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Masticatory muscle masses of murids

Comparison of Masticatory Muscle Masses between Cricetine and Murine Murids

KAZUHIKO SATOH and FUMIHIKO IWAKU

Department of Oral Anatomy, Division of Oral Structure, Function and Development
Asahi University School of Dentistry
(Chief : Prof. Fumihiko Iwaku)

Abstract *Masticatory muscle masses (i. e., the masseter, temporalis, internal pterygoid, and external pterygoid muscles) were compared between two murid subfamilies, transversely chewing Cricetinae (Old World hamsters : Mesocricetus, Tscherskia, Cricetulus, and Phodopus) and anteriorly chewing Murinae (Rats and mice : Rattus and Apodemus). Regression lines obtained from the plots of muscle weight versus cranial size indicate that cricetine murids have larger temporalis and internal pterygoid muscles than murine species with the same cranial size. Among the muscles examined, the temporalis grows at the highest rate in both subfamilies. The present findings suggest that a posterior shift of the hemimandible on the non-chewing side, associated with transverse food processing, requires a stronger backward pull of the temporalis than control of the forward chewing movement.*

INTRODUCTION

Murid rodent includes the species that chew with a transverse jaw movement and with a forward jaw movement[1~6]. These food processing patterns have little correlation with phylogeny or dietary habit[7]. Transverse chewing seems to be basic for murids, as it is common among mammals[8~15] and rodents with a primitive cuspal arrangement of cheek teeth (e. g., hamsters and squirrels)[1,2,16,17]. The forward chewing pattern appears multiple times through parallel evolution within rodents[3~6,16,18]. There is currently no hypothesis proposed for the evolutional advantage of this unique type of chewing.

Jaw-moving apparatuses might reflect the chewing direction. Assessment of the masticatory muscle masses might provide a clue to the advantage of forward food processing. These muscle weights, however, are closely related to dietary habit and body size, as well as jaw movement. Although quantitative data of the jaw muscles are available for several murid species[19~25], species with similar dietary habits and different chewing patterns have not been compared. In addition, the influence of body size on muscle mass has not been sufficiently evaluated.

In the present study the relation between the masticatory muscle mass and cranial size was compared in two granivorous murid subfamilies, Cricetinae (transverse-chewing group) and Murinae (forward-chewing group).

MATERIALS AND METHODS

The following species were used for the analysis: Subfamily Cricetinae, *Mesocricetus auratus* (n=7), *Tscherskia triton* (n=8), *Phodopus sungorus* (n=8), and *Cricetulus griseus* (n=8) ; Subfamily Murinae, *Rattus norvegicus* (n=36), and *Apodemus speciosus* (n=39). The cadavers of cricetine species were do-

nated by the Research Center for Frontier Bioscience, Bio-resource Division, Department of Biotechnology, Miyazaki University. Samples of murine murids were caught in Kyoto, Japan from 1993 to 1995. The heads of the specimens were preserved in 10% formaldehyde fluid for 1 month after decapitation and removal of skin. The masticatory muscles (Fig. 1) on the right side were then de-
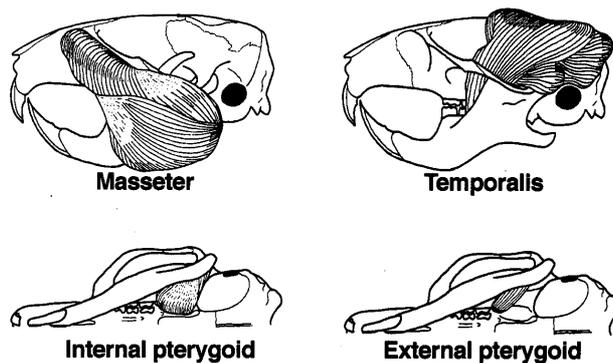
Fig 1. Masticatory muscles in a cricetine murid,
Mesocricetus auratus.

tached from the cranial bone and kept in an incubator at 40℃. After 10 days incubation dry muscle masses were measured.

