The role of occlusal stress and gingival infection in the formation of exostoses on mandible and maxilla from Neolithic China

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Summary

Exostoses on the mandible and maxilla is a frequently observed bone growth of controversial aetiology. The aim of this study is to analyse environmental factors that may stimulate the formation of exostoses on different regions of the maxilla and mandible. Sixty-six well-preserved crania from Neolithic China were studied for the presence of buccal exostoses on the maxilla (BE) and lingual exostoses on the mandible (LME). Other oral health indicators, such as occlusal wear on molars, pathology of temporomandibular joint (TMJ), carious lesions, calculus accretion, periodontal disease, and antemortem tooth loss were recorded. Buccal maxillary exostosis was unusually common on the Neolithic skulls from China, which thus resemble the *Sinantropus* crania described by Weidenreich (1943).

We report a significant Spearman correlation between BE and LME (rho = 0.54, P < 0.00001), suggesting a partially shared aetiology of these two types of exostoses. The highest correlations between either form of exostoses and any oral indicator of stress were found for pathology at TMJ (rho = 0.46, P < 0.0001 for both types of exostoses). Smaller but significant correlations were observed between LME and the age adjusted wear rate on lower molars, as well as between BE and indicators of oral/dental pathology, e.g. caries, calculus, periodontoses, and antemortem tooth loss. Both types of exostoses tended to increase in frequency with age, although a significant trend was observed only for BE. We conclude that formation of exostoses is a complex process that can be invoked by any agent causing damage and inflammation of gingival tissue. However, severe occlusal stress, which is often manifested in TMJ disorder, is the main environmental factor leading to exostosis development in genetically predisposed individuals.

Резюме

Костные разростания вдоль альвеолярного отростка верхней и нижней челюсти, экзостозы, именуемые также *torus mandibularis*, *torus maxillaris* и *torus palatinus*, имеют противоречевую этиологию и определяются как генетическими так и средовыми факторами. В представленной работе мы проанализировали различные средовые факторы, влияюшие на формирование экзостоза. Шестьдесят шесть взрослых черепов хорошей сохранности из Неолитического Китая были проанализированы на предмет присутствия разных типов экзостоза, а также индикаторов жевательного стресса, кариеса, периодонтоза, патологий темпоромандибулярного сочленения и потерей зубов. Неолитические черепа Китая характеризуются очень высокой частотой экзостозов на

мандибуле и максилле, чем напоминают черепа Синантропа, описанные Weidenreich (1943).

Значительная непараметрическая корреляция была показана для разных типов эгзостоза на мандибуле и максилле (rho=0.54, P<0.00001), что указывает на общую этиологию экзостозов на челюстном аппарате. Значительная корреляция между экзостозом и другими индикаторами была показана для остеоартрита в темпоромандибулярном суставе (rho=0.46, P<0.0001 для обоих типов эгзостоза). Более слабая, но значимая корреляция была найдена для экзостоза и степени стирания зубов, калькулюса и периодонтоза. Частота обоих типов экзостоза увеличивалась с возрастом, однако, статистически значимая корреляция с возрастом была достигнута только максиллярным экзостозом. Таким образом, мы считаем, что экзостоз на максилле и мандибуле имеет множественную этиологию. Его формирование может быть индуцировано любым агентом повреждающим соединительную ткань на альвеолярном отростке. В Неолитическом Китае таким повреждающим агентом наиболее часто был жевательный стресс.

Introduction

Localised cortical bone growth on the mandible and maxilla is known as exostosis or hyperostoses. It is usually found along the alveoli or on the hard palate and, depending on its location and extent, it can be classified as *torus mandibularis*, *torus palatinus*, buccal maxillar exostosis, or lingual maxillar exostosis. Among the different types of exostoses on jaws the palatal one is more common than other types. Mandibular exostosis is often 10–30% less frequent than the palatal one in the same population, while buccal and lingual maxillary exostoses are very rarely observed. When found on alveoli, exostosis occurs most frequently and tends to be thickest next to molars, extending anteriorly sometimes as far as P2 and, in rare cases, to the canine and incisors (Hrdlička 1940; Tadakuma & Ogasawa 1969).

Variable in expression, exostoses can be manifested as smooth and continuous ridges or consist of single or multiple more or less discrete nodules (Borghgraef 1973; Sellevold 1980). Given the diversity of the exostosis expression numerous metric and non-metric systems for scoring the morphology of exostoses have been developed and used (e. g. Woo 1950; Suzuki & Sakai 1960; Tadakuma & Ogasawa 1969; Martin 1973; Sellevold 1980; Kronenberger 1979, 1981; Sawyer et al 1979). Based on the exostosis thickness, precise location, nodule counts, or amount of bone involved in the trait's formation, these systems differ even in whether the trait should be scored as present or not. Despite the apparent complications this diversity of techniques presents for interpopulation comparisons, it is clear that the frequency, surface morphology, and extension of exostoses is patterned among populations (Roeder 1953; Sellevold 1980) and persists in families (Suzuki & Sakai 1960; Gould 1964; Gorsky et al 1998) suggesting the genetic nature of the trait. Thus, the trait has been frequently used as racial marker and latter for the studies of population dynamics (Carabelli 1844; Körner 1910; Weidenreich 1936; Oschinsky 1964).

