Patterns of Systemic Stress During the Agricultural Transition in Prehistoric Japan

Daniel H. Temple*

Department of Anthropology, University of Missouri, Columbia, MO 65211-1440

KEY WORDS enamel hypoplasia; cribra orbitalia; Jomon; Yayoi; bioarchaeology

ABSTRACT This study documents and interprets systemic stress during the agricultural transition in prehistoric Japan using linear enamel hypoplasia (LEH) defects and cribra orbitalia (CO) lesions. Middle to Final Jomon cultures (5000–2300 BP) from Honshu Island represent the foraging samples, while Yayoi cultures (2500–1700 BP) represent the early agricultural samples. Jomon foragers from eastern Japan had broad-based, intensive economies. Jomon foragers from western Japan had a greater focus on seasonally available, nutritionally poor resources, while Yayoi people were descendents of migrants from the East Asian continent and introduced wet rice economies to Japan. This study tests the hypotheses that wet rice economies will be associated with a lower prevalence of teeth/individuals affected by LEH defects in western Japan, while few differences in the prevalence of teeth/individuals with LEH defects will be observed between eastern Jomon people and Yayoi farmers. It is further predicted that similar CO prevalence will be observed between Jomon and Yayoi people given environmental similarities. Significantly greater frequencies of teeth affected by LEH defects are observed among western Jomon compared to Yayoi people. The prevalence of teeth with LEH defects is slightly elevated among eastern Jomon foragers compared to Yayoi agriculturalists. Significant differences in CO prevalence are not observed. Systemic stress prevalence in western Japan likely declined following wet-rice agriculture because this crop provided a predictable, renewable resource base. Systemic stress prevalence was similar between eastern Jomon and Yayoi people because both groups practiced intensive subsistence strategies. Similar CO prevalence reflects infectious diseases associated with living conditions. Am J Phys Anthropol 142:112–124, 2010.

*Correspondence to: Daniel H. Temple, Department of Anthropology, University of Missouri-Columbia, Columbia, MO 65211-1440.

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TABLE 1. Jomon and Yayoi sample data

<table>
<thead>
<tr>
<th>Site</th>
<th>Date</th>
<th>Group</th>
<th>Curation</th>
<th>N</th>
</tr>
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<tbody>
<tr>
<td>Kitamura</td>
<td>5000–3000 BP</td>
<td>Inland Jomon</td>
<td>Nagano</td>
<td>93</td>
</tr>
<tr>
<td>Ota</td>
<td>5000–4000 BP</td>
<td>Western Jomon</td>
<td>Kyoto University</td>
<td>42</td>
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<td>Tsukumo</td>
<td>3000–2300 BP</td>
<td>Western Jomon</td>
<td>Kyoto University</td>
<td>67</td>
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<tr>
<td>Yosekura</td>
<td>4000–3000 BP</td>
<td>Western Jomon</td>
<td>Tokyo University</td>
<td>59</td>
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<tr>
<td>Hobi</td>
<td>3000–2300 BP</td>
<td>Eastern Jomon</td>
<td>Tokyo University</td>
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<td>Inariyama</td>
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<tr>
<td>Nakazuma</td>
<td>4000–3000 BP</td>
<td>Eastern Jomon</td>
<td>Kyoto University</td>
<td>103</td>
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<tr>
<td>Yoshigo</td>
<td>3400–2400 BP</td>
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<tr>
<td>Daibuhama</td>
<td>2500–1900 BP</td>
<td>Yayoi</td>
<td>Kyushu University</td>
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<tr>
<td>Kanenokuma</td>
<td>2500–1900 BP</td>
<td>Yayoi</td>
<td>Kyushu University</td>
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<td>Koura</td>
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<td>Yayoi</td>
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<tr>
<td>Nagaoaka</td>
<td>2100–1900 BP</td>
<td>Yayoi</td>
<td>Kyushu University</td>
<td>20</td>
</tr>
</tbody>
</table>

a Approximate numbers of individuals available for study. The number of teeth and orbital vaults available for each sample differs from these numbers.

b Inland Jomon diet was likely similar to those from western regions (Akazawa, 1986; Minagawa and Akazawa, 1992).

c A skeleton from this sample was dated to ~2350 BP using AMS 14C methods with correction for the marine reservoir effect (Tanaka et al., 2005).

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First, it is predicted that the introduction of wet rice economies will be associated with a reduction in systemic stress in western Japan. Frequencies of teeth and individuals with LEH defects will significantly decline among prehistoric Yayoi compared to western Jomon communities. This decline will be associated with the introduction of a predictable, renewable resource base and exploitation of more nutritionally adequate dietary alternatives. Second, the hypothesis that a similar prevalence of teeth and individuals with LEH defects will be observed between Yayoi agriculturalists and Jomon foragers from eastern Japan is also tested. This prediction expects similar stress patterns between these two groups because both cultures practiced intensive subsistence strategies focused on high yield, reliable food sources, and consumed more nutritious fallback foods. Finally, the hypothesis that CO frequencies remained static following the transition to agriculture in prehistoric Japan is tested. This study predicts stasis in CO prevalence between Jomon and Yayoi period samples as each group thrived in contexts associated with elevated CO prevalence, specifically sedentary agricultural and maritime environments. Jomon samples from eastern and western Japan are combined to test this third hypothesis because similar rates of CO are observed between the two groups (Suzuki, 1998).

