Abstract

Introduction
Owing to the durable material nature and relatively compact size, teeth are well represented in the fossil record of mammals. Consequently, dental remains play a crucial role for paleo-anthropological/paleontological studies. Besides the taxonomic/phylogenetic studies, since dental developmental mechanism is well understood and its developmental process is recorded in fully formed tooth, tooth is a good subject for understanding relationship between development and morphological variation, which leads to morphological evolution. This study used geometric morphometrics for rigorous quantification of morphological variation of human molariform teeth, specifically focusing on the phenotypic variability. The principal aim of this dissertation is to understand morphological variability of human maxillary molar and to tackle following two specific questions:

I. How the patterns of morphological variability are structured during human molar odontogenesis?
   Patterns of size and shape variability among cusps were examined at total and each particular crown components. Under inspired by developmental genetic studies, The prediction that the location and the size of later-forming cusps are more variable than those of earlier-forming ones based on the patterning cascade model (PCM) of cusp development was assessed.

II. What types of properties of morphological variability exists through the odontogenetic process, and how they affect evolutionary morphological change? The strength of two components of phenotypic variability: canalization and morphological integration, plus the relevant evolutionary flexibility were compared between EDJ and OES and explored the effects on reconstruction of the phylogenetic relationships.

Materials and Methods
Unworn maxillary permanent first molar (UM1) and second deciduous molar (um2) excavated from Japanese archaeological sites were used. Specimens were μ CT-scanned, and 3D models of EDJ and OES were reconstructed. For the first question, 3D (semi) landmarks were digitized on each main cusp (paracone, protocone, metacone, and hypocone) region of four crown components (EDJ-ridge, OES-ridge, OES-circumferences, and CEJ) in a tooth. Using geometric morphometric methods, size and shape variation were compared among cusps. For the second question, I conducted the following analysis. Based on these models, landmark-based 3D geometric morphometric analyses were conducted. Among-individual phenotypic variation is used as the measurement of canalization of size and shape. To compare overall strength of morphological integration, we calculated the variance of the eigenvalues for the variance-covariance matrix for each four configuration. Evolutionary flexibility is evaluated by the mean cosine of angles between randomly generated selection vectors and the corresponding response vectors.

Results and Discussions
Size variability in both tooth types was generally consistent with the prediction yielded from the PCM, and the differences in size variation among cusps were smaller for the crown components that are completed in later stages of odontogenesis. However, regarding shape variability, the prediction was mostly unsupported, and UM1 and um2 showed different patterns. Our findings suggested that the
pattern of size variability would be caused by temporal factors such as the order of cusp initiation and the duration from the beginning of mineralization to the completion of crown formation, whereas shape variability may be affected by both topographic and temporal factors.

The lack of a significant difference in size variation between EDJ and OES suggested that the strength of canalization on size was almost constant throughout odontogenesis. In UM1, EDJ showed less shape variation and a higher level of morphological integration than OES, which indicated that canalization and morphological integration acted as developmental constraints. In um2, such a tendency appeared weaker, probably due to the thinner enamel and/or shorter period of enamel formation.

Evolutionary flexibility was not significantly different between EDJ and OES in either tooth, possibly because the pattern cascade mode of cusp development would cause a cusp-divided covariance structure. This crown formation would lead to the retention of a certain level of evolvability of EDJ despite the existence of developmental constraints.

In conclusion, the results of this study provided new information on the patterns and properties of morphological variability structured during odontogenesis in human molar, and its effect on evolutionary change, which point to future studies that would address the elucidation of the mechanisms of tooth morphological evolution.