A number of studies have examined a quasi-continuous multifactorial/threshold model of exostosis expression. According to this model, environmental stress must reach a certain threshold level before a genetically predisposed individual develops the trait (Eggen 1989; Hauser & De Stefano 1989; Haugen 1992; Seah 1995). The broad sense heritability for *torus mandibularis* has been estimated as a rather low, 30% (Eggen 1989). A full penetrance dominant mode of inheritance has been found for *tori palatinus* and *mandibularis* in some families (Gould 1964; Gorsky et al 1998). Differences in exostosis frequency and morphology among ethnic groups also support a strong genetic basis for the trait (Reichart et al 1988; King & King 1981), although variation among groups in diet and food preparation habits could also explain these differences. Asian populations often show higher frequencies of exostoses and presumably carry exostosis alleles in a greater frequency (Nery et al 1977).

Environmental factors affecting the expression of exostoses are not well understood, although masticatory hyperfunction has been proposed as the primary factor in exostoses formation (Hooton 1918; Hrdlička 1940; Weinmann & Sicher 1947; Ossenberg 1981). Clinical research supporting this hypothesis demonstrated significant co-occurrence of exostosis and para-functional oral activity, such as clenching and grinding as well as pathological alterations at the temporomandibular joint (TMJ) (Sirirungrojying & Kerdpon 1999; Kerdpon & Sirirungrojying 1999). The co-occurrence of exostosis with abnormal shapes of jaws and loss of posterior teeth suggested that exostosis might have performed a buttressing function reinforcing the alveolar process against excessive biting force (Hylander 1997; Listgarten & Tridger 1963; Salerno et al 1999). Compensatory response to periodontal disease has been proposed to explain some cases of exostoses (Glickman & Smulow 1965). The development of exostoses in response to chemical irritation has been also discussed (van den Broek 1941). As chemical irritation of periodontal tissues is likely to cause the periodontosis, the latter explanation is similar to the one suggested by Glickman and Smulow (1965). Lastly, an inadequate and nutritionally deficient diet is another possible inductor of exostoses (Schreiner 1935).

In bioarchaeological studies, an increase in prevalence of palatal exostoses has been reported with the transition from agriculture/animal husbandry to a more rough, wild game diet that also produced a higher rate of occlusal wear. In a study of Medieval Norse (Halffman et al 1992; Scott et al 1991), maxillary and palatal exostoses were reported to co-vary with heavy occlusal wear and enamel chipping on anterior teeth. In another skeletal series, the reduction of exostosis frequency from Vlasac I to Vlasac III in the Yugoslavian Mesolithic suggested a slight decrease in biomechanical stress over time (y'Edynak 1978).

Whether exostoses on different regions of the masticatory apparatus are related or independent features is another controversial issue. If occlusal stress is the main contributing environmental factor in formation of any jaw exostoses, high correlations among its different forms are expected. Yet, a near zero correlation for *torus palatinus* and *torus mandibularis* was found in several populations, e.g. contemporary Norwegians (Haugen 1992), Cubans (Balaez et al 1983), and the population of the United States (Kolas et al 1953). Lack of palatal tori in an Aleut population with a high incidence of mandibular tori (35%) implied an independent formation of exostoses on the jaws (Moorrees 1957). However, significant concordances of

the various forms of exostoses have been seen in other populations (Eggen & Natvig 1994; Jainkittivong & Langlais 2000).

In order to further investigate the role of environmental factors in a threshold model of exostosis formation we examined the correlation pattern among the different types of exostosis and indicators of oral health and occlusal stress. The masticatory stress indicators that we analysed include osteoarthritis at the temporomandibular joint and occlusal wear scores adjusted to age. Oral health was evaluated based on the incidence of periodontal disease, calculus accretion, carious lesions, and antemortem tooth loss.

Materials and methods

Sixty-six well-preserved skeletons from the Chinese Neolithic culture of Yangshao, Shaanxi province were examined for the presence of exostoses. The materials were provided to us by the Banpo Museum at Xi'an. These materials come from three Late Neolithic archaeological sites: Banpo Xi'an, Weinan Beilu, Lintong Jiangzhai, and Weinan Shijia. Radiocarbon dates from the three sites span the interval from 4 890 to 6 390 BP using a corrected half-life of 5 730 (The Institute of Archaeology, CASS 1991).

The exostosis formations were scored at two locations of the jaws. Buccal and labial aspects were recorded for buccal exostoses (BE) on the maxilla, and lingual mandibular exostoses (LME) on the lingual aspect of the mandible. Here we prefer the term exostosis to *torus mandibularis* since the later should refer only to continuous and well-developed bony ridges. With dry bone even minimal bone growth can be scored and the process of exostosis development can be more accurately traced than with living patients. In the living, a thick layer of soft tissue would disguise minor bone growth, so that it is very difficult to determine exostoses that forms less than a complete torus. Here we modified the scoring system discussed by Woo that was originally developed for *torus palatinus* to adequately reflect the expression of buccal maxillary and lingual mandibular exostoses in our sample. Following Woo (1950), we classified the exostosis formations as mild, moderate or severe based on degree of their expression. A mild score was assigned to any minor bone growth in the form of intermittent ridges or nodules along the alveolar process (figure 1a). A moderate score was given to thick and well-defined bone nodules forming continuous ridges at least 2 cm in length (figure 1b). A severe score was given to BE of more than 0.5 cm in thickness and to LME more than 1 cm in thickness, but only where they formed a true torus (figure 1c).

For the purpose of sex determination all skeletons were first seriated by robustisity and then pelvic morphology was used to define the boundary between sexes. The multifactorial approach proposed by Lovejoy et al (1985) was used for age estimation. All individuals were ranked by their morphology of *os pubis*, auricular surface, and ectocranial and endocranial suture closure. We used the first principal component scores of these ranks as the best composite indicator of age.