**BIOCULTURAL CONTEXT**

**Jomon**

Jomon period (13,000–2300 BP in eastern Japan) cultures were part of a 10,000 year foraging tradition in the Japanese Islands (Imamura, 1996a). Jomon foragers were the descendents of Pleistocene nomads who migrated to Japan around 20,000 BP and subsumed pre-existing “knife-blade” cultures (Kobayashi, 2005). These later groups were associated with a “microblade” technology that first appeared in Hokkaido, likely in relation to the expansion of cultural networks from eastern Siberia (Imamura, 1996a; Kobayashi, 2005). Microblade Paleoindic industries diversified from Hokkaido into Tohoku around 14,000 BP, evolved into Mikoshiba tradition, and formed the basis for the earliest spread of Jomon culture (Imamura, 1996a).

One set of hypotheses surrounding the earliest migrations to the Japanese Islands suggest that the ancestors of Jomon people migrated from Sundaland (Turner, 1990; Hanihara, 1991). These hypotheses are based on a dental morphological complex (i.e. Sundadonty) observed in Jomon people and shared with the early inhabitants of Sundaland (Turner, 1990, 1992; Matsumura and Hudson, 2005; and others). Multivariate analyses of cranial and dental measurements also find similarities between the Paleoindic foragers of Japan, Jomon people, and individuals from Sundaland (Hanihara, 1991; Baba et al., 1998; Hanihara and Ishida, 2005).

Other multivariate analyses of cranial and dental traits suggest a Northeast Asian “point of origin” for the Pleistocene ancestors of Jomon foragers (Doi et al., 1997; Dodo et al., 1998; Pietrusewsky, 2005; Seguchi et al., 2007; Hanihara and Ishida, 2009; and others). Cold-derived body size among Jomon foragers and the Pleistocene occupants of the Japanese Islands suggest that this region was initially populated by foragers from a colder environment such as Northeast/Central Asia (Temple et al., 2008). Analysis of classic loci and Y-chromosomes derived from the Ainu suggest a Northeast/Central Asian “point of origin” for the ancestors of Jomon people dating to −20,000 BP (Omoto and Saitou, 1997; Hammer et al., 2006). More recently, ancient DNA analysis of Jomon period skeletal remains from Hokkaido indicate that the Pleistocene ancestors of Jomon people migrated to the Japanese Islands from Northeast Asia (Adachi et al., 2009).

There is some disagreement regarding the use of the term “forager” to categorize the subsistence economies of Jomon people (Imamura, 2006; Underhill and Habu, 2006). It is, however, important to point out that the term “forager” does not describe a static subsistence framework. In fact, many “foraging” societies domesticate considerable numbers of plant species and are characterized by variation in mobility and social complexity (Binford, 1981; Harris, 1989; Smith, 2000). In this sense, Jomon people are encompassed within the foraging subsistence spectrum (Ikawa-Smith, 1986; Tsude, 2001; Matsui and Kanehara, 2006; Underhill and Habu, 2006).

Broad consumption of cariogenic cultigens is reported during the Jomon period, despite variation in resource availability (Turner, 1979; Fujita, 1995; Todaka et al., 2003; Temple, 2007a). Dietary changes among prehistoric Jomon people are related to the ubiquitous exploitation of a cariogenic food source such as taro or yams and resulted in elevated caries prevalence among Late/Final compared to Middle Jomon people (Fujita, 1995; Temple, 2007a) with exceptions reported on Hokkaido Island (Oxenham and Matsumura, 2008). Increased consumption of these products did not precipitate agricultural economies per se, as the types of energy expenditure, social organization, and caries frequencies are observed following climatic oscillations around 4300 BP indicating a shift in diet across eastern and western Japan (Fujita, 1995; Temple, 2007a). Dietary changes among prehistoric Jomon people are related to the ubiquitous exploitation of a cariogenic food source such as taro or yams and resulted in elevated caries prevalence among Late/Final compared to Middle Jomon people (Fujita, 1995; Temple, 2007a) with exceptions reported on Hokkaido Island (Oxenham and Matsumura, 2008).

Increased consumption of these products did not precipitate agricultural economies per se, as the types of energy expenditure, social organization, and caries frequencies are observed following climatic oscillations around 4300 BP indicating a shift in diet across eastern and western Japan (Fujita, 1995; Temple, 2007a). Dietary changes among prehistoric Jomon people are related to the ubiquitous exploitation of a cariogenic food source such as taro or yams and resulted in elevated caries prevalence among Late/Final compared to Middle Jomon people (Fujita, 1995; Temple, 2007a) with exceptions reported on Hokkaido Island (Oxenham and Matsumura, 2008).

**Yayoi**

Yayoi period (2500–1700 BP) were the first wet rice dependent communities in the Japanese Islands (Imamura, 1996a, b). Cranial and dental size and shape varied between Jomon and Yayoi people in association with environment and gene flow (Brace and Nagai, 1982; Mizoguchi, 1986; Hanihara, 1991; Turner, 1992; Nakahashi, 1993; Pietrusewsky, 2006). Yayoi period agriculturalists were the descendents of people from modern-day Korea or northern China who migrated to Japan and interbred to varying degrees with indigenous Jomon foragers around 2500 BP (Brace and Nagai, 1982; Hanihara, 1991; Nakahashi, 1993; Omoto and Saitou, 1997; Hammer et al., 2006; Pietrusewsky, 2006). Migrants from continental Asia during the Yayoi period introduced wet rice agriculture to the Japanese Islands (Imamura, 1996a,b; Hudson, 1999; Tsude, 2001).

