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Variation in regional diet and mandibular morphology in prehistoric Japanese hunter–gatherer–fishers

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ABSTRACT

Previous research has identified a relationship between mandibular morphology and diet (e.g., coarse or tough diets result in more robust mandibles). Prehistoric Japan is an excellent place to explore the significance of this relationship in shaping mandibular morphology due to the pronounced regional dietary variation. South/West Honshu Jōmon engaged in broad spectrum foraging, Northeastern Honshu Jōmon were fisher–gatherers, Hokkaido Jōmon were maritime (sea mammal) foragers. We test the hypothesis that diet variation across temporal and spatial zones will be reflected in mandibular morphological traits. Metric measurements were utilized to test for regional differences with both archaeological time period and biological sex as covariates. ANOVA results for region with time period as a covariate indicates all variables except corpus height and breadth are significantly different among regions but for the time period covariate, only corpus breadth and dimensions of ascending ramus are significant. ANOVA for region with biological sex as a covariate indicates all variables except corpus height are significantly different. Biological sex as a covariate demonstrates significant p-values for chin height, bicondylar breadth and minimum ascending ramus breadth. Generally, North Hokkaido and Southwest Hokkaido, exhibit the largest mandibular ascending rami and tallest anterior mandibles, whereas Northeast and South/West Honshu have smaller mandibles. Multivariate analysis indicates a separation between North and Southwest Hokkaido and South/West Honshu, whereas Northeast Honshu partially overlaps these dietary zones. Differences in mandibular morphology are better explained by regional diets than by temporal trends and biological sex.

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1. Introduction

One of the most influential factors shaping mandibular morphology is diet. When under strain from mastication (the mechanical processing of solid foods), muscles transmit biomechanical signals to the bones into which they are inserted. The evolution of mammalian teeth shows a marked trend towards increased tooth surface area to aid mechanical processing of food, maximize nutrient extraction, and reduce stress in mastication (Lucas, 2004). Within humans, biomechanical signals more so than natural selection and population history influence morphological variation in the mandible. Evidence from a large-scale global study of human populations with differing subsistence practices parsed the effects

of neutral evolution, population history and subsistence strategy and found that changes to mandibular morphology due to dietary practices erased the genetic signals of population history; further, masticatory pressure acts preferentially on the mandible rather than the maxillary region, which is secondarily influenced by changes in the mandible (von Cramon-Taubadel, 2011).

Plasticity during maturation alters the robusticity and size of the mandible, providing direct evidence of masticatory strain after consideration of other differentiating factors like biological sex, gender division of labor, and cultural practices such as using teeth as tools (Fig. 1). One well-documented phenomenon following the adoption of agriculture is an overall craniofacial reduction resulting from a diet of softer, processed foods that required little masticatory strain. Prior to the advent of agriculture and specialized tools for food processing, humans ate varied, regional, and seasonal diets that often included tougher/coarser foods requiring processing into smaller, easily digested particles via mastication. Generally, diets comprised of hard-object exploitation or foods difficult to

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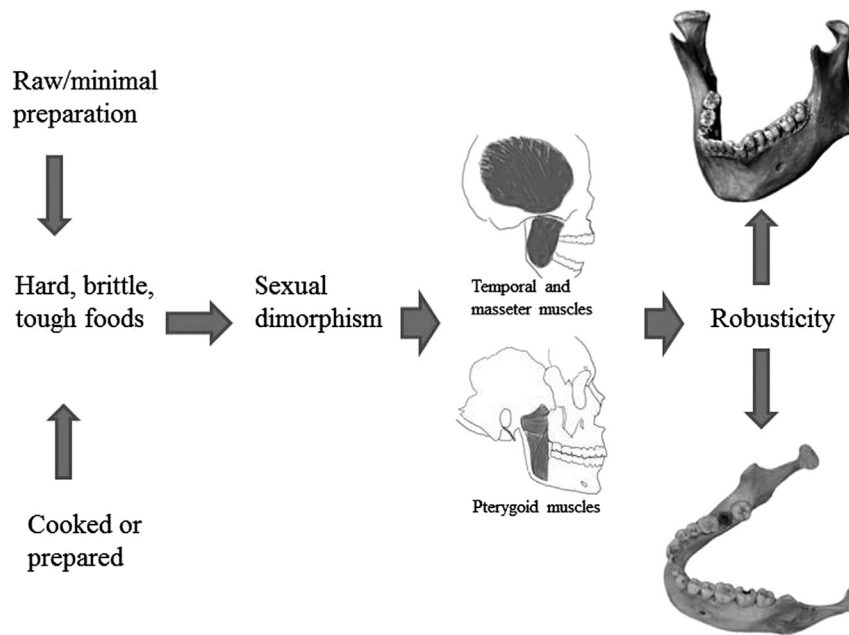