Degenerative changes at temporomandibular joint were scored on the mandibular condyle and on the temporal articulatory surface following the method outlined by Richards & Brown (1981) as absent; mild, or minimal erosion, localized to
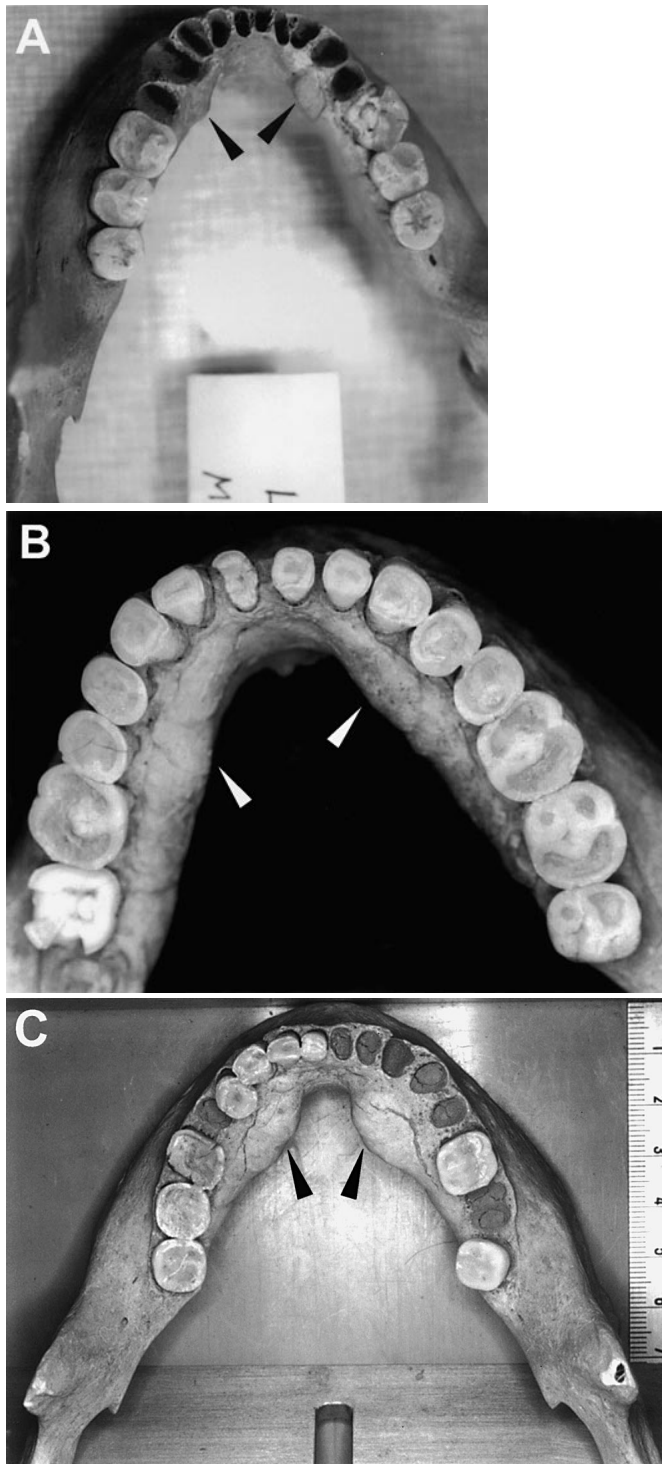
Fig. 1: Different degrees of exostoses expression on the mandibles from Neolithic China (marked by arrows): A – mild; B – moderate; C – severe.

either the anterior or posterior surface of the mandibular condyle or temporal surface, or mild lipping of mandibular condyles; moderate, presenting extended erosion that affects more than one surface of the TMJ or substantial oseteophytosis of the mandibular condyle occuring over most of the border; and severe, massive deterioration of the joint extending to the temporal arch and affecting most of the temporal articulatory surface and mandibular condyle.

An occlusal wear score was obtained independently for each of the four quadrants of the first and second molars on mandible and maxilla following the method proposed by Scott (1979). A total wear score was obtained as the sum of scores on the four quadrants. Whenever both left and right molars were present, the scores were averaged. Next, age was removed by regression on the principle components composite age scores. The obtained residuals are linearly independent of age and express the amount of wear as if each specimen were of the average age. These scores are instantaneous wear intensity scores. Anterior wear was not measured in this study due to the lack of material, since most of the skulls lost substantial numbers of anterior teeth post-depositionally.

Indicators of oral health scored by visual observation included carious lesions, antemortem tooth loss, calculus accretion and periodontal disease. The lesion had to completely penetrate the enamel as judged by a probe or bright light in order to be scored as carious. Teeth were scored as lost antemortemly if the dental socket was considerably remodelled. Calculus was scored following Brothwell (1981) as absent; mild, covering less than one-third of the crown; moderate, covering from one-third to two-thirds of the crown; and severe, covering more than two-thirds of the crown. Periodontal disease was noted as present when a substantial reduction in alveolar height was observed. Analysis of variance and covariance by the general linear model was used to compare average scores for the major analytical factors.

Spearman rank order correlation coefficients were used to assess the significance of the co-occurrence of BE and LME with indicators of wear and oral pathology. The metric variant of multidimensional scaling was selected to assess the pattern of the Spearman correlations, which are equivalent to Pearson correlation coefficients in value. Standardised stress values, representing the difference between the estimated and the observed values of trait, were computed to assess goodness of fit (Schiffman et al 1981: 367–369). Multidimensional scaling was accomplished with the SPSS version 5.0 statistical package for Windows.