Body parts of an organism usually develop according to the following allometric formula[26] :

$$Y = bX^a$$
thus $ln\ Y = a\ ln\ X + ln\ b$

where Y is the size of the body part, X is a parameter indicating the size of the whole organism (e. g., cranial length, body length, or weight), and a and b are allometric growth constants. In the present study, regression lines were obtained from scatter plots of the muscle mass (Y) versus the cranial length (X), each of which was transformed using the natural log. Cranial length was defined as the distance from the most anterior point of the upper incisor to the ventral notch of the magnum foramen. The differences in the regression lines between the two groups were tested using analysis of covariance (ANCOVA). Furthermore, the slope of the regression line (i. e., the allometric growth constant a) was compared among the muscles for each subfamily, and statistical significance was examined by Tukey's multiple comparison.

RESULTS

The regression line and values of its slope and y-intercept are shown in Figure 2 and Table 1, respectively. The masses of all muscles examined have a strong positive correlation with cranial size (r> 0.895). There is no significant difference between groups in the slope of the regression line for any muscle. On the other hand, the y-intercept for the temporalis and internal pterygoid muscles is larger in cricetine murids than in murine murids. These findings indicate that these muscles of cricetine murids are more developed than those of murine species with the same cranial size. There is no significant difference between the two subfamilies in the masseter and external pterygoid muscles.

Among the masticatory muscles, the slope of the regression line is largest for the temporalis and smallest for the external pterygoid for both subfamilies (Table 2). These findings suggest that the ratio of the temporalis to the whole masticatory muscle becomes higher as body size increases. There is no significant difference between the masseter and internal pterygoid muscles.

DISCUSSION

In rodents, the orbit and temporal fossa are not separated from each other by a septum. The eyeball limits the size of the temporalis, as they share a common space laterally bordered by the zygomatic arch. For example, certain rodents that inhabit the desert (e. g., pedetid, dipodid, and heteromyid species) have enormous eyeballs as an adaptation for nocturnal foraging[27]. Their temporales are rudimentary and occupy less than 5% of the whole masticatory muscle mass[16, 28~30]. In general, the relative size of a sense organ, including the eyeball, is inversely proportional to body size. This phenomenon is known as von Haller's law[31]. Thus, the increase in body size makes proportionally more space available for the temporalis. The present analysis reveals that the temporalis grows more rapidly than the other masticatory muscles in both of cricetine and murine murids. A similar developmental pattern is also re-

