

Functional Morphology of the Mastication Muscles in the Lesser and Greater Mouse Deer

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ABSTRACT. The mastication muscles were examined in the lesser (*Tragulus javanicus*) and greater mouse deer (*Tragulus napu*) to clarify the form of the mastication muscles in these primitive artiodactyls. The *M. masseter* was well-developed in both species, however the attachment area of its origin was not confirmed in the rostral facial part. The masseter bundles were not observed on the lateral side of the maxilla bone, and their origin was restricted to the zygomatic arch area. This suggests that the *M. masseter* may not act as a motor raising the mandible rostro-dorsally, but pull the insertion vertically unlike the highly derived grazer of Bovidae. The *Crista temporalis* was weak and the *M. temporalis* was thin in the mouse deer, and this indicates that the *M. temporalis* may not be important in the mastication in the primitive artiodactyls. These findings suggest that the browser such as mouse deer has been adapted for the feeding on soft leaves, and functional-morphologically different in mastication strategy from the grazer such as developed Bovidae species. The architecture of the mastication muscles was not different between the two species. However, in the muscle weight ratios per body weight, the *M. temporalis* and the *M. digastricus* were significantly smaller in greater mouse deer than in lesser mouse deer.

KEY WORDS: mastication, morphometry, mouse deer, osteometry, skull.

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Since the Tragulidae has been considered as one of the most primitive family in the artiodactyls [2, 8], the mastication muscles have been expected to examine in this group. The data will contribute to confirm the morphological evolution and the functional adaptation of the mastication mechanism in artiodactyls including the Bovidae and domesticated ruminants. At this standing point the mouse deer species have been used for the basic osteology [9, 13, 14], while the mastication mechanism has been morphologically examined in the representative highly-derived ruminants [4, 10, 11]. However, the architecture of the mastication has remained unclear in *Tragulus* species. In this study, therefore, the two species of mouse deer were dissected for the description and morphometry in the mastication muscles.

MATERIALS AND METHODS

We used 3 heads (2 males and 1 female) of the lesser mouse deer (*Tragulus javanicus*) captured in Peninsular Malaysia and maintained in the Universiti of Putra Malaysia (Selangor, Malaysia), and 2 heads (2 females) of the greater mouse deer (*Tragulus napu*) maintained in a livestock farm in Kota Kinabalu (Sabah, Malaysia). Since we selected the individuals of more than 400 mm in head and body length in the lesser mouse deer and more than 480 mm in the greater mouse deer (Table 1), we could consider all materials as

adult [1, 3]. The mastication muscles were observed and described by naked-eyes. Each mastication muscle has been excised and fixed in 10% formalin, stored in 70% ethanol and dried up in the 37°C incubator for 10 days. The muscles were weighed by the electronic balance at the nearest 0.001 g.

RESULTS

The mastication muscles are shown at various aspects in the lesser mouse deer (Figs. 1–3 and 5–8) and in the greater mouse deer (Fig. 4). The gross architecture of the mastication muscles was not morphologically different between the two species.

The *M. masseter* was the strongest in size in all mastication muscles (Fig. 1). The muscle could be divided into three layers: superficial, intermediate and deep (Fig. 2). The superficial layer was the most enlarged and thin. The origin of the layer was extended to the entire ventral region of the temporal process of the zygomatic bone, and few bundles reached the zygomatic process of the temporal bone. The layer was inserted to the most ventral area of the masseteric fossa of the mandible. The intermediate layer was restricted to the medial region of the superficial layer, and some bundles were fused to the deep layer in their dorsal part. The bundles of the deep layer arose from the zygomatic arch except for the most rostral part of the zygomatic bone,

Table 1. Comparison of body size and weight of mastication muscles between the two species*

