

# Variation and Variability of Skull Morphology in Rodents (Mammalia: Rodentia)

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## Abstract

### Background

Variation is the central concept in biological studies. A thematic focus is needed to clearly understand the wide-ranging perspectives of variation. Skull is the fundamental skeletal structure to study functional adaptation and evolution of the mammalian species. Skull typically tells the story about natural history of animals. Rodents are the most diversified mammalian group and occur in terrestrial, subterranean, arboreal, and aquatic habitats. Considering lifestyle diversity, rodent skulls are often used as model systems regarding functional, developmental, and evolutionary perspectives. In this dissertation, intra-and interspecific skull morphological variations were studied in rodent species by integration of different variation indices.

### Materials and Methods

I studied skulls of three species of rodents using both linear measurements and geometric morphometric methods. In linear measurements, different indices of variation such as coefficient of variation ( $CV$ ), Pearson's correlation coefficient ( $r$ ), and allometric coefficient ( $\alpha$ ) were used to investigate intraspecific variation. The different univariate, bivariate, and multivariate analyses were also used for interpreting skull variation. In geometric morphometrics, I used multivariate analyses integrating with allometric shape changes and modularity. All data were analyzed with the software PAST (ver. 3.16) and JASP (ver. 0.8.2.0)

for linear measurements, and geometric morphometric analyses were conducted using the MorphoJ software.

## Results

First, in a murid rodent (the large Japanese field mouse, *Apodemus speciosus*), present study revealed male-biased sexual dimorphism in cranium and mandible sizes. The CVs did not differ significantly between the sexes and exhibited an inverse relationship with the mean of skull measurements. Moreover, the CVs for the pre-orbital region tended to be larger than those for the inter- and post-orbital regions. Allometric trends revealed isometry and positive allometry in the pre-orbital region, and negative allometry in the inter- and post-orbital regions.

In a second analysis, females showed slightly larger mean size for all craniomandibular traits in the Japanese giant flying squirrel (*Petaurista leucogenys*). Females were significantly larger than males for the greatest length of skull, zygomatic breadth, and mandibular length. Discriminant functions indicated well distinctiveness between the sexes. Moreover, females showed significantly larger incisor resistance arm and moment arms of the superficial masseter (most ventral fibers) and the anterior deep masseter. Additionally, the CVs did not differ significantly between the sexes. Patterns of variability tended to differ in the cranial dimensions based on longitudinal and transverse axes, but not obviously in the major subdivisions of the skull. Allometric trends showed little deviation from isometry among the skull traits.

In a third analysis, interspecific skull shape differences were observed between two congeneric Japanese field mice, *Apodemus speciosus* and *A. argenteus*. This study found that *A. argenteus* showed relatively wider zygomatic arches, broader mandibular ramus, and a short mandibular diastema. The upper incisor, inter-orbital width, nasal region, and auditory bullae also showed interspecific differences. However, allometry revealed similar variability pattern in major parts of the skull within both species. The presence of two distinct modules in the

cranium (rostrum and braincase) and mandible (ascending ramus and alveolar region) was in agreement with common allometric trends.

## **Discussion**

The observed intraspecific variability patterns suggest the existence of developmental factors in both murid and sciurid rodents, and a general trend during ontogeny of the mammalian skulls. As allometry showed little deviation from isometry, this study also suggest that sciurid skull is more integrated than murid skull due to different evolutionary trends. The craniomandibular dimorphism observed in rodent species are mainly the size related phenomenon, despite similar trends in variability exhibited by both sexes are the consequence of morphological constraint. The relatively larger size in males of *A. speciosus* might have evolved to gain advantages in intra-sexual selection for mates. Moreover, larger females of *P. leucogenys* could have relatively greater absolute bite force, which may contribute to obtain more access for greater ecological resources. Therefore, female-biased dimorphism in *P. leucogenys* is mostly associated with resource benefits.

Present study indicated that interspecific skull shape variation between two *Apodemus* species might be associated with their ecological preferences. The relatively wider zygomatic arches and broader mandibular ramus in *A. argenteus* are linked to enlargement of the attachment sites for the masticatory muscles. The short mandibular diastema could increase the mechanical advantage of the lower jaw by reducing the out-lever arm. These suggest that *A. argenteus* has a greater relative bite force that is more suitable for diversified diets as a generalist feeder. The similar variability patterns in major components of the skull within both species may reflect similar patterns of intraspecific variation caused by common developmental factors.

## **Conclusion**

This dissertation suggests that trends in intraspecific variation of skull morphology in rodents are associated with functional and developmental factors. Craniomandibular dimorphism is an important source of variation, mostly depends on species in question. Interspecific variations are the consequence of species-specific ecomorphological adaptation linked to their diets and habitat utilizations, despite having similar variability patterns.