Results

Buccal maxillary and lingual mandibular exostoses in the Chinese Neolithic

The Chinese Neolithic sample expressed high frequencies of both types of exostoses. Buccal exostosis was observed in 31 of 66 (48%) of the maxilla. Among those affected, 22 cases were mild, eight were moderate, and one was severe. Morphologically, BE in the Chinese sample did not vary a great deal. In most individuals, BE was expressed as a continuous torus of bone along molars and premolars, reaching its maximum thickness in the alveolar area below the first or second molar. Buccal exostoses were always accompanied by short vertical ridges in the subnasal region of the alveolar process of the maxilla that often extended below alveolar margin (figure 2).

Fig. 2: Buccal exostoses on the maxillae from Neolithic China (marked by arrows). Note intermittent ridges on the anterior part of alveoli.

Lingual mandibular exostosis was present in 13 of 66 specimens, or 19.7% of individuals, with six mild, six moderate and one severe case. With a different morphology than that of BE, LME reached its maximal thickness in the area of third and fourth premolars and rarely extended beyond the first molar. Concordance between BE and LME was observed in 12 of 31 exostosis-positive skulls, while 19 cases were discordant. In the absence of a functional relationship between BE and LME, one would expect only 6.1 out of 31 cases concordant. Thus, the observed concordance exceeded the one expected by chance by a factor of two. The Spearman rank order correlation of BE and LME was, as would be expected, significant (rho = 0.54, t(N-2) = 5.11, P < 0.00001).

Sex and age factors in exostosis formation and masticatory stress

Both BE and LME showed an increase in frequency with age. The presence of BE increased from 31.3% among adult individuals below 30 years, to 53.3% in 30 to 50 year olds, and to 57.9% in individuals over 50. The frequency of LME also increased with age, from 13.3% in the 20–29 year range, to 20.0% in the 30–49 age group, to 26.3% in those older than 50 years. However, positive correlations with age attained a 0.05 level of significance only for BE and not for LME (table 1). The frequencies between sexes for either type of exostosis were not significantly different, even though both BE and LME were more prevalent among males, with male/female ratios of 1.2:1 for BE and 2.3:1 for LME.

Table 1: Buccal maxillar and lingual mandibular exostoses: Spearman correlations with age, sex, and indicators of oral health and masticatory activity.

| Trait	Buccal Maxillar Exostoses		Lingual Mandibular Exostoses	
	Spearman rho	t(N-2)	Spearman rho	t(N-2)
Age	0.30 (63)	2.41*	0.17 (63)	1.39
TMD	0.46 (61)	3.96***	0.46 (63)	4.09***
Antemortem molar loss	0.25 (66)	2.00*	0.05 (66)	0.41
Calculus	0.34 (36)	2.09*	0.24 (37)	1.48
Calculus severity	0.37 (36)	2.31*	0.05 (37)	0.33
Caries	0.39 (36)	2.47*	0.31 (36)	1.91
Periodontal d	0.34 (66)	2.83**	0.22 (66)	1.81
Wear M1	0.01 (47)	0.07	0.13 (47)	0.85
Wear M2	0.06 (43)	0.39	0.27 (43)	1.81
Wear M1	0.06 (35)	0.37	0.21 (37)	1.26
Wear M2	0.32 (32)	0.12	0.19 (34)	1.07
Wear rate M1	–0.25 (47)	–1.79	0.02 (47)	0.12
Wear rate M2	–0.00 (43)	–0.05	0.21(43)	1.40
Wear rate M1	–0.11 (36)	–0.66	0.44 (37)	2.89**
Wear rate M2	0.08 (34)	0.46	0.38 (34)	2.36*
Total wear rate	0.02 (34)	0.12	0.46 (34)	2.90**

*p < 0.05; **p < 0.01; ***p < 0.001
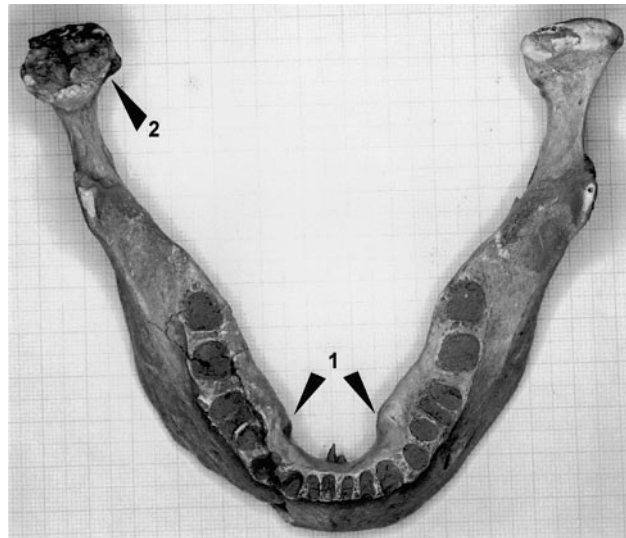
Fig. 3: An example of lingual mandibular exostoses (1) co-occurring with unilateral osteo-arthritis (2) on mandibular condyle.

Correlations of BE and LME with total unadjusted wear scores did not reach the 0.05 level of significance for either of the molars (table 1). When wear scores were adjusted for age to estimate the intensity of occlusal wear, a significant positive correlation was found between LME and the instantaneous wear rate on the lower first and second molars. Total intensity of wear, an index calculated as the sum of age-adjusted wear scores across the first and second molars on both mandible and

maxilla, also showed a significant correlation with LME. Individuals with LME exhibited an average intensity of wear that was 2.6 standard deviations higher than that for individuals without LME.