The earliest dates for migrant arrival correspond with the earliest dates for wet rice production in Northern Kyushu and Southern Honshu Island, specifically those obtained from the Dojagahama, Itatzuke, and Notame sites (Imamura, 1996b). Tool types and irrigation systems that closely resemble those found at farming sites from southern China and Korea also suggest that wet-rice agriculture was brought to Japan by migrant people (Tsude, 2001). For example, the paddy field excavated at the Itatzuke site is remarkably similar to wet rice fields found in southern China and North Korea between 4000 and 3000 BP (Tsude, 2001).
Significant energy expended on the care of domesticated plants is recorded during the Yayoi period in the form of large-scale agricultural ecosystems based around wet rice farming (Imamura, 1996b; Hudson, 1999; Tsude, 2001). Precipitous increases in carious tooth frequencies follow this economic shift and bear further testament to the importance of carbohydrate-heavy crops during the Yayoi cultural horizon (Sanui, 1960; Inoue et al., 1986; Oyamada et al., 1996; Todaka et al., 2003; Temple and Larsen, 2007). This increase in caries prevalence is associated with the consumption of a starch-heavy carbohydrate, variation in food preparation techniques (i.e., boiling and processing rice), and increased malocclusion among Yayoi compared to Jomon people (Temple and Larsen, 2007). General variation in cranial morphology between historic Japanese compared to Yayoi people suggest in situ behaviorally-related changes in morphology after the arrival of these migrants to the Japanese Islands (Mizoguchi, 1986).

**MATERIALS**

All bioarchaeological data (LEH, CO) were collected by the author (DHT). Human skeletal remains recovered from eight Jomon period sites (Fig. 1; Table 1) represent the foraging component of this study. These sites are dated from the Middle (5000–4000 BP), Late (4000–3300 BP), and Final (3300–2500 BP) Jomon period and include remains from the eastern and western regions of Honshu island. Human skeletal materials recovered from four Yayoi period archaeological sites represent the agricultural component of this study (Fig. 1; Table 1). These sites yielded the largest numbers of skeletal remains for all early agricultural sites in the Japanese Archipelago. Wet rice dependence among these groups is supported by archaeological and isotopic studies (Imamura, 1996a,b; Chisholm and Koike, 1999). All sites were dated using pottery chronology and/or radiocarbon methods. The use of pottery chronology is an accurate method to estimate site occupations in prehistoric Japan because these methods have achieved significant precision over many years of description and comparison to absolute dating methods (Aikens, 1995; Imamura, 1996a; Habu, 2004; Tanaka et al., 2005).

This study compares Yayoi assemblages recovered from western Japan to Jomon assemblages recovered from eastern Japan. Eastern Yayoi skeletal collections are fragmentary and small in sample size due to highly acidic soil. Those in western Japan were preserved in sand-dunes, while those from eastern locations were interred in soil (Imamura, 1996a). Soil in Japan has a low pH level and is responsible for fragmentation and disintegration of skeletal materials interred outside of shell mounds or sand dunes (Imamura, 1996a).

Comparing these two groups could be problematic as these comparisons may not measure a “direct” biological impact of wet rice agriculture in eastern Japan. These comparisons are, however, important because Yayoi samples from western Japan represent the earliest wet rice farmers in the Japanese archipelago. In this sense, comparisons between eastern Jomon communities with the earliest wet rice farmers from western Japan will enhance knowledge of the more immediate differences/impacts in stress associated with this transition.

**METHODS**

**Age estimation**

CO prevalence was compared between age groups. Age was estimated on the basis of long bone epiphyseal fusion (Scheuer and Black, 2000) tooth development/eruption stages (Smith, 1991), and tooth wear scores obtained from premolar and molar teeth (Scott, 1979). Samples were then divided into two age groups based on these estimations. Age Group 1 includes individuals younger than 15 years, while Age Group 2 includes individuals aged 15 years and older.

**LEH defects**

LEH defects were recorded as deficiencies in enamel thickness appearing as horizontal grooves or pits on mandibular and maxillary anterior, permanent one of these teeth for both adults and subadults with at least one tooth. LEH defect presence was determined by macroscopic observation aided by the use of a magnifying glass (10×), natural fluorescent lighting, and a 100-W Toshiba desk lamp. Identification of LEH defects follow Skinner et al. (1995) and Guatelli-Steinberg (2003), where adjacent perikymata were compared to possible LEH defects to prevent confusing normal variation in tooth morphology with disrupted enamel production. The minimum limit for LEH defect identification was set at the point where horizontal grooves appeared larger than adjacent perikymata under 10× magnification. The maximum limit includes LEH defects that were clearly visible as furrows of enamel deficiency in the absence of magnification. Methods for documenting intraobserver error in LEH defect recognition are reported in Temple (2007a,b). These methods determined a level of “substantial agreement” between two rounds of observation.
It is important to note that LEH defects are most objectively identified by increased perikymata spacing using microscopic measurements (Hillson and Bond, 1997). Since this study relies on macroscopic identification, the prevalence of LEH defects reported here represents a minimum estimate. LEH prevalence is first reported using individual and overall frequencies. These frequencies were calculated using the following methods: Number of anterior, permanent teeth with at least one LEH defect divided by the total number of observed anterior, permanent teeth (overall prevalence); number of individuals with at least one observable LEH defect on an anterior, permanent tooth divided by number of individuals with at least one anterior, permanent tooth (individual prevalence).