	Sex	Head and body length	Body weight	<i>M. temporalis</i>	<i>M. masseter</i> **	<i>M. masseter</i> ***	<i>M. digastricus</i>	<i>M. pterygoideus</i>
<i>T. javanicus</i>	Male	440.0	1340.0	0.198	0.140	0.204	0.0710	0.220
<i>T. javanicus</i>	Male	415.0	1120.0	0.204	0.201	0.138	0.0980	0.183
<i>T. javanicus</i>	Female	417.0	1400.0	0.231	0.259	0.187	0.0830	0.150
Average		424.0	1286.7	0.211	0.200	0.176	0.0840	0.184
S.D.		13.9	147.4	0.018	0.060	0.034	0.011	0.035
<i>T. napu</i>	Female	512.0	2800.0	0.314	0.271	0.338	0.0909	0.380
<i>T. napu</i>	Female	498.0	2500.0	0.332	0.239	0.367	0.0519	0.251
Average		505.0	2650.0	0.323	0.255	0.353	0.0714	0.316
S.D.		9.9	212.1	0.102	0.072	0.021	0.028	0.105

* Head and body length is given in mm, and weight in g.

** The superficial layer of the *M. masseter*.

*** The intermediate and deep layers of the *M. masseter*.

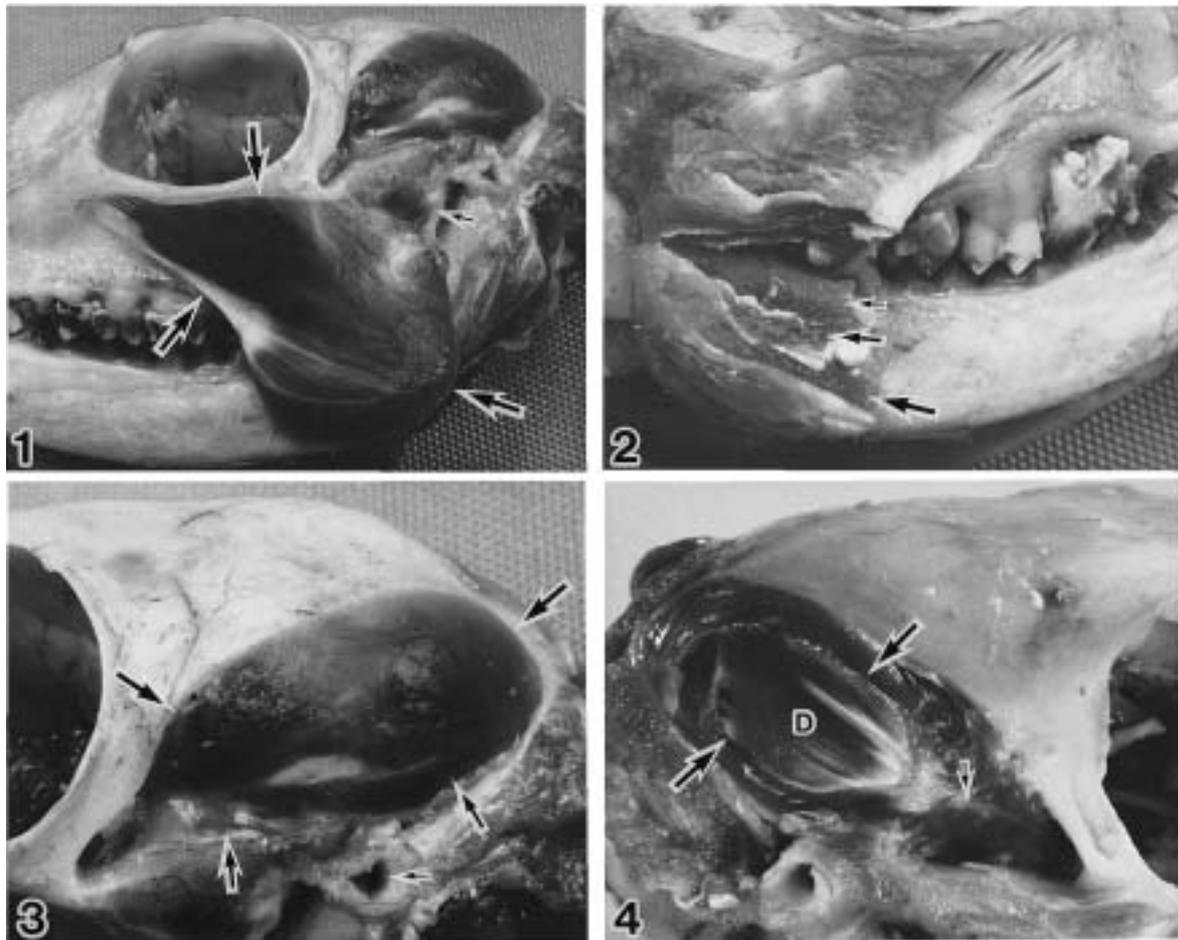


Fig. 1. Left side of the head of the lesser mouse deer. The superficial layer of the *M. masseter* (large arrows) is well-developed between the zygomatic arch and the masseteric fossa of the mandible. The deep layer of the *M. masseter* (small arrow) originates from the zygomatic process of the temporal bone.