Masseter

Temporalis

Internal pterygoid
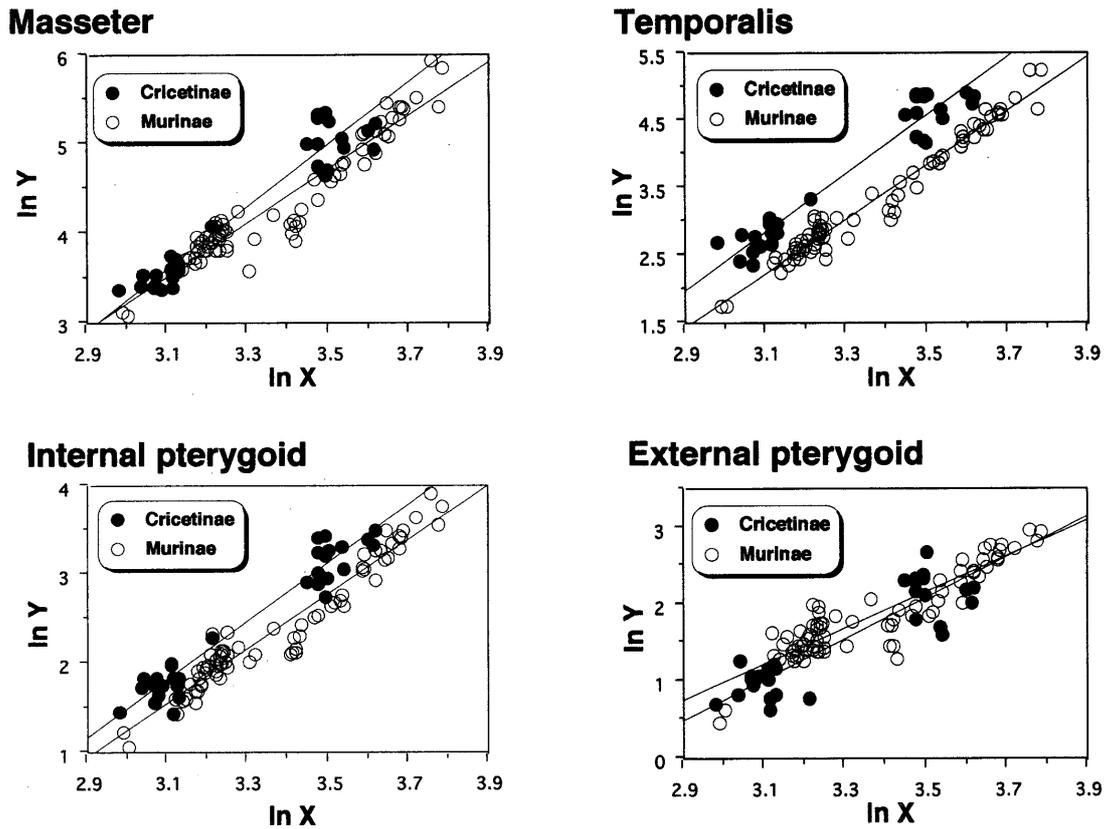
External pterygoid

Fig 2. Plots of cranial length (X) versus muscle mass (Y), each of which is transformed using natural log, with regression line.

Table 1. Slope and y-intercept of regression line, correlation coefficient (r), and statistical difference of y-intercept between two groups (Cr, Cricetinae ; Mu, Murinae ; *Significantly different at p<0.01) for each masticatory muscle.

	Cricetinae (transversely chewing group)			Murinae (forward chewing group)			Difference of y-intercept
	slope	y-intercept	r	slope	y-intercept	r	
Masseter	3.417	-7.157	0.963	2.999	-5.784	0.956	Cr = Mu
Temporalis	4.346	-10.643	0.970	4.029	-10.261	0.981	Cr > Mu*
Internal pterygoid	3.267	-8.307	0.970	3.065	-7.949	0.966	Cr > Mu*
External pterygoid	2.649	-7.197	0.895	2.328	-6.001	0.911	Cr = Mu

Table 2. Comparison of slopes of regression line among masticatory muscles (Cricetinae / Murinae). Upper right, difference in each combination of the muscle ; lower left, level of sigfnficance.

	Masseter	Temporalis	Internal pterygoid	External pterygoid
Masseter	----------	M < T / M < T	M = IP / M = IP	EP < M / EP < M
Temporalis	* / *	----------	IP < T / IP < T	EP < T / EP < T
Internal pterygoid	ns / ns	* / *	----------	EP < IP / EP < IP
External pterygoid	* / *	* / *	* * / *	----------

EP, external pterygoid ; IP, internal ptergoid ; M, masseter ; T, temporalis.
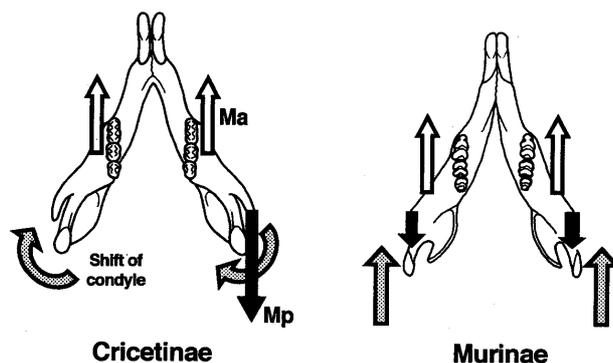*, p<0.01 ; **, p<0.05 ; ns, not significant.