LEH defects arising from disrupted physiological homeostasis following severe traumatic injuries may bias interpretations by mimicking hypoplastic lesions normally attributable to stress (Hillson, 1996). LEH defects associated with traumatic injuries are rare in archaeological contexts (Goodman and Rose, 1991). Nevertheless, LEH defects associated with systemic stress are possible to differentiate from those arising as a consequence of physical trauma by chronological matching: LEH defects associated with systemic stress are observable at similar chronological positions on tooth antimeres, whereas trauma-induced LEH defects are generally observed on isolated teeth (Hillson, 1996). Antimere refers to side-specific identical structures in bilaterally symmetric organisms (e.g., right and left mandibular canines). In an attempt to offset the potential for including trauma-induced LEH defects in the study, LEH defect prevalence on maxillary first incisor (MxFI) and mandibular canine (MaC) tooth antimeres were calculated. MxFI and MaC teeth were selected in association with previous observations that suggest these teeth are most susceptible to LEH defect formation (Goodman and Armelagos, 1985). Numbers of mandibular canine (MaC) and maxillary first incisor (MxFI) antimeres with at least one observable LEH defect on both teeth divided by the total number of observed MaC and MxFI antimeres, respectively were used to calculate the prevalence of antimeres affected by LEH defects.

**Cribra orbitalia**

CO lesions were identified using a 10× magnifying lens under florescent lighting and a 100-W desk lamp. CO was identified as sieve-like lesions on the orbital roof. The presence of marrow hyperplasia through the orbital cortex and/or remodeling on the borders of sieve-like lesions helped differentiate this condition from post-mortem damage. CO was scored following methods reported by Steckel et al. (2002) and described by Temple (2007b). Prevalence of this condition was compared as the total number of individuals with at least one orbital roof with evidence of CO divided by the total number of individuals with at least one orbital roof.

**Statistical methods**

The G-statistic with continuity correction is a more conservative version of the chi-square test in assessing the independence of nominal data (Sokal and Rohlf, 1995). The G-statistic with continuity correction compares the goodness-of-fit between observed and expected cell frequencies and corrects for greater than expected Type I errors (Sokal and Rohlf, 1995). The G-statistic is applied to data where the observed minus expected cell frequencies are greater than the expected cell frequencies or studies that rely on limited sample sizes—small samples confute the numerator in the chi-square calculation and produce unusually large degrees of difference between data sets (Sokal and Rohlf, 1995). G-tests for independence are employed by previous studies using similar sources of data (Temple, 2007a; Temple and Larsen, 2007).

**RESULTS**

**LEH defects**

Overall prevalence of teeth with at least one observable LEH defect is significantly greater among eastern Jomon foragers compared to Yayoi agriculturists (Table 2). G-values for the overall prevalence of anterior, permanent teeth with at least one LEH defect are elevated for the western Jomon and Yayoi comparison in relation to a ~26% difference in teeth affected by LEH defects. Differences in the frequencies of anterior, permanent teeth affected by LEH defects between eastern Jomon and Yayoi samples are less extensive at ~6%.

Eastern Jomon foragers have significantly fewer individuals with at least one anterior, permanent tooth affected by at least one LEH defect compared to Yayoi agriculturists (G = 7.91; P ≤ 0.05) (Table 3). No significant differences in individuals with at least one anterior, permanent tooth affected by at least one LEH defect are observed between the western Jomon and Yayoi samples (G = 0.077).

No significant differences are observed in MxFI antimeres affected by LEH defects between the eastern Jomon and Yayoi samples (G = 3.2), while significantly greater frequencies of MxFI antimeres affected by LEH defects are observed among western Jomon compared to Yayoi groups (G = 5.5; P ≤ 0.05) (Table 4). No significant difference in MaC antimeres affected by LEH defects are observed between the eastern Jomon and Yayoi samples (G = 0.644). Significantly greater frequencies of MaC antimeres are affected by LEH defects among western Jomon compared to Yayoi people (G = 7.8; P ≤ 0.05).

### Table 2. Overall prevalence of anterior, permanent teeth with LEH defects

<table>
<thead>
<tr>
<th>Group</th>
<th>N Teeth</th>
<th>% LEH</th>
<th>(Y): P ≤*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yayoi (Y)</td>
<td>965</td>
<td>30.3</td>
<td>0.05</td>
</tr>
<tr>
<td>Eastern Jomon (EJ)</td>
<td>559</td>
<td>36.8</td>
<td>0.001</td>
</tr>
<tr>
<td>Western Jomon (WJ)</td>
<td>495</td>
<td>56.7</td>
<td></td>
</tr>
</tbody>
</table>

* Probability values for Yayoi compared to eastern and western Jomon.

### Table 3. Percentages of individuals with at least one anterior, permanent tooth expressing an LEH defect

<table>
<thead>
<tr>
<th>Group</th>
<th>N individuals*</th>
<th>% LEH</th>
<th>(Y): P ≤</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yayoi (Y)</td>
<td>182</td>
<td>63.1</td>
<td>0.05</td>
</tr>
<tr>
<td>Eastern Jomon (EJ)</td>
<td>164</td>
<td>48.2</td>
<td>0.05</td>
</tr>
<tr>
<td>Western Jomon (WJ)</td>
<td>122</td>
<td>64.8</td>
<td>NS b</td>
</tr>
</tbody>
</table>

* Number of individuals with at least one anterior, permanent tooth.

b Does not reflect a statistically significant result compared to Yayoi samples.
Several significant differences in the prevalence of teeth affected by LEH defects between Yayoi and western Jomon people support the first hypothesis of this study. Few differences in teeth affected by LEH defects between Yayoi and eastern Jomon people confirm the second hypothesis.

