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Original Article

Masseter muscle structure and its relationship with medial chewing movement in Pallas's squirrel, *Callosciurus erythraeus*

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Here we describe the architecture of the masseter muscle in Pallas's squirrels, Callosciurus erythraeus, and discuss the relationship of its anatomical features with a medial chewing pattern on the basis of comparisons with previous information about cricetine and murine murids, which masticate food by medial and forward movements of the mandible, respectively. Callosciurus and cricetine murids share some characteristics of the masseter muscle, such as the absence of the medialy-reflected part of the superficial layer, the simple structure of the anterior part of the deep layer, and the strong anterodorsal inclination in some units of the deep layer. Those features are not observed in murine murids. Because cricetine and murine murids have similar dietary habits, interspecific differences in the anatomy of the masseter muscle do not seem to reflect a particular dietary adaptation, but rather appear to reflect a chewing mode. Further mechanical analyses are required to elucidate the functional significance of the present findings.

Key words: *Callosciurus*; masseter muscle; medial chewing; murid rodents

Introduction

Rodent species exhibit a variety of mandibular movements during molar occlusion for food processing, i.e., medial, forward, and oblique directions, irrespective of their dietary habits[1-7]. Thus, this mammalian group is an ideal model for examining the relationship of the jaw muscle structure, direction, and attachment site with the chewing direction. The rodent masseter muscle is very large and more structurally complicated than the other jaw-closing muscles[8]. To clarify the relation of anatomical structures of the masseter muscle with the chewing pattern, detailed observations of the compartments within the muscle are necessary. Although some information about the muscle fiber direction, and aponeurotic distribution of these compartments is available concerning murid species such as rats, mice, hamsters, and voles[9-16], little is known about the architecture of the masseter muscle in most of other rodent taxa.

Sciurid rodents masticate food by a medial shift of the mandible[6,7]. Detailed studies have reported the masseter muscle structure of sciurid[17-19], but several characteristics, such as the distribution of the aponeuroses and origin-insertion relationship of each muscle fiber bundle, remain obscure. In the present study we describe the architecture of the masseter muscle in a sciurid species, Pallas's squirrels, *Callosciurus erythraeus*, and discuss the relationship of its anatomical features with the medial chewing pattern based on our observations in comparison with previous reports concerning cricetine and murine murids[13,15].

Materials and methods

The carcasses of two adult specimens (1 male and 1 female) were used for examination. These specimens were captured for pest control, and donated from the Environment Conservation Division Animal protection management charge, Kamakura City Office, Kanagawa, Japan. For clear separation of the muscle fiber bundles, the heads of the specimens were fixed in 10% formaldehyde solution for at least 1 month after removing the skin. To distinguish the muscle subunits, the aponeurosis distributions and the attachments of each muscle fiber bundle were carefully observed under a stereoscopic microscopy (10–32X magnification; SZX 9, Olympus, Tokyo). Terminology for the subunits of the masseter muscle and their aponeuroses was applied in accordance with Satoh and Iwaku[13].

Results

Superficial layer

The superficial layer of the masseter muscle (SM: Fig. 1) runs nearly horizontal, and laterally wraps around the ventral portion of the deep layer. The superficial layer originates on the inner surface of the broad inferior zygomatic plate aponeurosis (IZPAP: Fig. 1), which arise from an anteriorly-projected process near the lower border of the infraorbital foramen (Fig. 4a), The superficial layer inserts on the ventral side of the angular process, dorsally bordered by the masseteric ridge (Fig. 4d), The ventral fibers of the superficial layer turn slightly inward and attach to the medial side of the anteroventral area of the angular process.

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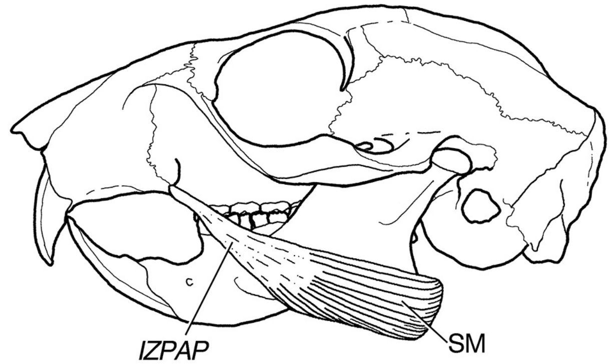

Fig. 1. The superficial layer of the masseter muscle in *Callosciurus erythraeus*. Abbreviations for aponeuroses are indicated in italics to distinguish them from those of the muscles. IZPAP, inferior zygomatic plate aponeurosis; SM, masseter superficial layer.