Both BE and LME showed high correlations with disorders of the TMJ; all correlations were significant (P < 0.001; see table 1 and figure 3). Among 21 skulls exhibiting osteoarthritis at TMJ, 76.9% were also noted for BE and 42.9% for LME. Skulls with no bone evidence of TMJ pathology had BE with a frequency of 35.0% and LME with a frequency of 9.5%. Thus, the likelihood of having exostoses in the presence on TMJ pathology was 2.2 times higher for the maxilla and 4.5 times higher for the mandible. Skulls exhibiting osteoarthritis at TMJ also showed a greater concordance of the two exostosis types: 56.3% of BE and LME were concordant in the presence of TMJ pathology, while only 21.4% were found concordant for skulls with non-pathological TMJ. Loss of posterior teeth, which could have moved the chewing stress from molars to the anterior dentition, had a significant correlation with BE, but not with LME (table 1).

Exostosis and infection indicators

Frequencies of oral health indicators characterise the sample as one with low caries and high calculus rates, when judged by percent of teeth affected. Only 19% of all individuals and 2.1% of individual teeth had carious lesions, while teeth with calculus accretion were found in 76% of the crania and 26.3% of all teeth. Calculus accretions were predominantly mild, so that average severity of observed calculus was 1.2. Periodontal disease was found in only 14% of the crania.

Buccal exostoses showed a significant correlation with caries and calculus occurrence, calculus severity, and a particularly strong association with periodontal disease (table 1). Correlations between these indicators and LME did not attain significance. So, while eight out of nine cases of periodontal disease were noted for BE, only four also exhibited LME. Among seven individuals with caries, four had BE and only one, LME. Out of 28 individuals with calculus, 17 were concordant with BE and only four with LME, a slight association that was still higher than would be expected by chance.

Multidimensional scaling: pattern of correlation among oral pathology/masticatory stress indicators

The bivariate pattern of variation of oral indicators is complex, with environmental factors, such as occlusal stress, diet, and gingival infection presumably affecting a number of indicators simultaneously, but in varying degrees. Therefore, a multidimensional scaling was computed to help understand the multivariate pattern of correlation. We used the metric model due to the limited number of variables (13). The multidimensional scaling was computed from a Spearman correlation matrix, and produced stress values that converged for three dimensions after 63 iterations, yielding a final standardised Kruskal stress of 0.046 for a three-dimensional model, indicating an acceptable fit (Kruskal & Wish 1978: 56).

The final configuration is shown on figure 4. The first and second dimensions cluster traits into three subsets: (1) exostoses formations (BE and LME) are associated
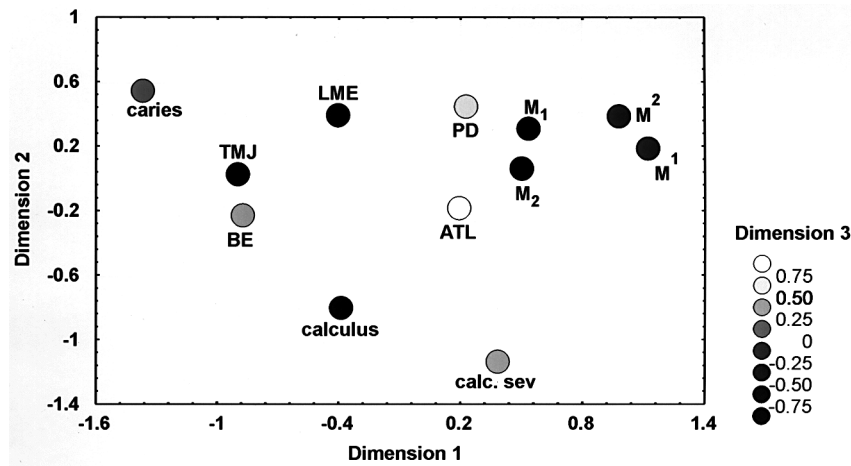
Fig. 4: The results of multidimensional scaling analysis of masticatory stress and oral health indicators. The third dimension is shown as shades of grey. Abbreviations: ATL – antemortem tooth loss, BE – buccal maxillar exostoses, caries – presence of carious lesions on a dental set, calculus – number of teeth with calculus deposits on a dental set, calc. sev. – average severity score of calculus deposits on a dental set, LME – lingual mandibular exostoses, M^1, M^2, M_1, and M_2 – intensity of wear on corresponding molars, PD – presence of periodontal disease, TMJ – severity score of osteoarthritis at temporomandibular joint.

with osteoarthritis on TMJ (upper left); (2) wear rates on molars cluster together with periodontal disease and antemortem tooth loss (upper right), and (3) calculus indicators are found at the bottom centre of the chart. The third dimension is shown on the figure by the intensity of grey, with light grey to white tones being more positive and dark grey shades more negative. This dimension outlines another pattern linking LME and TMJ osteoarthritis with the intensity of wear on molars, and BE with caries, calculus severity, periodontal disease, and antemortem tooth loss.

Discussion

The moderate but highly significant correlation of LME with BE and their strong association with TMJ pathology support the shared aetiology of these two types of exostoses. Co-occurrence of the different forms of exostoses has been previously reported in several studies (Topaz & Mullen 1977; Antoniades et al 1998; Eggen & Natvig 1994; Jainkittivong & Langlais 2000). Similar to our results, Jainkittivong & Langlais (2000) found high concordance of tori and exostoses. At the same time, non-significant correlations between palatal and mandibular exostoses were observed among Norwegians (Haugen 1992) and for an ethnically mixed population of North Americans (Kolas et al 1953). The lack of association reported in these studies could be the consequence of the low frequency of the traits themselves. Populations with higher frequencies of exostoses, particularly those from Northern and Eastern Asia, show higher concordance than those from Europe, as in the comparison of Thais with Germans (Reichart et al 1988). It could be that the

two forms of exostoses are inherited independently, but are influenced by similar environmental factors. In this case, if allele frequency for either form of exostosis were low, their higher segregation would lead to the discordance of the different forms of exostoses. Being drawn from Eastern Asia, where exostosis frequencies are usually high and genetic variation is low, it is not surprising that most of the exostosis variation in our sample can be explained by environmental factors. Alternatively, different vectors of biting force could stimulate exostosis formation on different regions of the jaws. Thus, forces causing frequent mandibular exostoses would not necessarily result in *torus palatinus,* a pattern observed in an Aleut population by Moorrees (1957), a population that would have experienced strong stress from chewing.