Fig. 1. Relationship between diet, mastication, and mandibular robusticity. Mandibular robusticity is greatly influenced by the foods consumed and the degree of preparation involved. Sexual dimorphism also contributes to morphological differences, with males generally exhibiting larger and more rugose mandibles compared to females, although a gendered division of labor with females heavily utilizing their teeth as tools, for example, to process hides, may result in greater robusticity. During development, increased recruitment of the temporalis, masseter and pterygoid muscles results in a larger, more robust mandible in adulthood.

masticate (e.g., tough meats, roughly ground grains and/or underground storage organs) result in larger, robust lower jaws compared to diets comprised of softer foods (e.g., fruits, processed or cooked foods) which result in smaller, more gracile mandibles (von Cramon-Taubadel, 2011). A functional stimulation of mandibular growth and development suggests diets with increased masticatory strain produce longer dental arches that accommodate teeth more rapidly (Enlow and Hans, 1996). Western ‘soft’ diets tend to result in shorter dental arches due to the lack of biomechanical signaling to the mandible (Corruccini, 1991). In addition, the joint connecting the mandible to the face via the temporal bone (the temporal-mandibular joint) has undergone a reduction in size and form in the transition from hunting–gathering to agriculture due to reduced masticatory muscle robusticity and associated changes in craniofacial form (Hinton and Carlson, 1979).

Several craniofacial muscles are recruited during mastication as well as in work tasks, such as using the teeth as a gripping organ in hide and tool production. Consistent chronic increases in mechanical stress expand muscle attachment sites and increase the maximum and minimum breadths of the ascending ramus (Bastir et al., 2004) and the robusticity of the mandibular corpus (Kanazawa and Kasai, 1998; Holmes and Ruff, 2011). Of the large number of muscles involved in oral function, the majority of those recruited in food processing attach to the mandible: food fracturing muscles (masseter, temporalis, medial pterygoid); jaw-closing muscles that aid bite force (adductors); jaw-opening muscles (abductors); other muscles that aid in rotation of the mandible (lateral and anterior-posterior); and a few involved in lip movement (Lucas, 2004). These muscle groups create mechanical strain on the mandibular bone throughout life resulting in a dynamic remodeling of bone relative to changes in muscle use (Lucas, 2004). In addition to muscle strain, other biomechanical signals for mandibular bone growth (and loss) are influenced with respect to the energy absorbed per unit of the volume of tissue, and the rhythm of loading patterns (Lucas, 2004).

Prehistoric Japan is an excellent place to examine the relationship between mandibular robusticity and diet because there are clear regional, temporal, and cultural differences in diet. During the Jōmon period (c. 15,000–2500 cal BP), populations were mostly sedentary hunter–gatherer–fishers that were well adapted to the postglacial environmental fluctuation characteristic of Japan during the Neolithic (Habu, 2004). The Jōmon subsistence system can be described as broad spectrum foraging with no specific staple resources, regionally variable, and adapted to the seasonality of available food resources which ultimately allowed for the adoption of sedentary life (Takahashi et al., 1998). The focus of this research is the subsistence and diet changes occurring from the Middle through Later Jōmon periods on Honshu and the Middle Jōmon through the Epi-Jōmon periods on Hokkaido. We are particularly interested in whether the mandible will capture dietary variation across space and time via measurements of robusticity and size.

Is regional dietary variation a main factor shaping mandibular morphology in prehistoric hunter–gather–fishers in Japan? To address this question, we analyzed the validity of regional groupings on the basis of diet (from archaeological data) using a suite of metric traits that assess mandibular robusticity. Regions include South/West Honshu, Northeastern Honshu, North Hokkaido, and Southwestern Hokkaido. We consider two covariates. First, Jōmon diet is variable across space and time so we use archaeological periods as a covariate: Middle Jōmon (including one Early Jōmon site), Later Jōmon (pooled Late and Final Jōmon) and Epi-Jōmon (on Hokkaido). Second, we use sex as a covariate because sex can be a proxy for a gender-based division of labor and previous research (Hinton and Carlson, 1979) indicates sexual dimorphism in hunter–gatherer mandibular metrics. With the transition to agriculture, differences decreased due to a marked reduction in male morphology.

We expect the main effect of regional diet to be significant in defining groups; populations engaging in diets with foods requiring extra masticatory strain (e.g., nuts, tubers, tough meats) will have

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