The functional anatomy of the masticatory muscles of the Malayan pangolin, *Manis javanica*

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**Abstract.** The masticatory muscles of the Malayan pangolin, *Manis javanica*, were observed in dissection, and relative positions of the cranium and the mandible were examined under soft-X ray photographs. The *M. temporalis* was well-developed in the medial area of the zygomatic process of temporal bone. The *M. masseter* was found to consist of three large well-developed bundles between the zygomatic arch and the mandible. Based on these observations, it is suggested that the thin V-shaped mandible may act as a substantial support in the ventral portion of the oral cavity, and that the *M. masseter* and *M. temporalis* may serve to help fix the shape of mouth, when the pangolin uses the specialized tongue for feeding. We demonstrated that the *M. digastricus* is at least functionally able to depress and open the mandible. In addition, the well-developed *M. mylohyoideus* may contribute to the control of intraoral pressure during mastication.

**Key words**: digastric muscle, mandible, masseter muscle, pangolin, temporal muscle.

Although the tongue structure of pangolins has attracted the interest of a number of anatomists (Ehlers 1894, Edgeworth 1923, Sonntag 1923, 1925, Lubosch 1938, Kubota *et al.* 1962, Saban 1968, Doran and Allbrook 1973, Yen 1984, 1985, Chan 1995), who have pointed out that the Manidae species use their uniquely elongated tongue for feeding on termites and ants, the morphology of the masticatory muscles and of the mandibular bone of the pangolins has been overlooked. The mastication system has so far been considered functionally vestigial or insignificant (Doran and Allbrook 1973, Walker 1991, Chan 1995), but without there having been detailed descriptions of the masticatory muscles.
The purpose of this study therefore was to examine macroscopically the three dimensional relationship between the cranium and the mandible, and the development of the masticatory muscles in order to clarify their functional significance.

**Materials and Methods**

One formalin-fixed head and three skulls of the Malayan pangolin, *Manis javanica* that had been stored in Thailand Institute of Scientific and Technological Research, in the Department of Veterinary Anatomy of The University of Tokyo and in the Department of Zoology of National Science Museum, Tokyo were used in this study.

The skin, subcutaneous tissue and globe were removed from the fixed head, then the masticatory muscles, *Musculi masseter, digastricus, temporalis, pterygoidei* and *Musculus mylohyoideus* were observed macroscopically. Soft-X ray photographs were taken to examine the articulation and the positional relationship between the mandible and the cranium, and the areas of attachment of the masticatory muscles on the skulls were observed. The anatomical nomenclature of the muscular system was based on Miller's Anatomy of the Dog (Evans 1993).

Fig. 1. Lateral soft-X ray photograph of the head of a Malayan pangolin. Rostral direction at the top. The thin mandible (small arrow) is gently curved and connects to the ventro-caudal area of zygomatic process of the temporal bone (large arrow). Arrowheads, incomplete zygomatic arch.

Fig. 2. Dorso-ventral soft-X ray photograph of the head of a Malayan pangolin. Rostral direction at the top. The thin mandible represents the V-shape (arrow). Arrowhead indicates the auditory bulla. The atlas vertebra is present in this specimen.
RESULTS

The relative positions of the mandibular bones and the cranium were observed using soft-X ray photographs (Figs. 1, 2). The mandibular body was found to be slender and gently curved dorso-ventrally, but was not generally well-developed (Figs. 3, 4). The symphysis was relatively long and strong in comparison with the thin mandibular bone. The lateral surface of the mandible was flat and lacked processes for the insertion of muscles, while the medial side had a shallow groove to which *M. mylohyoideus* was attached. The mandible connected to the ventro-caudal area of the zygomatic process of the temporal bone. The articulation area was slightly depressed, and the zygomatic process had no specialized surfaces for articulation (Figs. 3, 4). All three skulls and the preserved head possessed incomplete zygomatic arches which varied in their developmental state (Figs. 1-4). The temporal bone was well-developed dorso-rostrally in the area of the zygomatic process (Fig. 3), which we have called the “temporal-muscle process”. The orbit was surrounded by depressed frontal and developed temporal bones, and there was a deep hollow in the caudal part of the orbit.

Fig. 3. Left side of the skull of a Malayan pangolin. Rostral direction at the top. The mandible has been artificially attached to the cranium. The skull is elongated and simple in lateral view, while the mandible bone is slender. The zygomatic arch is not developed (arrows). The temporal bone is dorso-rostrally well-developed in the part of zygomatic process (arrowhead). The depressed orbit is surrounded by the temporal muscle process in the caudal part.

Fig. 4. Ventral view of the skull specimen of a Malayan pangolin. Rostral direction at the top. The mandible articulation area is slightly depressed (arrow).
Fig. 5. Right side of the head of a Malayan pangolin. Rostral direction at the top. The wedge-shaped *M. temporalis* is well-developed in the caudal part of the orbit and in the medial side of the temporal-muscle process of the temporal bone (small arrows). The *M. masseter* consists of three main bundles reaching from zygomatic arch to the caudal part of the mandible (intermediate arrows). Large arrows, zygomatic arch. Arrowhead, mandible.

Fig. 6. Dorso-lateral view of the orbit region of a Malayan pangolin. Rostral direction at the top. The wedge-shaped *M. temporalis* is well-developed in the medial side of the zygomatic arch (small arrows). The large arrow indicates a part of the *M. masseter*.