The high correlation between both types of exostosis and pathology at the TMJ and other oral health indicators cannot be accommodated by the hypothesis of a full penetrance mode of exostosis inheritance, and indicates a substantial role for environment in the expression of the trait in some populations. This finding, however, does not compromise the conclusions drawn from the family studies, that the trait is inherited with a single dominant allele (Gould 1964; Gorsky et al 1998). The contributing environment could be conserved within families over a few generations that were analysed in those studies. It is also possible that different alleles influencing susceptibility to exostosis may have different degrees of penetrance.

A weak correlation with age that reached a significant level only for BE and not LME indicates that most cases of buccal maxillary exostosis are induced by masticatory overload at an early age, although a few may develop later in life. Indeed, high frequencies of exostoses can be found in a very young age cohorts, for example, 36% of Icelandic children exhibited palatal tori by the age of six (Axelsson & Hedegård 1985).

The studies of other populations provided somewhat contradictory data on the relationship of exostosis with age. Gradual decline of the palatal and mandibular tori after the age of 30 was observed in the Habana population (Balaez et al 1983). Similarly, a reduction of exostoses was observed after the third decade of life among African Americans (Austin et al 1965; Schaumann et al 1970) and after the fourth decade of life in Norwegians (Eggen & Natvig 1994). A different pattern, one in which the incidence of exostoses increased throughout the entire lifespan, was found in a population of Canadian Eskimos (Mayhall & Mayhall 1971). In this sample exostosis varied from 28% in the 11–20 age cohort to 46% with the 21–30 age cohort, and to 89.5% in the 51–60 age cohort. As the samples for these studies were composed of contemporaries, recent dietary shifts and cultural changes in food preparation or stress could have contributed to the observed patterns. For instance, Mayhall and Mayhall (1971) noticed that indigenous individuals with a predominantly European diet exhibited exostoses less frequently than those on aboriginal diet. Still another pattern is exhibited by an increase of palatal exostoses with age in degree of expression but not frequency in medieval Norse of Greenland (Halffman et al 1992).

Despite the variety of age trends of exostoses that have been reported, one rule consistently applies: exostosis reduces with age in frequency and degree of expression in those populations where masticatory demand subsides after the third or fourth decade of life. The reduction in muscular force or high frequency of edentu-

Table 2: Frequencies of torus mandibularis in skeletal and living populations around the world. * studies of living populations.

Population	%	No. examined	Source
Yukagirs (Yakutia)	85.7	7	Zoubov 1973
Eskimo Greenland	84.7	215	Fürst & Hansen 1915
Icelanders (1100–1650)	81.1	55	Steffensen 1969
Eskimo Canada	77.8	79	Dodo & Ishida 1987
Eskimo Greenland	75.8	165	Jørgensen 1953
Aleuts	70.0	20	Zoubov 1973
Icelanders (1000–1563)	67.9	56	Steffensen 1969
Aleuts	66.7	75	Dodo & Ishida 1987
Icelanders (900–1100)	66.2	133	Steffensen 1969
Greenlandic Icelanders (1275–1350)	66.1	56	Fischer-Møller 1942
Eastern Aleuts	61.4	44	Moorees 1957
Coimbra (20th c)	54.9	195	Galera et al 1995
Nomads of TransBaikal	52.7	36	Zoubov 1973
Irishmen (Gallen Priory) 700–1600	50.5	99	Howells 1941
Sinantropus, China	50	6	Weidenreich 1941
Eskimo	47.1	51	Schreiner 1935
Koniags	46.1	89	Hrdlička 1940
Icelanders (1650–1840)	44.8	67	Steffensen 1969
Alaskan Eskimo	40.1	116	Dodo & Ishida 1987
Irishmen (Castleknock) 850–1050	40	133	McLoughlin 1950 in Axelsson & Hedegård 1981
Canadian Eskimo, Igloolik*	39.7	315	Mayhall & Mayhall 1971
Japanese*	39.7	1010	Sakai 1954
Canadian Eskimo, Hall Beach*	37.3	118	Mayhall & Mayhall 1971
Aleuts, Atka and Umnak Islands*	35.2	108	Moorees et al 1952
Lapps	32.5	308	Schreiner 1935
Mongolians	32.1	67	Dodo & Ishida 1987
Chinese, Shantung	31.6	380	Miyasita 1935
Japan	31.5	127	Dodo & Ishida 1987
Icelandic schoolchildren*	30.0	763	Axelsson & Hedegård 1981
Evenks	30.0	10	Zoubov 1973
Ainu	30.0	145	Dodo & Ishida 1987
Thai*	29.9	182	Kerdpon & Sirirungrojying 1999
Norwegians, Gudbransdalen*	27.5	829	Eggen & Natvig 1994
modern Amicans	27	328	Sonnier et al 1999
Bushmen	26.9	78	Drennan 1937
Japanese, Kyoto	26.6	244	Akabori 1939
Students Maryland USA	26	~200	Krahl 1949
Western Aleuts	25.7	35	Moorees 1957
Ancient Chinese	23	(?)	Rouas & Midy 1997
Chinese, Xinjiang	20	5	Djurić-Srejić & Nikolić 1996
Chinese Yangshao, 7000–5000 BP	19.7	66	Pechenkina & Benfer this study
Norwegians (Oslo), Middle Ages	17	100	Schreiner 1935
Norwegian	17	100	Schreiner 1935
Finns, Haiuoto*	14	400	Alvesalo & Kari 1972
North American Indians	13.6	2000	Hrdlička 1940
Norwegians, Loften*	12.7	1181	Eggen & Natvig 1994
African Americans	11.3	53	Hrdlička 1940
Alaskan Eskimo, Wainwright*	10.7	168	Mayhall et al 1970
Hottentot	10	10	Drennan 1937
Nubia	9.5	652	Nielsen 1970
Thai*	9.2	947	Reichart et al 1988

Table 2: Continued.