Fig. 2. Right side of the head of the lesser mouse deer. Rostral direction at the right. The superficial (large arrow), intermediate (intermediate arrow) and deep (small arrow) layers are confirmed in the section of the *M. masseter*.

Fig. 3. Left dorso-lateral aspect of the head of the lesser mouse deer. Rostral direction at the left. The *M. temporalis* (large arrows) originates from the temporal fossa. In the lateral region the thin slip (intermediate arrows) is extended from the dorsal area of the occipital process of the temporal bone. The slip originates also from the lateral surface of the *M. temporalis* in this individual. Small arrow, external acoustic pore.

Fig. 4. Right dorso-lateral aspect of the head of the greater mouse deer. Rostral direction at the right. After partial removing of the superficial layer (large arrows), the deep layer of the *M. temporalis* (D) is seen from the temporal fossa. In the lateral region the thin slip (small arrow) is extended from the dorsal area of the occipital process of the temporal bone.

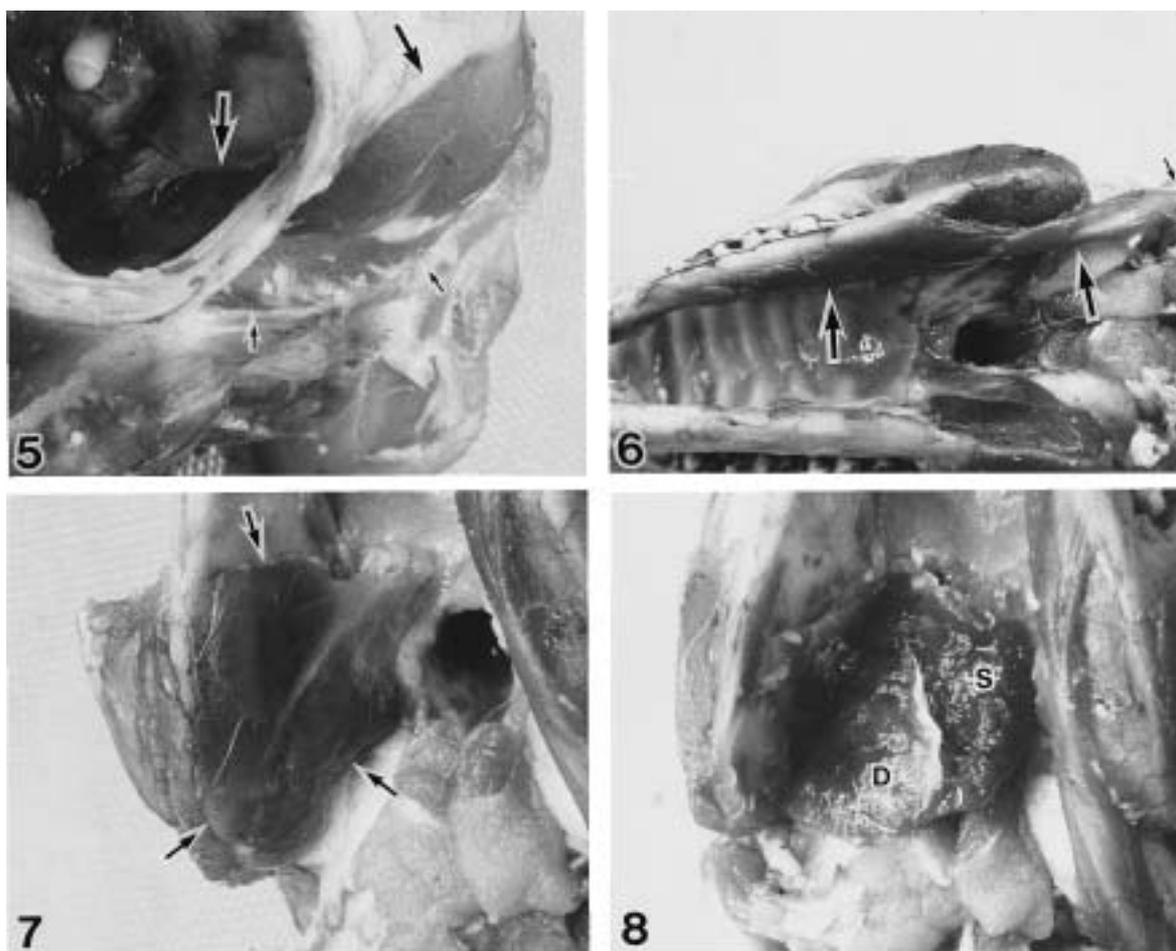


Fig. 5. Left dorso-lateral aspect of the head of the lesser mouse deer. The caudo-ventral area of the orbit and the ventral part of the temporal fossa are observed. The *M. temporalis* (large arrows) arises from the dorsal area of the temporal fossa, runs through the medial space of the zygomatic process of the frontal bone, occupies the caudo-ventral space of the orbit and inserts to the coronoid process. The lateral slip of the *M. masseter* arises from the occipital process (small arrows).

Fig. 6. Ventral aspect of the head of the lesser mouse deer. The *M. digastricus* (large arrows) can be seen from the jugular process (small arrow) to the ventro-medial area of the mandibular body.

Fig. 7. Ventro-medial aspect of the head of the lesser mouse deer. The *M. pterygoideus* (arrows) shows the triangle shape in the medial side of the mandibular ramus.

Fig. 8. The *M. pterygoideus* cannot be divided into the *lateralis* and *medialis*. However the muscles are separated into the two layers: superficial (S) and deep (D).