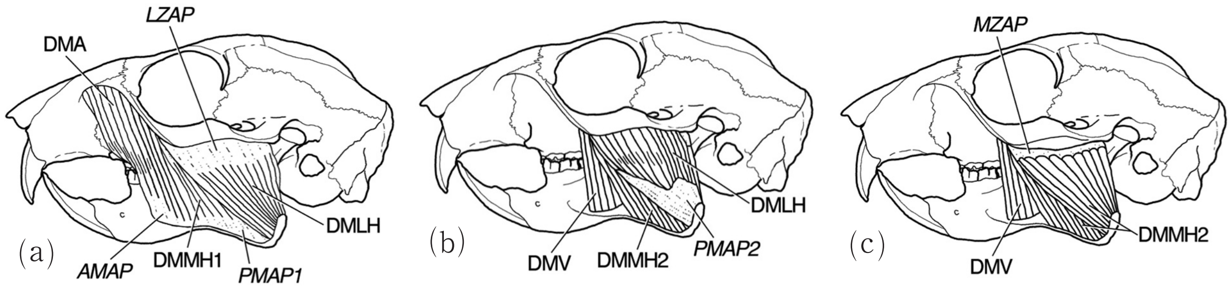

Fig. 2. The deep layer of the masseter muscle in *Callosciurus erythraeus*. The deeper view is successively illustrated from a to d. Abbreviations for aponeuroses are indicated in italics to distinguish them from those of the muscles. AMAP, anterior mandibular aponeurosis; DMA, anterior part; DMLH, lateral horizontal part; DMMH 1 – 2, 1 st and 2 nd portions of medial horizontal part; DMV, vertical part; LZAP, lateral zygomatic aponeurosis; MZAP, medial zygomatic aponeurosis; PMAP 1 – 2, 1 st and 2 nd sheets of posterior mandibular aponeurosis.

Deep layer

The deep layer of the masseter muscle (Fig. 2) originates along the dorsal border of the zygomatic plate, and the lateral and ventral sides of the zygomatic arch. It inserts on the masseteric ridge, and the lateral side of the mandibular ramus. The deep layer contains several aponeuroses. For the origin, two sheets of aponeurosis lie along the zygomatic arch, but no aponeurosis is observed on the zygomatic plate. The lateral zygomatic aponeurosis (LZAP: Fig. 2a) starts at the posterior end of the zygomatic plate. It then runs along a dorsally convex ridge on the lateral aspect of the middle part of the zygomatic arch, and terminates at the area ventral to the glenoid fossa (Fig. 4a). The anterior and posterior ends of the medial zygomatic aponeurosis (MZAP: Fig. 2c) are situated at the same points as those of the lateral zygomatic aponeurosis. The former aponeurotic sheet attaches to the ventral edge of the zygomatic arch (Fig. 4b).

For the insertion of the deep layer, there is a series of aponeuroses aligned along the masseteric ridge. The anterior mandibular aponeurosis (AMAP: Fig. 2a) is located along the anterior one-third of the ridge (Fig. 4d). Based on the origin-insertion relationship of the muscle fiber bundle, as mentioned below, the other two sheets appear to correspond to the posterior mandibular aponeurosis (PMAP) in murid rodents. The anterior one (PMAP1: Fig. 2a) is thin and occupies one-half of the masseteric ridge (Fig. 4d). On the other hand, the posterior sheet (PMAP2: Fig. 2b) broadens dorsoventrally and lies on the groove near the tip of the angular process (Fig. 4d).

Based on the uniformity of the attachment site, five subunits are recognized within the deep layer of the masseter muscle: anterior, lateral horizontal, medial horizontal 1 and 2, and vertical parts. The anterior part (DMA: Fig. 2a) directly originates from the dorsal margin of the zygomatic plate (Fig. 4b) and runs mostly in the dorsoventral direction. It then inserts on the medial side of the anterior mandibular aponeurosis. The posterior end of the origin of the anterior part is situated dorsally to the upper first molar.