Population	%	No. examined	Source
Neolithic of TransBaikal	9.1	22	Zoubov 1973
Precolumbian Peruvians	8.5	1000	Sawyer et al 1979
Mediaeval Portugal	8.5	59	Cunha 1994
American Whites*	7.9	1953	Kolas et al 1953
African Americans*	7.9	956	Schaumann et al 1970
Norwegian*	7.32	100	Haugen 1992
American Whites	7.2	139	Corruccini 1974
American Blacks	6.6	182	Corruccini 1974
British Columbia	6.4	501	Cybulski 1975
American Whites	6.1	766	Hrdlička 1940
Germans*	5.2	1317	Reichart et al 1988
Franzhausen Bronze Age	5.1	205	Wiltschke-Schrotta 1988
Cubans, La Habana*	4.5	744	Balaez et al 1983
Pamirians	3.7	81	Zoubov 1973
Peruvian Precolumbian	3.5	455	Hrdlička 1940
Malaysian	3	1044	Yaacob et al 1983
Swedes (Halland and Scania) 1000–1700	2.7	963	Mellquist & Sandberg 1939 in Axelsson & Hedegård 1981
Indian	2	710	Yaacob et al 1983
Ancient Egypt	2	428	Rösing 1990
India*	1.4	1000	Shah et al 1992
South-Western France	1.2	80	Rouas & Midy 1997
Chinese*	1	600	Yaacob et al 1983
Brazilian Indian*	0.5	200	Bernaba 1977
Chileans*	0.05	1906	Witkop & Barros 1963
Australian Aborigines	0	100	Campbell 1925
Neolithic of Ukraine 6000–5000 BP	0	20	Zoubov 1973
6 South African tribes	0	287	Rightmire 1972
Chinese, 5000–2000 BP	0	24	Pechenkina et al 2002

* marks studies of living populations.

lous individuals in older age cohorts likely leads to remodelling of the exostosis with obliteration in some old individuals (Axelsson & Hedegård 1985). This hypothesis is supported by the greater frequencies of LME and palatal exostosis in dentulous skulls than on edentulous (Sonnier et al 1999). In populations with low frequencies of antemortem tooth loss, such as the Chinese Neolithic and Norse, masticatory demands are likely to remain constant or increase with age. Indeed, when any teeth are lost, the strain distribution during mastication becomes uneven and less efficient. Strain increases in the alveolar arch and around the rim of the nasal cavity as the chewing loading moves anteriorly (Arbel et al 2000). This also explains the frequent exostosis ridges underneath the nasal cavity observed in our sample (figure 2) where the majority of teeth lost were molars (Pechenkina et al 2002).

Patterns in which exostosis occurs significantly more frequently between one of the sexes are known (Roeder 1950; Balaez et al 1983; Reichart et al 1988) although a lack of significant differences have also been reported (Axelsson & Hedegård 1985; Muller & Mayhall 1971). These differences, where present, are probably established by the same environmental stresses being applied differen-

tially by sex. Between sexes variation of diet, oral pathology, robusticity, or extra-masticatory activities performed on daily basis could result in a differential distribution of exostoses by sex. In Eskimo populations, women exhibit exostoses more frequently than men because they often use teeth for hide preparation (Larsen 1997). In our samples the prevalence of exostoses on male crania covaries with a more frequent calculus accretion and probably represents more mastication of meat (Pechenkina et al 2002).

Moderate correlations of exostoses with TMJ disorder favour the hypothesis that a high and probably abnormal loading of the masticatory apparatus will lead to the development of exostoses. Osteoarthritis at the TMJ can be interpreted as a non-specific indicator of masticatory overloading. Anterior or incisor loads, rather than posterior chewing, are more likely to overload TMJ due to the greater leverage in the application of force. Severe and prolonged occlusal stress resulting in substantial wear tends to alter the plane of mastication, which can lead to abnormal loads at TMJ (Osborn 1982; Richards & Brown 1981). The latter interpretation of the aetiology of TMJ pathology is supported in our study by the multidimensional scaling analysis, where osteoarthritis at TMJ, LME and the rate of molar wear lie close together in the third dimension, indicating a pattern of covariation among the three.

Taken all together, the severe and abnormal occlusal stress, stress so strong that it can lead to pathological alterations at TMJ, is the leading contributor in exostosis formation. In addition, severe occlusal wear alters the masticatory plane and changes the distribution of strain and pressure forces along the alveolar bone. The redistribution of strain and pressure forces exerted by a molar on surrounding tissue has been experimentally shown to induce bone remodelling in rat maxillas (Waldo & Rothblatt 1954). The molecular mechanism relevant to the transmission of mechanical stress to the bone remodelling cell units in masticatory apparatus was tentatively outlined by Takano-Yamamoto et al (1994). In their experiments the expression of osteopontin, the protein mediating osteoclast attachment, has been detected during physiological tooth movement.