**DISCUSSION**

**LEH defect prevalence**

Several significant differences in the prevalence of teeth affected by LEH defects were observed between western Jomon and Yayoi samples. Assuming a decline in stress between the western Jomon and Yayoi samples, these results may be related to variation in resource availability and nutritional quality. LEH defects reflect inadequate intake of proteins, vitamins, and iron (Wolbach and Howe, 1933; Mellanby, 1939; Schour et al., 1944). Poor intake of these nutrients is associated with atrophy of the enamel organ (Wolbach and Howe, 1933; Schour et al., 1944) and damage to the Tomes' process (enamel producing organ) of ameloblasts (Witzel et al., 2006). The enamel organ is a condensation of cells that differentiate into ameloblasts (Ten Cate, 1998). Nutritional deprivation causes enamel organ atrophy through vasoconstriction (Mellanby, 1939; Schour et al., 1944). Poor organizational capacity for the differentiation of ameloblasts and odontoblasts from the enamel organ combined with LEH defect formation follows (Mellanby, 1939; Schour et al., 1944). Tomes’ process damage impairs the capacity for the ameloblast to produce enamel (Witzel et al., 2006) and also results in the production of LEH defects.

Similar findings are reported among children in developing countries. Prevalence of children in Guatemala with teeth affected by LEH defects and overall frequencies of teeth affected by LEH defects were increased among groups that lacked adequate nutritional supplementation (i.e., protein and vitamin fortifications) (Goodman et al., 1991; May et al., 1993). These findings suggest that poor consumption of essential nutrients is associated with the formation and greater prevalence of LEH defects.

**Cribrar orbitalia**

Comparisons of CO prevalence are reported for Age Groups 1 and 2 in Table 5. CO prevalence is not significantly different between the Middle to Final Jomon and Yayoi agriculturalists from Age Group 1 ($G = 0.013$) or 2 ($G = 0.014$). These results are consistent with the third hypothesis of this study that predicted similar frequencies of CO would be observed between Jomon and Yayoi period people.

**TABLE 4. Percentage of antimeric tooth pairs expressing LEH defects on both teeth**

<table>
<thead>
<tr>
<th>Group</th>
<th>N MxFl antimeres</th>
<th>%LEH</th>
<th>(Y:) $P \leq$</th>
<th>N MaC antimeres</th>
<th>% LEH</th>
<th>(Y:) $P \leq$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yayoi (Y)</td>
<td>77</td>
<td>35.1</td>
<td>--</td>
<td>76</td>
<td>34.2</td>
<td>--</td>
</tr>
<tr>
<td>Eastern Jomon (EJ)</td>
<td>47</td>
<td>21.2</td>
<td>NS</td>
<td>23</td>
<td>56.5</td>
<td>NS \textsuperscript{a}</td>
</tr>
<tr>
<td>Western Jomon (WJ)</td>
<td>28</td>
<td>60.7</td>
<td>0.05</td>
<td>39</td>
<td>61.5</td>
<td>0.01</td>
</tr>
</tbody>
</table>

\textsuperscript{a} Number of maxillary first incisor antimeres.
\textsuperscript{b} Percentage of antimeres expressing LEH defects.
\textsuperscript{c} Number of mandibular canine antimeres.
\textsuperscript{d} Does not reflect a statistically significant result compared to Yayoi samples.

**TABLE 5. CO prevalence by age group and time period**

<table>
<thead>
<tr>
<th>Age group 1$^{b}$</th>
<th>N individuals</th>
<th>% Cribra</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jomon</td>
<td>24</td>
<td>50.0</td>
</tr>
<tr>
<td>Yayoi</td>
<td>33</td>
<td>50.1</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Age group 2$^{b}$</th>
<th>N individuals</th>
<th>% Cribra</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jomon</td>
<td>209</td>
<td>8.6</td>
</tr>
<tr>
<td>Yayoi</td>
<td>111</td>
<td>8.8</td>
</tr>
</tbody>
</table>

\textsuperscript{a} Age Group 1 includes individuals less than 15 years.
\textsuperscript{b} Age Group 2 includes individuals aged 15 years and greater.

Teeth and individuals with LEH defects are also observed in great prevalence from a variety of contexts with presumably elevated levels of malnutrition, and especially, regions with resource limitations such as famine-era China and the Protohistoric American Southwest (Zhou and Corruccini, 1998; Stoddler et al., 2002). Hunter-gatherer people from Southwest Asia have elevated LEH defect frequencies for teeth and individuals in association with seasonal food scarcity (Lukacs and Pal, 1993). These findings suggest that nutritionally inadequate food and seasonal scarcity were responsible for the elevated prevalence of LEH defects among western Jomon compared to Yayoi people.

It is also possible that increased population density during the Late/Final Jomon period may have added pressure on resource availability in western Japan. Population density declined in eastern and central Japan during the Late to Final Jomon period; western Japan did, however, experience significant increases in population density during this same time period (Koyama, 1978). This population expansion appears to be part of a broader response to climatic cooling, where migrations into northern and western Japan combined with dietary change are noted, rather than increased reproductive output within a stressed community (Hudson, 1999; Habu, 2004; Temple, 2007a).

