior part inserts into the ventro-medial area of the mandible (arrow).

Table 2. Weight (grams) and hypothesized primary function of each masticatory muscle.

		Primary function of each muscle	Actual effect to the mandible
masseter muscle	6.695	pull cranially the ventral area of the mandible	medial rotation
profound temporal muscle	1.630	elevate dorsally the mandible	medial rotation
superficial temporal muslce	2.471	elevate dorsally the mandible	medial rotation
zygomatic part of superficial temporal muscle	1.845	elevate dorsally the mandible	medial rotation
digastric muscle	0.232	pull caudally the ventral area of the mandible	stabilization
lateral pterygoid muscle	0.878	slide medially the condyle area of the mandible	medial shift of the condyle and stabilization
medial pterygoid muscle	1.554	pull medially the ventral area of the mandible	lateral rotation

medial area of the mandible (Fig. 4). The muscle bundle rises from the pterygoid fossa ventro-laterally and reaches the ventral edge of the posterior portion of the mandible. The muscle extends to the medial area of the angular process of the mandible. After removal of the medial pterygoid muscle, the two thin, fleshy parts of the lateral pterygoid muscles were discernable (Fig. 5). The inferior part runs from the pterygoid plate posteriorily to the antero-medial area near the temporomandibular joint, whereas the superior part arises from the ventro-lateral part of the temporal bone and inserts into the ventro-medial area near the temporomandibular joint.

Muscle-weight data

Wet weights of the seven bundles of the masticatory muscles are given in Table 2. Since the superficial and profound masseter muscles and the two parts of the lateral pterygoid muscle were partially fused, their total weights were examined.

Although the masseter muscle is not well-developed in macroscopic observations, its weight is much larger than that of the other muscles. The total weight of the temporal muscle bundles is relatively larger, whereas the digastric muscle is much the smallest among all of the masticatory muscles.

Three-dimensional image analysis

The three dimensional images were helpful in elucidating the movements of the mandibles (Figs. 6–11). Although elevation and depression of the mandibles was not observed, the medio-lateral rotations of the mandibular ramus were indicated during the artificial opening-closing movements of the mandibles. The mandibular symphysis is not fused and thus does not restrict the independent movement of the left and right mandibles. Certain images (Figs. 8–10) show that the oral cavity changes drastically in both shape and size during the rotational movement of the mandibles. The oral cavity can be expanded bilaterally during the mandibular opening state when the dorsal part of the mandibles bend medially (Figs. 8B, 9B, 10B).