The lateral horizontal part (DMLH: Fig. 2ab) arises from the zygomatic arch posterior to the zygomatic plate, and converges toward the posterior mandibular aponeurosis 2. This subunit is considerably inclined in the anterodorsal direction, as the aponeurosis of insertion lies near the tip of the angular process. The superficial fibers of the lateral horizontal part (Fig. 2a) originate from the inner surface of the lateral zygomatic aponeurosis, and insert on the lateral side of the lower half of the posterior mandibular aponeurosis 2. The deep fibers of the muscle (Fig. 2b) directly attach to the lateral side of the zygomatic arch, ventromedial to the lateral zygomatic aponeurosis (Fig. 4 b).Their insertion lies on the dorsolateral area of the posterior mandibular aponeurosis 2.

The medial horizontal part1 (DMMH1: Fig. 2a) arises from the medial side of the medial zygomatic aponeurosis. The origin of this subunit is restricted to a small area near the anterior end of the medial zygomatic aponeurosis. The medial horizontal part 1 radiates from the origin, and terminates on the medial side of the posterior mandibular aponeurosis 1. Therefore, the direction of the posterior fibers is more anterodorsally inclined than that of the anterior fibers.

The medial horizontal part 2 (DMMH 2: Fig. 2c) comprises two fiber groups that differ in direction. The superficial portion arises from the lateral and dorsomedial sides of the medial zygomatic aponeurosis, and then converges toward the bony surface just dorsal to the posterior mandibular aponeurosis 2. The direction of the superficial portion resembles that of the lateral horizontal part. On the other hand, the deep portion of the medial horizontal part 2 runs more vertically than its superficial portion. The origin and insertion of the deep portion lie on the ventromedial aspect of the medial zygomatic aponeurosis and the whole lateral side of the angular process, respectively (Fig. 4d).

The vertical part of the deep layer (DMV: Fig. 2bc) has a fleshy attachment at both the origin and insertion. The origin is situated on a small area posterior to the end of the zygomatic plate (Fig. 4a). The site of the insertion

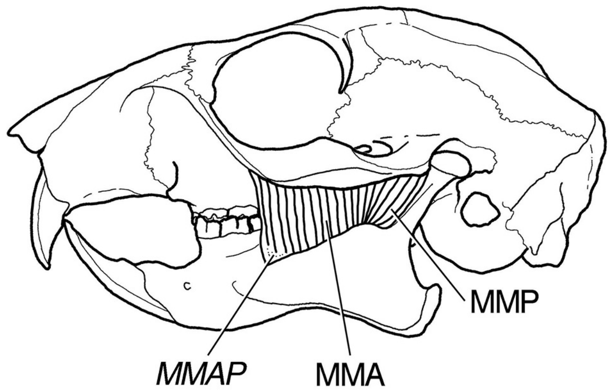

Fig. 3. The medial layer of the masseter muscle in *Callosciurus erythraeus*. Abbreviations for aponeuroses are indicated in italics to distinguish them from those of the muscles. MMA, anterior part; MMAP, medial mandibular aponeurosis; MMP, posterior part.