Age compositions of deer hunted by Jomon people changed to include large quantities of younger animals during the Late/Final Jomon period suggesting that increased population density was associated with overuse of environmental resources (Koike and Ohtaishi, 1985; Koike, 1992). Similar trends are observed in gastropod exploitation patterns, where range of shell heights expanded to include smaller organisms during the Late/Final Jomon period (Koike, 1986). Finfish consumed by western Jomon people were subjected to seasonal depletion (Kobayashi, 2005), while fallback foods were nutritionally poor (Akazawa, 1986). This suggests that increased population density during the Late/Final Jomon period in western Japan may have encroached on the carrying capacity of an already limited environment and exacerbated nutritional status.
In contrast, Yayoi people were reliant on a predictable and renewable source of food in the form of wet rice economies (Imamura, 1996a,b) and consumed nutrient rich fallback foods (Chisholm and Koike, 1999; Takahashi, 2009). The earliest form of wet rice produced in prehistoric Japan was resistant to cold weather and able to survive drastic seasonal shifts in temperature (Tsude, 2001). In addition, the form of paddy-field agriculture imported to the Japanese Islands was at an advanced stage, having evolved in Northeast Asia over 5,000 years before arriving in this region (Tsude, 2001). Yayoi people also supplemented this diet with maritime resources (Chisholm and Koike, 1999; Takahashi, 2009) and even cultivated various species of freshwater fish (Nakajima et al., 2009). It is, therefore, likely that the lower prevalence of teeth with LEH defects among Yayoi people is attributable to resource stability and nutritional quality. Similarity in systemic stress prevalence between the Yayoi and eastern Jomon people is associated with exploitation of consistently available subsistence bases and wide dietary breadths. Hypotheses by Yesner (1994) predict that resource abundance and dietary breadth are associated with systemic stress patterns among prehistoric foragers and incipient agriculturalists. For example, patterns of LEH defects in Southeast Asia indicate continuity between foragers and agriculturalists in association with continued broad-spectrum subsistence economies following the transition to wet rice agriculture (Pietrusewsky and Douglas, 2002a,b; Douglas and Pietrusewsky, 2007). Eastern Jomon people relied on a wide dietary breadth with consistently available, calorically dense resources (Akazawa, 1999). Yayoi people continued this trend, incorporating maritime and terrestrial game into agricultural economies (Terasawa and Terasawa, 1981; Chisholm and Koike, 1999; Nakajima et al., 2009). To be certain, Jomon people from eastern Japan and the Yayoi groups relied on different foods and resource procurement/production systems. Both groups were, however, active participants in economies characterized by intensive subsistence behavior and the exploitation of calorically dense resources.

Cribra orbitalia and parasite infection

Similar frequencies of lesions associated with CO are observed between Jomon and Yayoi samples in both age groups. Prevalence of CO was originally thought to form a straightforward relationship with diet, specifically iron status (El-Najjar et al., 1976). These relationships were later questioned on the basis of various parasites found in the coprolites of prehistoric North Americans (Reinhard, 1990). Cranial porosity also reached significant levels among maritime foragers from the California coast (Walker, 1986) and densely populated desert agriculturists (Walker, 1985) further indicating that dietary factors are only loosely associated with CO. These lesions are, in populous maritime and agricultural environments, associated with iron deficiency anemia stemming from parasitic infection, prolonged weaning due to poor resource availability, and diarrhea caused by the use of contaminated water supplies (Walker, 1985, 1986, 2006).

A recent survey does, however, suggest that iron deficiency anemia alone will not produce the hypertrophic marrow expansion observed in cases of CO and that these lesions are more likely attributable to other nutritional deficiencies or infectious conditions of the eye orbit (Walker et al., 2009). Primary diseases contributing to the development of CO include scurvy, rickets, megaloblastic anemia (MA), and trachoma (Schultz, 2001; Wapler et al., 2004; Walker et al., 2009). It is difficult to differentiate these conditions without histological (Schultz, 2001) or radiographic (Ortner, 2003) sections. It is, however, possible to “infer” specific conditions associated with CO based on environmental context and lesion distribution (Larsen and Sering, 2000).

Rickets is a pathological condition associated with a lack of vitamin D intake (Ortner, 2003). Humans cannot independently synthesize vitamin D and must obtain this nutrient from environmental surroundings. Vitamin D is available in a variety of foods, but in most cases, humans directly synthesize adequate amounts of this nutrient from sun exposure (Ortner, 2003). Under circumstances where sun exposure is negligible, for instance among indigenous foragers of Siberia and Northern North America, consumption of marine products provide an adequate source of vitamin D (Jablonski and Chaplin, 2000). The climate of Japan is temperate (Honshu Island and regions south) and continental microthermal (Hokkaido) (Fukui, 1977). These regions experience adequate sunlight for vitamin D synthesis in the context of industrially and urban environments (Lips, 2007). This suggests rickets arising from dietary/clinical factors was an unlikely contributor to the observed patterning of CO lesions. Rickets is, however, observed in cases of parasite infection (Walker et al., 2009), and therefore, cannot be effectively ruled out as a contributor to these lesions.

Scurvy is another diagnostic option for these lesions. Scurvy is a pathological condition attributed to insufficient levels of vitamin C (Auferheide and Rodriguez-Martín, 1998). Considerable levels of vitamin C are found in citrus fruits, vegetables, and shellfish (Rivers, 1987). Significant consumption of shellfish as well as a wide variety of vegetables is reported among Jomon people (Koike, 1986; Crawford, 1992, 2006; Matsui and Kanehara, 2006). Some level of caution is, however, necessary in ruling out scurvy as a diagnostic option. Surprisingly elevated frequencies of scurvy were observed in early historic Florida—a region with abundant access to citrus fruits (Ortner et al., 2001). Underlying infection by parasites and infant diarrheal disease may also significantly deplete vitamin C and result in scurvy (Walker et al., 2009). As a consequence, scurvy cannot be effectively rejected as a diagnostic option for the observed lesions.

The marrow hyperplasia of CO is also attributable to megaloblastic anemia (MA) (Walker et al., 2009). MA is associated with inhibited DNA production in red blood cells and produced by poor levels of vitamin B-12 or folic acid (Antony, 1995). This condition is rare in adults, but children lacking significant stores of vitamin B-12 are particularly susceptible to the disease as are individuals exposed to parasitic infection (Walker et al., 2009). This suggests that MA also contributed to the patterning of CO observed by this study.