The dorso-posterior area of the mandible, including parts of the mandibular ramus and the coronoid process, is medially curved (Figs. 7, 11). The temporal and pterygoid muscles are attached to the dorsal horizontal surface of the mandibles (Figs. 2, 3, 7, 8). The position and angle of the rotating mandible are seen in some aspects (Figs. 6, 7), and in the transverse sections of the skull (Figs. 8, 9). The head
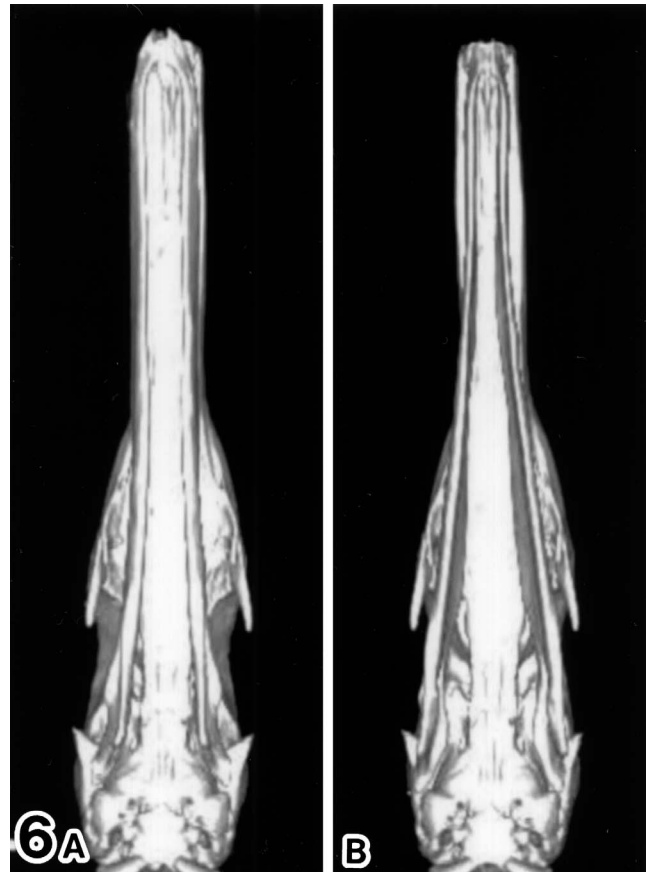
Fig. 6. Ventral aspect of three-dimensional reconstructed images of the head of the giant anteater. Rostral direction is at the top. **(A)** Mandibular closing state. **(B)** Mandibular opening state.