The role of root apex pressure applied on the periodontal ligament in formation of torus mandibularis has been proposed by Ossenberg (1981). Since the roots of upper molars are tilted lingually and the roots of lower molars are tilted buccally, they would exert pressure on the periodontal ligament in opposite directions. The micro-ruptures in the ligament are likely to result in periodontitis, an infection that could trigger exostosis formation. This would explain why exostoses on the maxilla form along the buccal surface, while exostoses on the mandible are to be found on the lingual surface of the bone.

While the role of occlusal overload in exostosis formation seems well established, BE, the more common feature in our sample, has additional factors affecting its expression. Buccal exostosis was significantly correlated with the indicators of dental and gum disease, such as caries, calculus, and periodontal disease, as well as with antemortem tooth loss. All these indicators can be either a cause or an outcome of chronic gingival infection, and their shared aetiology was supported by their pattern in the third dimension of the multidimensional scaling analysis. At the same time, with the exception of caries, they are not independent of occlusal stress. The variables of periodontal disease occurrence and antemortem tooth loss are

located near the intensity of tooth wear indicators on the first and second dimension of the multidimensional scaling (figure 4). Indeed, extreme wear intensities, may reduce crown mesio-dental lengths until they cause the loss of interproximal contact between adjacent teeth, permitting access of microbial infection to gingival tissue (Aufderheide et al 1998: 401). The traumatic effect of high masticatory stress can be the main contributor in antemortem tooth loss in populations with low rates of caries, as in the case of our population. Exostoses from periodontosis due to a prolonged gingival infection can be accepted as a minor contributing factor in the formation of exostoses on the buccal aspect of maxilla.

Both infection in gingival tissue and severe pressure applied to alveoli during mastication can invoke an inflammatory response in the fibrous tissue that is directly adjacent to the cortical bone. Subsequent mineralisation of the inflamed tissue would result in exostosis formation. Since a number of vitamin deficiencies, such as scurvy, lead to the damage of connective tissue and frequent haemorrhages, an inadequate diet can also cause exostosis formation, as was earlier suggested by Schreiner (1935). In other words, while environmental factors causing exostoses may vary, the immediate mechanism activating exostosis growth is probably the same: an inflammatory process in the fibrous tissue.

As both allele frequencies and environmental factors contributing to exostosis formation vary worldwide, the role of exostoses for epigenetic studies of population dynamics needs to be addressed. Table 2 summarises the frequencies of LME, or torus mandibularis, in human populations around the world. A substantial part of the trait's variation might be due to interobserver errors and different criteria for coding. Studies on living patients tend to produce smaller exostosis frequencies because of soft tissue masking the mild exostosis cases. However, despite the great variety of scoring techniques and the large chronological framework a definite geographic pattern emerges. In the circumpolar populations of Eskimo, Yukagirs, Icelanders, and Aleuts, LME is very common. Indigenous populations of South America and North America south of Canada have low frequencies of LME, as do the populations of America and Europe. Ancient Chinese populations had moderate frequencies of LME that resemble some modern Thai and Japanese samples. More recent Chinese samples have very low frequencies of mandibular exostosis (Yaacob et al 1983; Pechenkina et al 2002).

Unfortunately, there is only one systematic comparison among populations of BE (Hrdlička 1940). In his samples, many of which were drawn from Asian populations, the trait never exceeded a frequency of 5.2%. We observed a frequency of BE in the Chinese Neolithic of 48.0%, a figure much larger than that reported by Hrdlička. In this respect the sample reported here resembles the crania of Sinanthropus described by Weidenreich (1936; 1943) where buccal exostosis was observed on all three maxillae classified as *Sinanthropus pekinensis* (*Homo erectus*). Interestingly, the morphology of BE on Sinantropus maxillae was similar to the one observed in Neolithic China, where it often extends into the area of anterior teeth. This form of exostosis appears to be rare in cranial samples dated to latter times (Hrdlička 1940).

Lingual mandibular exostosis was also present in *Sinanthropus* as three out of six mandibles exhibited *torus mandibularis* (LME) (Weidenreich 1943). Some of the European presapiens crania also exhibit exostosis, e. g. Krapina 1 and Spy 1,

but in a lesser frequency than Sinanthropus (Nikitiuk 1966: 340–359). Various types of exostosis were also present on the jaws of four out of seven crania from ancient China dated between 3 800 and 2 000 BP (Djurić-Srejić & Nikolić 1996). Whether these similarities between *Sinanthropus* and crania from the Chinese Neolithic represent evidence of genetic continuity or an outcome of similar environmental demands on the masticatory apparatus, or both, is unclear. It is obvious that dietary similarity between Yangshao millet farmers (Pechenkina et al 2002) and early *Homo* could not be responsible for the high frequencies of BE in both groups, although intensity of mastication might. Agricultural products, mainly millet, constituted close to 75% of Yangshao diet (Pechenkina & Ambrose, unpublished data), an agricultural diet that is very different from the foraging diet expected for early Homo. However, the similarity of BE morphology between *Sinanthropus* and Neolithic skulls of Northern China, rather than the high frequency of exostosis itself, may result in part from genetic continuity in the region.

Conclusions

The immediate cause of exostosis formation is microdamage and inflammation in periodontal tissue in genetically susceptible individuals. Extreme and abnormal biting forces, resulting in the deterioration of the temporomandibular joint, is the most likely factor that could produce this effect. Any other stress that creates abnormal loads during mastication or introduces infection to gingival tissue is also capable of inducing exostoses. The threshold nature of exostosis development is suggested by its exhibiting significant correlations only with wear intensity scores that were corrected for age. Considering the strong environmental influence on the expression of maxillar and mandibular exostosis, its variation, if to be used for studies of population histories, should be interpreted with referral to masticatory loads, cranial robusticity, diet, and oral health of the analysed populations.

Acknowledgements

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