It is important that parasites specific to prehistoric Japan be considered as contributing factors to cranial porosity induced by MA, rickets, or scurvy. These conditions include but are not limited to schistosomiasis, trichuriasis, roundworm (Ascaris), and Diphyllobothrium infections. In Asia, schistosomiasis is a disease associated with infection by the cercariae of Schistosoma japonica that survive on snails living in brackish water, depart this vector during daylight hours, penetrate
human skin, and disseminate to various organ systems (Mascie-Taylor and Mohamed, 1995). Eggs of Schistosoma japonica are re-released into surrounding environments by urination, mature into cercariae, reattach to snails, and perpetuate new rounds of infection. Environmentally, Schistosoma japonica infections increase in concert with the square acreage of wet rice fields in rural China suggesting a link between paddy field agriculture and schistosomiasis (Yi-Xin and Manderson, 2005). Schistosomiasis inducing parasites are also spread through contact with or consumption of unsanitary environments by urination, mature into cercariae, reattach to snails, and perpetuate new rounds of infection. Environments by urination, mature into cercariae, reattach to snails, and perpetuate new rounds of infection. Environments by urination, mature into cercariae, reattach to snails, and perpetuate new rounds of infection. Environments by urination, mature into cercariae, reattach to snails, and perpetuate new rounds of infection. Environments by urination, mature into cercariae, reattach to snails, and perpetuate new rounds of infection.

Trichuriasis is a pathological state caused by the consumption of eggs laid by Trichuris trichiura or Trichocephalus trichiuri in dry areas, specifically those found associated with stored rice and other grains (Stephenson et al., 2000). The disease is also related to accidental ingestion of soil contaminated by the eggs of Trichuris (Stephenson et al., 2000). These eggs hatch in the small intestine, with larvae and mature worms moving into various regions of the digestive system (Crompton and Nesheim, 2002). Subsequent spread through contact with stool is reported (Stephenson et al., 2000; Crompton and Nesheim, 2002).

Roundworms are another potential contributor to nutritional depletion and CO distribution among the Jomon and Yayoi people. Parasitic roundworms include members of the genus Ascaris. Ascaris infection occurs when pigs consume the meat of infected rats and humans consume the meat of infected pork, especially in circumstances where meat is raw or undercooked (Aufferheide and Rodriguez-Martín, 1998). Immature larvae are deposited into the small intestine with later migration into the large intestine by mature parasites. Mature parasites then reproduce in the large intestine, depositing larvae into the intestinal mucosa.

Finally, infection by the Diphyllobothrium genus of marine parasite is reported in a variety of coastal contexts (Reinhard, 1990; Bathurst, 2005a,b). In Japan, Diphyllobothrium latum and nihonkaiense infect hosts following consumption of raw or undercooked fish, with mature organisms migrating to the small intestine (Scholtz et al., 2009).

Parasite loads are particularly heavy among maritime foragers, where contact with contaminated, stagnant water and consumption of undercooked fish provide vectors for infection and reinfection (Reinhard, 1990; Bathurst, 2005a,b; Walker, 2006). Jomon people occupied coastal, populous environments and procured maritime resources on the open water (Koyama, 1978; Imamura, 1996a). Fishing behavior, maritime resource consumption, and exposure to contaminated water supplies likely acted as a primary source of Diphyllobothrium and Schistosoma infection. Jomon people also consumed pig meat (Hongo et al., 2006), and as a consequence, were likely exposed to Ascaris parasites. In addition, Jomon people stored foods including various acorns and walnuts in underground storage units (Imamura, 1996a). Food storage may have placed Jomon people at risk for infection by Trichuris. In fact, whipworms (Trichuris) were observed in coprolites from the Jomon period Sannai Maruyama site (Matsui et al., 2003). The totality of these findings indicate that CO patterning among Jomon people reflect nutrient deficiencies brought about by parasite infection, with specific reference to Trichuris species.

Yayoi people stored wet rice as dry grain (Imamura, 1996a,b), continued to rely on maritime resources, and consumed pigs (Aikens and Akazawa, 1992; Chisholm and Koike, 1999). These behaviors likely exposed Yayoi people to Ascaris, Diphyllobothrium, Schistosoma, and Trichuris infection. It is also possible that infection by parasites such as Schistosoma japonica were transmitted through contact with stagnant water in wet rice fields. More specifically, however, whipworms (Trichuris) and roundworms (Ascaris) were found in coprolites recovered from the Ikegami-Sone Yayoi site (Matsui et al., 2003). This suggests that the patterning of CO observed among Yayoi people was associated with parasite infection, particularly Trichuris and Ascaris species. It is also important to consider trachoma as a possible contributor to these lesions (Walker et al., 2004; Walker et al., 2009). Trachoma is an infectious disease of the eye caused by direct contact with the bacteria Chlamydia trachomatis (Wright et al., 2008). Elevated frequencies of trachoma are reported in dense populations lacking access to sanitary bathing and drinking facilities as well as those where young people lack access to clean water for proper facial cleansing and sleep near infected individuals (Wright et al., 2008).

Access to sanitary bathing and drinking facilities were a major environmental hazard for prehistoric coastal communities, particularly those with dense populations (Walker, 2006). Both Jomon and Yayoi people occupied regions of high population density (Koyama, 1978). Poor sanitation among these groups is indicated by reports of fecal material within water sources around settlements (Matsui et al., 2003). In this sense, both Jomon and Yayoi people occupied environments where trachoma was a likely environmental hazard and an additional contributor to the CO lesions observed by this study.