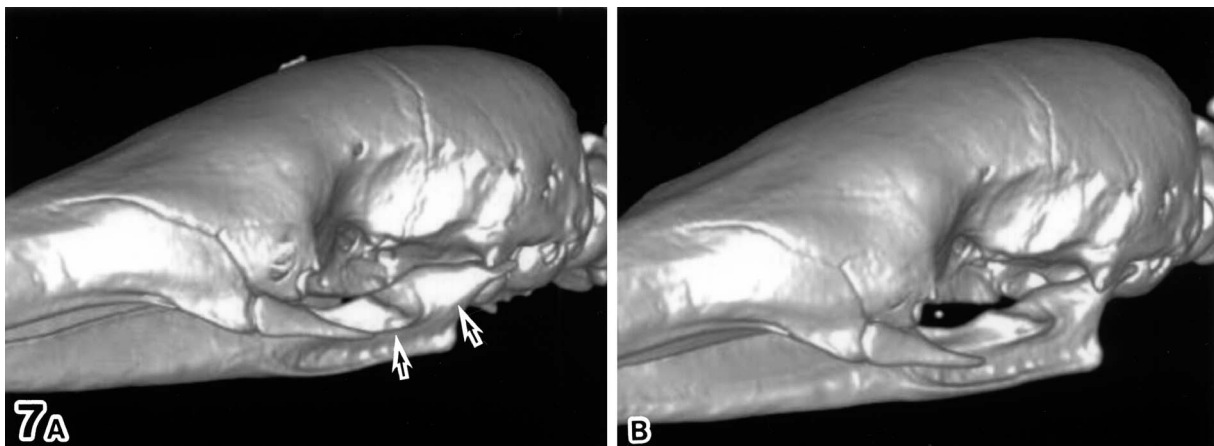
Fig. 7. Cranio-lateral aspect of three-dimensional reconstructed images of the head of the giant anteater. **(A)** Mandibular closing state. **(B)** Mandibular opening state. Arrows indicate the areas of the medially curved surface, including the coronoid process and mandibular ramus.
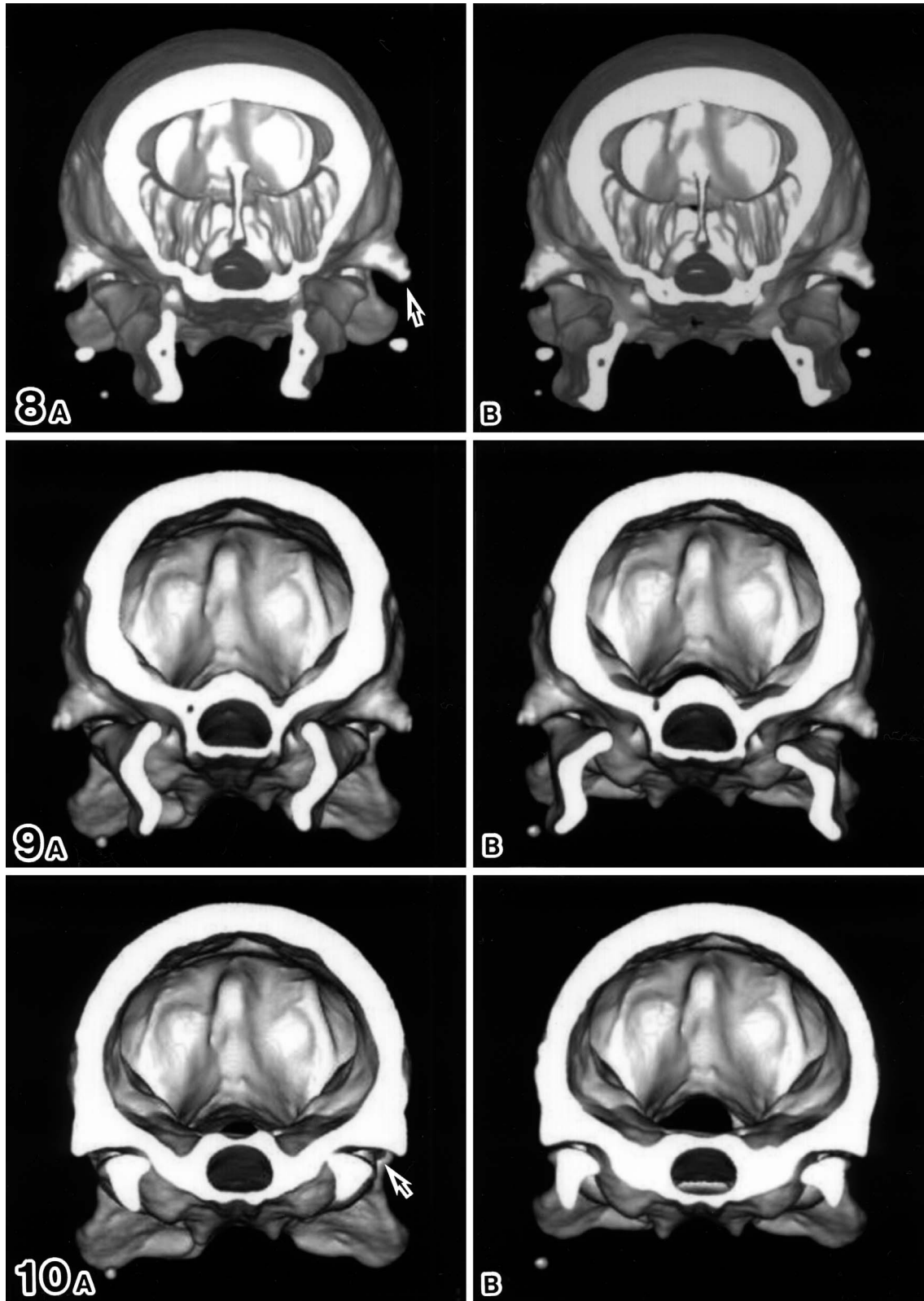
Fig. 8. Transverse section of three-dimensional reconstructed images of the head of the giant anteater at an anterior level of the mandibular ramus. Rostral aspect. **(A)** Mandibular closing state. **(B)** Mandibular opening state. Arrow, temporal process of the zygomatic bone.