where only the superficial layer originated. The area of the temporal bone in the zygomatic arch was substantially occupied by the deep layer (Fig. 1). The bundles ran beneath the superficial and intermediate layers, and were attached to the lateral bundles of the *M. temporalis* in the lateral space of the mandibular ramus. Many bundles reached the dorsal area of the masseteric fossa, but the part attached to the *M. temporalis* ran into the rostro-lateral region of the coronoid process of the mandibular ramus. Any bundle of the *M. masseter* was not extended to the rostral area of the zygomatic arch, and the *Crista facialis* was not well-developed in the zygomatic and the maxilla bones.

The *M. temporalis* was small and thin. The weak *Crista*

temporalis was found in the temporal fossa, and the muscle bundles arose from the ventro-lateral area of the *Crista temporalis* (Fig. 3). The muscle partly originated from the dorso-medial area of the zygomatic process of the frontal bone. The *M. temporalis* could be divided into the thin superficial and thicker deep layers in the temporal fossa region (Fig. 4), although the two layers were fused together near the insertion. The bundles of the *M. temporalis* ran through the medial space of the zygomatic process of the frontal bone, occupied the caudo-ventral space of the orbit, and inserted to the coronoid process (Fig. 5).

The large slip was noteworthy in the lateral region of the temporal fossa (Figs. 3 and 4). The slip gave a rise from the

occipital process of the temporal bone in the dorso-caudal region of the external acoustic pore (Figs. 3–5), and also originated from the lateral surface of the *M. temporalis* (Fig. 3). The bundles of the slip seemed different in width among the individuals (Figs. 3–5).

The *M. digastricus* showed the typical twin bellies at medio-ventral aspect of the head (Fig. 6). The muscle arose from the rostro-lateral side of the jugular process. The muscle bundles were concentrated into tendinous structure at the level of the masseteric fossa, and then possessed the rostral fleshy belly. It inserted to the elongated area of the medial side of the mandibular body. The insertion was not confirmed in the lateral side of the mandible.