**Stress and the agricultural transition**

The results presented here differ from previous research addressing patterns of systemic stress during the agricultural transition (i.e., Cohen and Armelagos, 1984; Larsen, 1987, 1995, 1997, 2002, 2006; Cohen and Crane-Kramer, 2007), but are consistent with reports from Southeast Asia (Oxenham, 2000; Domett, 2001; Pietrusewsky and Douglas, 2002a,b; Domett and Tayles, 2007; Douglas and Pietrusewsky, 2007). A general decline/continuity in systemic stress is noted with regard to prevalence of teeth with LEH defects, while CO frequencies remained static. Two major reasons for these systemic stress patterns are important to note. Wet rice agriculture arrived in Japan as a fully functioning subsistence strategy and was supplemented by a sophisticated system of maritime exploitation. The development of agricultural ecosystems implies a fairly long-term process of human/environmental interaction with early systems subjected to failure due to climatic or other environmental fluctuation (Harris, 1989, 1996). The earliest wet rice fields in Japan best resemble those from China and have significantly more complex features than the earliest paddy sites such as Caoxieshan (6000 BP) (Imamura, 1996a;b; Tsude, 2001). In fact, Yayoi paddy fields post-date the earliest development of wet rice paddies in China by ~3,000 years (Takahashi, 2009) and exemplify modified versions of these earlier sites (Imamura, 1996b; Tsude, 2001). It is, in this sense, likely that Yayoi period agriculturalists did not experience stressors associated with poor control over environmental resources. Instead, these early agricultural people enjoyed the benefit of a well developed subsistence system. It should be noted.
that systemic stress experienced as a consequence of introducing this behavioral strategy into new landscapes may have been experienced, though stress prevalence among Yayoi people still did not exceed levels reported for eastern or western Jomon people.

In addition, Yayoi period agriculturalists continued to exploit maritime products following the agricultural transition. Maritime resources provide an excellent source of nutrition, particularly when mixed with cereal products (Layrisse et al., 1968; Larsen, 2003; Murphy and Allen, 2003; Rivera et al., 2003). Prehistoric foragers reliant on terrestrial mammals experienced an increase in the frequency of teeth affected by LEH defects after the transition to intensive plant-based agriculture, in part due to dietary stress (Cook, 1980, 1981, 1984; Lukacs, 1992; Larsen et al., 2002; Hutchinson et al., 2007).

In contrast to dietary shifts experienced during the agricultural transition in the New and Old World, there is ample evidence suggesting continued reliance on the procurement of maritime resources among Yayoi people. Similarities in fishing tool kits are noted between Jomon people from eastern Japan and a number of Yayoi period sites (Aikens and Akazawa, 1992; Imamura, 1996a; Takahashi, 2009). Stable isotopic analysis of human remains indicates that Yayoi people consumed greater amounts of maritime products than early agricultural people from North America (Chisholm and Koike, 1999). Additionally, previously mentioned studies report evidence that Yayoi people actually cultivated some species of fresh-water fish (Nakajima et al., 2009).

CONCLUSIONS

Jomon foragers from western Japan had significantly greater frequencies of teeth with LEH defects than Yayoi agriculturalists. Reduction in the prevalence of teeth with LEH defects following the agricultural transition is likely related to the introduction of a predictable, renewable subsistence base into western Japan combined with a system of exploiting more nutritious fallback foods. More specifically, Jomon foragers from western Japan were reliant on calorically dense finfish, but consumed nutritionally poor fallback foods. The introduction of wet rice agriculture provided this region with an economic system of exploiting more nutritious fallback foods. The introduction of wet rice agriculture provided this region with an economic system of exploiting more nutritious fallback foods. The introduction of wet rice agriculture provided this region with an economic system of exploiting more nutritious fallback foods. The introduction of wet rice agriculture provided this region with an economic system of exploiting more nutritious fallback foods.

Similar frequencies of teeth with LEH defects were observed between Jomon foragers from eastern Japan and Yayoi agriculturalists. The similar prevalence of systemic stress observed between these two groups is attributable to the fact that eastern Jomon and Yayoi people both had significant control over environmental resources and relied on nutritionally rich fallback foods that included terrestrial mammals and marine resources.

Finally, CO prevalence between the two groups remained stable. Both Jomon and Yayoi people were exposed to environments that were hospitable to organisms such as *Schistosoma japonica*, *Trichuris*, *Diphyllobothrium*, and roundworms (*Ascaris*). *Trichuris* and *Ascaris* parasites were, in fact, observed in Jomon and Yayoi coprolites. In addition, both groups occupied environments where exposure to bacteria such as *Chlamydia trachomatis* was likely significant. This suggests parasite induced malnutrition and bacterial infection was responsible for the observed pattern of CO among Jomon and Yayoi people.

These results depart from general models of Post-Pleistocene human evolution that suggest increases in systemic stress followed the agricultural transition. Two primary reasons for the trend in Japan are reported. First, wet rice agriculture was based on a well developed system of paddy farming that evolved over 3,000 years before arriving in the Japanese Islands. Second, Yayoi people continued to rely on maritime products as a dietary source. In contrast, early agricultural people from other regions of the globe relied upon newly developed subsistence systems and nutritionally inadequate cultivars. It is also important to note that Jomon and Yayoi people represent distinct biological groups with unique migratory histories (see references above). Variation in systemic stress between these groups may also represent differences in genetic capacity to buffer against environmental perturbations (see: Hoover and Matsumura, 2008). Research addressing finite aspects of stress including chronology, duration, and periodicity may further resolve this issue (see: Temple, 2008).

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