Fig. 9. Transverse section of three-dimensional reconstructed images of the head of the giant anteater at the level of the medial curved surface, including the coronoid process and mandibular ramus. Rostral aspect. **(A)** Mandibular closing state. **(B)** Mandibular opening state.

Fig. 10. Transverse section of three-dimensional reconstructed images of the head of the giant anteater at the level of the temporomandibular joint (arrow). Rostral aspect. **(A)** Mandibular closing state. **(B)** Mandibular opening state.
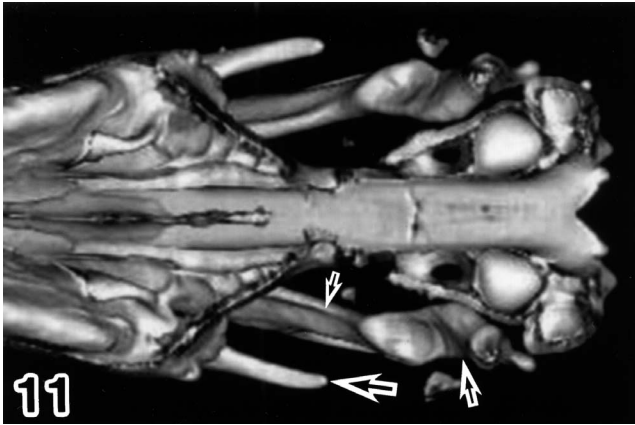
Fig. 11. Dorso-caudal aspect of three-dimensional reconstructed images of the head. Rostral direction is to the left. Mandibular opening state. The dorsal region of the skull has been partially removed to show the dorsal part of the mandible and the space between the mandible and the skull. This view clearly shows that the medially curved mandible (small arrow), low mandibular ramus (intermediate arrow), and incomplete zygomatic arch (large arrow) prevent the collision of the mandible with the skull during medial rotation of the mandible.

of the condylar process of the mandible slides medio-laterally along the articular surface of mandibular fossa in the squamous part of the temporal bone (Fig. 10). From the data on the normal vectors related to the cranium and left mandible, we demonstrate that the rotation angle of the mandible is at most 35.4 degrees.

DISCUSSION

The bilateral rotational movement of the mandibles of the giant anteater revealed by image analysis is most note-worthy. Observers of the anteater's behavior have pointed out that it is able to rapidly protrude and retract its long tongue through the oral cavity and the mouth opening to allow food ingestion (Montgomery and Lubin, 1977; Redford, 1981; Montgomery, 1985; Naples, 1986). The long tongue acts as a belt conveyor to transfer food from the mouth opening to the esophagus through the oral cavity and phar-ynx (Naples, 1985). Changing the shape and size of the oral cavity allows the anteater quickly and stably to protrude its elongated tongue (Naples, 1999). It also permits the animal to house the relaxed tongue within the oral cavity during the mandibular opening state. We conclude that the giant ant-eater medially bends the dorsal part of its mandibles in the mandibular opening state so as to smoothly pull the elon-gated tongue, along with its cargo of ants and termites, through the enlarged oral cavity.

The echidna (*Tachyglossus aculeatus*) is equipped with similar mechanisms controlling the action of the tongue and also feeds on termites and ants (Doran, 1973; Murray, 1981). As suggested in the anatomical description (Naples, 1999), the rotation of the mandibles contributes to the rapid movement of the elongated tongue. We suggest that the maximum rotational angle of about 35 degrees is sufficient and appropriate for this functional requirement in the masti-cation mechanism.

The shape of the mandible is morphologically adapted

to its rotational movement. We suggest that the medially curved surface, including the coronoid process and mandib-ular ramus validly receives the dorsally oriented force of the temporal muscles (Figs. 2, 3, 7, 9). Each bundle of the tem-poral muscle acts primarily as an elevator and secondarily as a medial rotator of the mandible during the opening action. The medial pterygoid muscle generates the main power of the lateral rotation, whereas the temporal muscle group functions as medially rotating motors in the mandibu-lar movement. The superficial temporal muscle and the medial pterygoid muscle are relatively heavier (Table 2). We suggest that these muscles function as the main medial and lateral rotators of the mandible, respectively.