Fig 3. Role of temporalis during chewing in Cricetinae and Murinae. Ma (white arrow), anteriorly directed force, which can be produced by masseter, internal pterygoid, and external pterygoid muscles ; Mp (black arrow), posteriorly directed force by temporalis. Length of Mp, relative to that of Ma, indicates magnitude required for jaw movement.

ported in another murid subfamily, Arvicolinae[23]. Therefore, the high growth rate of the temporalis is common among murids, and indirectly reflects allometry of the visual organ.

The transverse food processing pattern of a cricetine species *Mesocricetus auratus* is created by a horizontal mandibular rotation (Fig. 3, left). At this time the mandibular condyles on the chewing and non-chewing sides have opposite directions of movement[1]. The forward shift of the chewing side results from activities of the masseter, internal pterygoid, and external pterygoid muscles. For the non-chewing side, the posterior horizontal fibers of the temporalis are important for producing backward jaw movement. On this side, however, the deep layer of the masseter, quite developed part in murid rodents[19~25], applies a powerful forward pull to the hemimandible[1]. Thus, the posterior part of the temporalis needs to be massive to overcome the force of the masseter (Fig. 3, left).

On the other hand, the temporalis of murine murids seems less important than that of cricetines in terms of chewing function. In a murine species *Rattus norvegicus*, the masticatory muscles symmetrically contract and both mandibular condyles slide nearly along a sagittal line[3~5] (Fig. 3, right).

This propalinal jaw shift is produced by the masseter, internal pterygoid, and external pterygoid muscles. The temporalis, however, does not act to move the jaw in a chewing direction, but rather acts to control the movement[24] (Fig. 3 : right). The present finding on the temporalis weight of the two groups strongly supports the above prediction.

The main role of the internal pterygoid muscle in rodents is to create a medial shift of the hemimandible during molar occlusion[32] and to prevent large tensile strain on the flexible mandibular symphysis due to masseter contraction[33]. The difference in the mass of this muscle between cricetine and murine murids, however, is difficult to interpret in terms of chewing function. In sciurid rodents, which masticate in the same way as cricetine murids, the internal pterygoid muscle is larger than in murine murids relative to the whole masticatory muscle[20]. Further functional analysis is required to clarify why the large internal pterygoid muscle is required for transverse chewing.

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ネズミ科キヌゲネズミ亜科とネズミ亜科における咀嚼筋重量の比較

佐 藤 和 彦　　岩 久 文 彦

朝日大学歯学部口腔構造機能発育学講座口腔解剖学分野（主任：岩久文彦教授）

501-0296　岐阜県瑞穂市穂積1851

キーワード：咀嚼筋，咀嚼方向，ネズミ科齧歯類

抄録　咀嚼筋（咬筋，側頭筋，内側翼突筋および外側翼突筋）重量を顎運動の異なるネズミ科の 2 亜科，側方咀嚼をおこなうキヌゲネズミ亜科（旧世界ハムスター類：*Mesocricetus*，*Tscherskia*，*Cricetulus*，および*Phodopus*の各属）と前方咀嚼をおこなうネズミ亜科（狭義のネズミ類：*Rattus*属および*Apodemus*属）とで比較した．頭蓋基底長に対する筋重量のデータを基に得られた回帰直線から，キヌゲネズミ亜科の側頭筋および内側翼突筋が同サイズのネズミ亜科に比べてより発達することが示唆された．また，いずれの亜科においても側頭筋の成長速度が咀嚼筋中最大であることが示唆された．本研究の結果から，側方咀嚼に不可欠な下顎骨非咀嚼側の後方移動には前方咀嚼時の顎運動の制御に比べてより強力な側頭筋による後方への牽引力が必要であると考えられた．