The *M. temporalis* was well-developed on the medial side of the zygomatic arch of the temporal bone and the temporal muscle process (Figs. 5, 6). The *M. temporalis*, which was found to be wedge-shaped, was largely attached to the caudal part of the orbit, and was rostrally extended to the medial surface of the zygomatic arch. The muscle was inserted vertically into the caudal mandible body. The *M. masseter* consisted of three well-developed main bundles (Figs. 5, 7). The two cranial bundles originated form the medial side of the zygomatic arch and the most caudal bundle arose from the ventral part of the arch. All three bundles reached the caudal half of the mandible laterally (Fig. 7).

The *M. digastricus* consisted of two thin parts, the lateral part originating from the ventral area of temporal and occipital bones inserting into the ventral edge of the mandible (Figs. 7, 8), while the thinner medial part arose from the ventral surface of the *M. mylohyoideus* (Fig. 7), and did not attach to the caudal part of the mandible. The *M. mylohyoideus* was thick and occupied the space between the mandibular bones, and provided an area of attachment for the medial portion of the *M. digastricus* (Fig. 8).

The *M. pterygoideus lateralis* was found to consist of two small, short bundles lying parallel and rostro-laterally oriented from the palatine bone to the medial side of the mandible (Fig. 9).
Fig. 7. Ventro-lateral view of the head of a Malayan pangolin. Rostral direction at the top. Superficial muscles are removed. The *M. masseter* consists of three main bundles (small arrows). The *M. digastricus* can be seen. The lateral part of the *M. digastricus* (intermediate arrow) originates from the ventral area of the temporal and the occipital bones (arrowheads), while the thinner medial portion (large arrow) rises form the ventral surface of the *M. mylohyoideus*. Asterisks, the ventral edge of the mandible. S, submandibular gland.

Fig. 8. Ventro-lateral view of the head of a Malayan pangolin. Rostral direction at the top. The *M. digastricus* is turned out, and the two distinctive parts can be observed (small arrows). The *M. mylohyoideus*, which is thick and occupies the space between mandibles (large arrow).

Fig. 9. Ventral view of the head of a Malayan pangolin. The *M. pterygoideus lateralis* consists of two small and short bundles (small arrows). The large arrow indicates the ventral edge of mandible to which the *M. digastricus* is attached. Rostral direction at the top.

**DISCUSSION**

The possibility of morphological differences between species of Manidae in the developmental of the masticatory muscle should be taken into account, particularly given that previous descriptions have not been consistent (Lubosch 1938, Saban 1968, Yen 1985, Chan 1995).

Firstly, it is suggested that the thin V-shaped mandible may provide significant support for the ventral portion of the oral cavity. It became clear during this study of the Malayan pangolin that the *M. temporalis* was developed and had the enlarged attachment to the temporal-muscle process. The multi-bundled *M. masseter* was also found to be a strong mastication motor. Although the developmental state of the zygomatic arch was found to vary between individuals, we believe, contrary to Saban (1968), that the arch is not
vestigial. Although active movement of mandible is certainly not important for feeding in this species, we suggest that the zygomatic arch and its temporal-muscle process, the *M. masseter* and *M. temporalis*, may all serve to help fix the shape of mouth. Although the mandible is simple and thin, the symphysis is relatively well-developed in the pangolins (Lubosch 1938, Saban 1968) indicating that mandibular bones may support the shape of the oral cavity while feeding with the tongue.

In comparison with the *M. masseter* and *M. temporalis*, the *M. digastricus* of the Malayan pangolin is not comparable with that of other mammals (Edgeworth 1923, 1935, Evans 1993). Although Chan (1995) pointed out that the *M. digastricus* disappears into the submandibular gland, in this study we have demonstrated that the lateral part of the *M. digastricus* is at least functional in depressing and raising the mandible. It is further suggested that the medial part of the *M. digastricus* only assists the action of the well-developed *M. mylohyoides*. The *M. mylohyoides* may support the function of *M. digastricus* and act as a depressor of the mandible. In addition, the well-developed *M. mylohyoides* may contribute to the control of intraoral pressure during mastication. Specimens with intact hyoid bones should be examined morphologically in the future to elucidate this.

Our description of *Mm. pterygoidei* is similar to that of Yen (1984). The *M. pterygoidei* lateral is could not be confirmed in this specimen. It remains unclear how this muscle has changed in form and function.

The functional significance of masticatory muscles of certain rodents has been described (Kesner 1980, Bekele 1983, Druzinsky 1995), and functional models of mandibular movement have also been established for some rodents (Weijs 1975, Gorniak 1977, Byrd 1981, Satoh 1997). On the basis of data from *Apodemus* and *Clethrionomys* species (Satoh 1997), it has been suggested that patterns of mandibular movement are directly modified by adaptations in dental morphology. We speculate, however, that the masticatory muscles in toothless mammals such as the pangolin have also been functionally affected by their special feeding pattern. In such mammals, the primary function of masticatory muscles may not be to generate occlusal force, but to control the air pressure within the oral cavity.

In contrast with previous speculations (Doran and Allbrook 1973, Chan 1995), the present study has clearly demonstrated that the masticatory muscles of the Malayan pangolin are not vestigial, but functional, well-developed, fix the mandibular bones, support the shape of the oral cavity, and help control the pressure in the oral cavity during feeding with the tongue.

The masticatory muscles of other toothless mammals may also be a functional part of the mastication system and may also have been adapted for special feeding as a form of functional convergence.

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