The lateral pterygoid muscle is much lighter in weight than the adjacent medial pterygoid muscle. The lateral pterygoid muscle certainly connects the pterygoid plate with the dorsal area of the mandibular ramus; however, its inser-tion is much closer to the condyle. From the position of the lateral pterygoid muscle, we suggest that this muscle may not contribute to the lateral rotation of the mandible, but instead contributes to the medial shift of the head of the condylar process and to stabilization of the mandible (Table 2). We think that the digastric and buccinator muscles may act mainly as stabilizers of the mandible during rotation.

The masseter muscles are much heavier than the other masticatory muscles, indicative perhaps that these muscles are a strong medial rotator of the mandible; however, their main bundles run cranio-caudally in the lateral space of the mandible (Fig. 1). The direction of the bundles is not effec-tive for rotation of the dentary. The masseter muscles do, however, show the oblique running to the sagittal plane, consequently, the contractive power is generated cranio-laterally for the ramus area of the mandible by the masseter muscles. It seems, therefore, that the masseter muscles contribute to the medial rotation of the mandible, even though the contractile direction of the muscles is not optimal for this function (Table 2). Although it has been reported that the giant anteater lacks a profound masseter muscle (Naples, 1999), we were able to distinguish bundles of the profound masseter muscle in deep regions of the superficial masseter muscle.

On the temporal muscles, the originating area is located in the lateral area of the insertion part. This positioning of the temporal muscles is not exactly effective for medially rotat-ing the mandible. We suggest that the temporal muscles may primarily act as an elevator of the mandible. The mus-cle force reaching the ramus area can easily elevate both sides of the mandible, since the characteristic curved sur-face (Figs. 7, 8, 9) receives the power of the muscles from the dorso-lateral side. Finally, the dorsally oriented contrac-tion of the temporal muscles and the cranially directed force of the masseter muscles can effectively complete the medial rotation of the dentary during the opening action (Table 2).

It should be noticed that the height of the mandible is extraordinary short in the giant anteater. The dorsally pro-truded ramus generally helps mammals to elevate the mandible to crush food. However, if the anteater rotated a mandible that was larger and taller, the ramus would collide with the side of the skull. The mandibular ramus, including the coronoid process, bends medially to form the curved surface of the dorsal portion (Figs. 7, 11). The medially bent

surfaces of the dorsal area are also seen in the rostral part of mandibular body (Fig. 7). The zygomatic arch is incomplete in the lateral area. We suggest that these characteristics are functionally important to maintain space between the cranium and mandible during rotation of the mandible (Figs. 7, 11). Reduction of the zygomatic arch and mandibular ramus have been recorded in some taxonomic groups of Pilosa, however, one of the oldest of the Myrmecophagidae, *Eurotamandua*, possessed a complete zygomatic arch and a high ramus of the mandible (Carroll 1987; Rose and Emry, 1993). So, these characteristics are due not only to phylogenetic restrictions but also to functional requirements of the highly specialized mastication mechanism adapted for feeding on ants and termites.

The mylohyoid muscle was cut during pathological examination of the carcass before image analysis was conducted. Since this muscle may have an influence on the rotation of the mandibles, as discussed by Naples (1999), examination of an intact head will be necessary for the complete simulation of muscle functions based on CT analysis.

Reiss (1977) detailed the innervation of each muscle related to the masticatory apparatus of the giant anteater. Our identification of the masticatory muscles is consistent with his theory on homology and phylogenetic context. In the less-derived xenarthrans, such as various armadillos, the functional significance and evolutionary status of the masticatory apparatus have been discussed (Smith and Redford, 1990; Vizcaíno and Bargo, 1998). These authors concluded that living *Dasypus* and *Euphractus*, and fossil *Eutatus* and *Proeutatus*, were each equipped with a specialized feeding apparatus adapted to an insectivorous, carnivorous, or omnivorous dietary pattern. This suggests that the Cingulata might have functionally-specialized masticatory mechanisms derived during evolutionary history, as well as during adaptation to myrmecophagy in the phylogeny of the anteaters.

ACKNOWLEDGMENTS

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