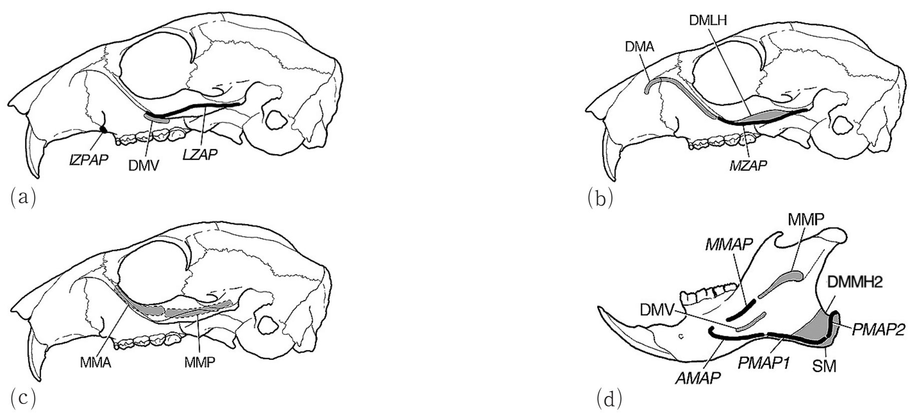

Fig. 4. Attachment sites of the masseter muscle and corresponding aponeuroses (abbreviated in italics for distinction from the muscles) on the cranium (a-c) and mandible (d) in *Callosciurus erythraeus*. Heavy lines and gray areas indicate attachments to the aponeurosis and the muscular origin or insertion, respectively. See text for the correspondence of these aponeuroses with the muscle units. AMAP, anterior mandibular aponeurosis; DMA, anterior part of deep layer; DMMH 2, 2 nd portion of medial horizontal part of deep layer; DMLH, lateral horizontal part of deep layer; DMV, vertical part of deep layer; IZPAP, inferior zygomatic plate aponeurosis; LZAP, lateral zygomatic aponeurosis; MMA, anterior part of medial layer; MMAP, medial mandibular aponeurosis; MMP, posterior part of medial layer; MZAP, medial zygomatic aponeurosis; PMAP 1 – 2, 1 st and 2 nd sheets of posterior mandibular aponeurosis; SM, superficial layer.

starts at a point dorsal to the middle portion of the anterior mandibular aponeurosis. It then runs posterodorsally and terminates at the area dorsal to the boundary between the anterior mandibular aponeurosis and posterior mandibular aponeurosis 1 (Fig. 4d).

Medial layer

The medial layer of the masseter muscle comprises the anterior, and posterior parts (Fig. 3). The anterior part (MMA) originates from the anterolateral border of the orbit (Fig. 4c) and inserts on the mandibular ramus dorsal to the insertion of the vertical part of the deep layer with a weak tendinous sheet, the medial mandibular aponeurosis (MMAP: Figs. 3 and 4d). The anterior part and cheek teeth row cross at nearly right angles, as viewed from the lateral side.

The posterior part (MMP) arises from the medial aspect of the posterior two-thirds of the zygomatic arch (Fig. 4c). Its insertion obliquely runs from the area just behind the attachment of the anterior part to the masseteric fossa formed by the root of the lower incisor (Fig. 4d). The anterior fibers run in the same direction as the anterior part, whereas the posterior fibers are posterodorsally inclined.

Discussion

Comparison of the masseter muscle architecture with murid rodents

Among rodent species, the internal architecture of the three layers of the masseter muscle, especially the deep layer, varies widely[9–16, 18–22]. In most rodents the deep layer of the masseter muscle contains two aponeuroses of origin along the zygomatic arch and a series of aponeuroses of insertion along the masseteric ridge as in *Callosciurus*. To date, the division of the posterior mandibular aponeurosis into two sheets has not been reported in other rodents.

In previous anatomical studies of the masticatory muscles of sciurids[17–19], the masseter deep layer was classified into the anterior part, which inserts on the entire length of the masseteric ridge, and the posterior part, which converges into the tip of the angular process. Furthermore, within the anterior part, its anterior and posterior regions have been recognized. Based on the origin-insertion relationships, the posterior region of the anterior part seems to correspond to the medial horizontal part 1 and the deep portion of the medial horizontal part 2 in the present study. In murid rodents, these units are not included in the anterior part of the masseter deep layer, but are rather included in its posterior parts[10, 23].

The subunits within the deep layer of the masseter muscle are noticeably different between *Callosciurus* and murid rodents[9, 10, 12–16]. In murid rodents, the lateral horizontal part arises from the medial aspect of the lateral zygomatic aponeurosis, whereas in *Callosciurus,* the origin of this unit extends to a slightly concave area on the middle portion of the zygomatic arch. Furthermore, in murid rodents, the medial horizontal part 1 and 2 uniformly insert on the posterior mandibular aponeurosis and the whole lateral side of the angular process, respectively. The muscle fibers of these units run parallel with each other. In *Callosciurus*, however, the medial horizontal part 1 diverges from the origin to the insertion. For medial horizontal part 2, although the deep portion runs similarly to that of murid rodents, the superficial portion converges toward the tip of the angular process. In murid rodents, a distinct unit, called the medial horizontal part 3, is observed along the dorsal edge of the angular process, whereas in *Callosciurus* there are no muscle fibers in this area.