Under the *M. digastricus*, the *M. pterygoideus* was observed on the medial side of the mandible (Fig. 7). The bundles indicated a triangle shape at the medial aspect. It originated from pterygoid process of the sphenoid bone and the lateral side of the horizontal plate of the palatine bone. We cannot distinguish the *M. pterygoideus medialis* from *lateralis*, and concluded that the *M. pterygoideus medialis* was fused into the well-developed *M. pterygoideus lateralis*, although the muscles could be simply separated into two layers (Fig. 8).

The quantitative data in muscle weight and their ratio to body weight are arranged in Tables 1 and 2. The differences of the ratio were examined by Student's *t*-test between the two species (Table 2).

DISCUSSION

The functional morphology in the artiodactyls has been undertaken in the evolutionary highly-derived groups as modern Bovidae [7, 10, 12]. The anatomical description and the functional analysis have been carried out in domesticated cattle, goat and sheep [4]. These materials have been specialized to graze the crude grass in the plain [5, 6, 10, 11], and the data has not contribute to discuss the mastication system in primitive herbivorous artiodactyls, so-called

browser, feeding on soft leaves in woods.

The rostral area in Bovidae grazer is much wider than that in the mouse deer [4]. The splanchnocranium at the level of the premolar area is dorsally developed in highly-derived artiodactyls. These characters give the attachment surfaces to the facial muscles regulating in detail the movement of rostral part of the mouth. It enables the grazer species to crop and feed on crude and coarse grass. And in the modern Bovidae species the lateral region of the maxilla bone including *Crista facialis* is enlarged where the *M. masseter* could be inserted. These morphological peculiarities represent highly-specialized forms of the grazer. In contrast the origin of the *M. masseter* is restricted to the zygomatic area in the mouse deer, and the smaller facial surface does not contribute to the attachment of the *M. masseter*. We suggest that the *M. masseter* may not act as a motor raising the mandible rostro-dorsally, but pull the insertion area of the mandible vertically in the mouse deer. The *Crista temporalis* is not developed in the mouse deer unlike the domesticated ruminants. It may have influences on the original surface area of the *M. temporalis*.

From these data, we obtained two functional peculiarities in the mastication muscles of the mouse deer. 1) The origin of *M. masseter* is not enlarged in the facial area and the bundles simply pull up the mandible; this suggests that the mouse deer has not been highly-adapted to move the mandibular body complicatedly and rostro-ventrally. 2) The *M. temporalis* is not well-developed in the temporal fossa region, and the muscle does not act as a crushing motor for crude plants unlike the developed grazer. The two findings may be related to the mastication strategy of browser adapted for soft leaves on which the primitive artiodactyls mainly feed in woods [5, 6, 11].

The weight ratio in total is obviously different between the two species. This indicates that the greater mouse deer possess the relatively lighter mastication muscles for their body weight (Table 2). The *M. temporalis* and *M. digastricus* contribute to the interspecies differences of muscle

Table 2. Muscle weight ratios to body weight and significant differences between the two species*

	Sex	<i>M. temporalis</i>	<i>M. masseter</i> **	<i>M. masseter</i> ***	<i>M. digastricus</i>	<i>M. pterygoideus</i>	Total
<i>T. javanicus</i>	Male	1.478	1.045	1.522	0.530	1.642	6.216
<i>T. javanicus</i>	Male	1.821	1.795	1.232	0.875	1.634	7.357
<i>T. javanicus</i>	Female	1.650	1.850	1.336	0.593	1.071	6.500
Average		1.650	1.563	1.363	0.666	1.449	6.691
S.D.		0.140	0.367	0.120	0.150	0.267	0.485
<i>T. napu</i>	Female	1.121	0.968	1.207	0.325	1.357	4.978
<i>T. napu</i>	Female	1.328	0.956	1.468	0.208	1.004	4.964
Average		1.225	0.962	1.338	0.266	1.181	4.971
S.D.		0.146	0.008	0.184	0.083	0.250	0.010
t-test****		3.27	8.54	43.56	3.45	20.20	1.51

* Each ratios are given as muscles weight per body weight $\times 10^4$.

** The superficial layer of the *M. masseter*.

*** The intermediate and deep layers of the *M. masseter*

**** Each number indicates the limit percentage in which the significant differences are confirmed between the two species.

weight ratio (Table 2), although the other muscles did not show the significant differences between the two species

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