Anatomical features relating to medial chewing movement

Murid rodents include species that grind food by medial, forward, and oblique mandibular movements[1–4, 6]. Among those species, the internal structure of the masseter muscle has been well investigated in cricetine (Old World hamsters) and murine (rats and mice) species, which chew with medial and forward mandibular movements, respectively[10, 13, 15]. There is a clear difference between cricetine and murine murids in the insertion and direction of the lateral horizontal part of the masseter deep layer. This unit inserts on the whole lateral surface of the posterior mandibular aponeurosis in murine species, whereas it inserts on the mere posterior half of the sheet in cricetine murids. As a result, the lateral horizontal part of cricetine murids runs in more anterodorsal direction than that of murine murids. Such cricetine features resemble the lateral horizontal part and superficial portion of the medial horizontal part 2 of *Callosciurus*, which show a strong anterodorsal inclination due to the convergence of fibers toward the tip of the angular process. This phenomenon suggests that the medial movement of the mandible during chewing requires more anterior force than forward movement.

The masseter muscles of *Callosciurus* and cricetine murid also share some other characteristics. In those two taxa, ventral muscle fibers of the superficial layer attach to the ventral aspect of the base of the angular process. In addition, no subdivision is recognized within the anterior part of the deep layer, as all muscle fibers directly originate from the zygomatic plate and insert on the anterior mandibular aponeurosis. On the other hand, in murine murids, the superficial layer of the masseter muscle has a distinct slip that turns inward and inserts on the medial side of the condylar process, just beneath the lower incisor root. The anterior part of the deep layer contains some aponeuroses of origin, and attaches to the mandible directly and via an aponeurosis. Therefore this part can be subdivided into several units in murine species. Because the dietary habits are similar between cricetine and murine murids, interspecific anatomical differences of the masseter muscle do not seem to reflect a certain dietary adaptation. Consequently, common characteristics between cricetine murids and *Callosciurus*, i. e., the absence of the medialy-reflected part of the superficial layer, simple structure of the anterior part of the deep layer, and strong anterodorsal inclination in some units of the deep layer, appear to be related to the medial chewing pattern. Further mechanical analyses are required to elucidate the functional significance of those features.

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タイワンリス *Callosciurus erythraeus* の咬筋構造と内側への咀嚼運動との関係

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齧歯類の臼歯によるすりつぶし運動には，食性とは無関係な前方型，内側型，斜前方型という３つのパターンが存在する（Offermans and De Vree, 1990）．しかし，顎運動のパターンと咀嚼筋形態との関連性については十分に明らかにされていない．そこで本研究では，内側型の咀嚼運動がみられるタイワンリス，*Callosciurus erythraeus*，の咬筋表層・深層・内側層の内部構造および走行について詳細な観察をおこない，これまでに報告されているネズミ科キヌゲネズミ亜科（内側型）およびネズミ亜科（前方型）との比較をもとに顎運動パターンと咬筋の解剖学的特徴との関係について考察した．ともに内側型の咀嚼をおこなうタイワンリスとネズミ科キヌゲネズミ亜科の咬筋では，表層における下顎骨内側面に停止する部位の欠如，深層前部の単純な構造，深層のいくつかの区画における強く前傾した走行という共通の特徴が認められた．これらの特徴は，前方型の運動がみられるネズミ科ネズミ亜科では認められない（Satoh and Iwaku, 2004, 2008）．ネズミ科キヌゲネズミ亜科とネズミ亜科の食性が類似していることから，これら２亜科間で異なり，キヌゲネズミ亜科とタイワンリスとの間に共通する咬筋の特徴は，食性への適応ではなく咀嚼運動の違いを反映したものと考えられる．本研究で得られた結果の機能的意義を説明するためには，さらなる力学的解析が必要である．

キーワード：タイワンリス，咬筋，内側型咀嚼，ネズミ科齧歯類

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