

Northern exposure: Mandibular torus in the Greenlandic Norse and the whole wide world

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Abstract

Objectives: In the first issue of the *American Journal of Physical Anthropology*, E.A. Hooton noted the expression of Eskimoid characteristics in the Icelandic skull, one of which was mandibular torus. Our goal is to evaluate this trait in another North Atlantic population, the Greenlandic Norse.

Materials and methods: An investigation of mandibular torus was carried out on all Greenlandic Norse skeletons disinterred up to 1986 ($n = 109$), along with comparative samples from Iceland ($n = 82$), Norway ($n = 98$), and Denmark ($n = 64$). Torus expression was scored on a six grade scale with absence and five degrees of trait presence.

Results: Greenlanders and Icelanders show extraordinarily high frequencies (65–97%) and pronounced expressions of mandibular torus. More surprising was the almost complete absence of this trait in a Danish Viking sample (9%) and a significantly lower frequency in medieval Norwegians (48%).

Discussion: The dramatic expression of mandibular torus in the Greenlandic Norse and their contrast to related Scandinavian populations in Europe stimulated the collection of data from the literature and the database of Christy G. Turner II for 49,970 individuals in 335 populations. When plotted on a global scale, mandibular torus shows a strong clinal distribution with the highest frequencies in northern latitudes and the lowest frequencies around the equator. Although mandibular torus has some hereditary component, as indicated by family studies, the trait has a strong environmental component of variance. How factors of a northern environment, including climatic stress and dietary behavior, influence torus expression remains enigmatic.

1 | INTRODUCTION

The Norse colonized Greenland from Iceland in A.D. 986. During their 500 year occupancy of the island, the Norse exhibited a number of temporal trends, including decreases in tooth, brain, and body size and an increase in third molar agenesis (Scott, Halfman, & Pedersen, 1992). Another trait that exhibits an interesting pattern of variation is mandibular torus, a bony growth on the lingual side of the mandible. Mandibular torus has long been known to be common among northern groups, especially Eskimos, Aleuts, and Lapps (Hrdlička, 1940; Moorrees, 1957; Oschinsky, 1964; Schreiner, 1935). None, however, exhibit this torus to such a degree as the Greenlanders (Scott, Halfman, & Pedersen, 1992; Sellevold, 1980).

Researchers have long debated the etiology of mandibular tori. The higher frequencies in Asians compared to Europeans (Jainkittivong & Langlais, 2000) led some to argue the trait is heritable (Carson, 2006; Sawyer, Allison, Elzay, & Rezzia, 1979). Even granted this pattern of variation, there is disagreement as to how genes contribute to the development of these bony exostoses. Early studies described the mode of inheritance as either autosomal dominant or autosomal recessive (Alvesalo & Kari, 1972; Johnson, Gorlin, & Anderson, 1965; Krahl, 1949; Suzuki & Sakai, 1960). Some studies suggest mandibular torus is inherited as a monoallelic trait with complete or partial penetrance, an explanation utilized when patterns of segregation are not consistent with simple Mendelian models (e.g., Gould, 1964). Moorrees, Osborne, and Wilde (1952) suggested three independent loci control tori

expression. In a recent study, researchers found 93.6% of monozygotic twins were concordant for mandibular torus expression. Dizygotic twins, by contrast, had a concordance rate of 79.4% (Auskalnis et al., 2015). The most parsimonious interpretation holds that mandibular torus is a threshold trait with a polygenic mode of inheritance. Despite disagreement on mode of inheritance, family and twin studies nonetheless indicate heredity plays some role in mandibular torus development.

Several environmental causes have been proposed to explain the presence and variation in mandibular torus. Eggen (1989) examined individuals with mandibular torus in two categories: those who brux and those who do not. From this comparison, he estimated that ~30% of mandibular torus expression is dictated by genes with the remaining 70% reflecting environmental factors (e.g., occlusal stress). Occlusal stress and parafunctional activity may be important components of the production of these exostoses (Hassett, 2006; Igarashi, 2016; Johnson, 1959; Kerdpon & Sirirungrojying, 1999; Pechenkina & Benfer, 2002). Mayhall (1970) and Eggen and Natvig (1991) suggest a coarse diet promotes the development of mandibular torus. Eggen (1993) also proposed that a marine diet with high levels of omega-3 fatty acids and vitamin D might promote excessive bone growth with a possible influence on unusually large mandibular and palatine tori. This idea was tested by Baumann, Lynnerup, and Scott (in press) who examined the relationship between torus expression and stable carbon and nitrogen isotope compositions in Greenlandic Inuit and Norse. For the most part, these authors found no significant association between stable isotopes and torus. The only statistically significant finding was an inverse relationship between mandibular torus expression and stable nitrogen isotope levels in the Inuit (but not the Norse).

Mandibular torus is uncommon in young individuals although relatively high frequencies have been reported for Lapp and Aleut children (Moorrees, Osborne, and Wilde, 1952). Haugen (1992) found a larger number of individuals with mandibular torus in the 35- to 65-year-age group. Jankittivong and Langlais (2000) identified a statistically significant prevalence that increases with age in a Thai sample. Topazian and Mullen (1977) suggest those with a predisposition for mandibular torus exhibit continuous growth of this exostosis throughout life. Other researchers have found it becoming more pronounced over the course of an individual's lifetime relative to specific climatic, dietary, and lifestyle factors (Axelsson & Hedegård, 1981; Eggen, 1989; Hrdlička, 1940; Ihunwo & Phukubye, 2006; Jankittivong & Langlais, 2000; Pechenkina & Benfer, 2002). This suggests that while mandibular torus is heritable, environmental factors such as masticatory stress influence the degree to which tori are expressed (Carson, 2006; Moorrees, Osborne, and Wilde, 1952).

There is disagreement among researchers regarding sex differences in mandibular torus. Some have found no sex differences in torus expression while others report higher frequencies in either males or females. No consistent pattern has emerged across dozens of studies and hundreds of samples. This contrasts with palatine torus, which shows a consistent bias in favor of females (Halffman, Scott, & Pedersen, 1992).

Our goal is to evaluate the geographic and temporal variation of mandibular torus among Norse populations in the North Atlantic, with

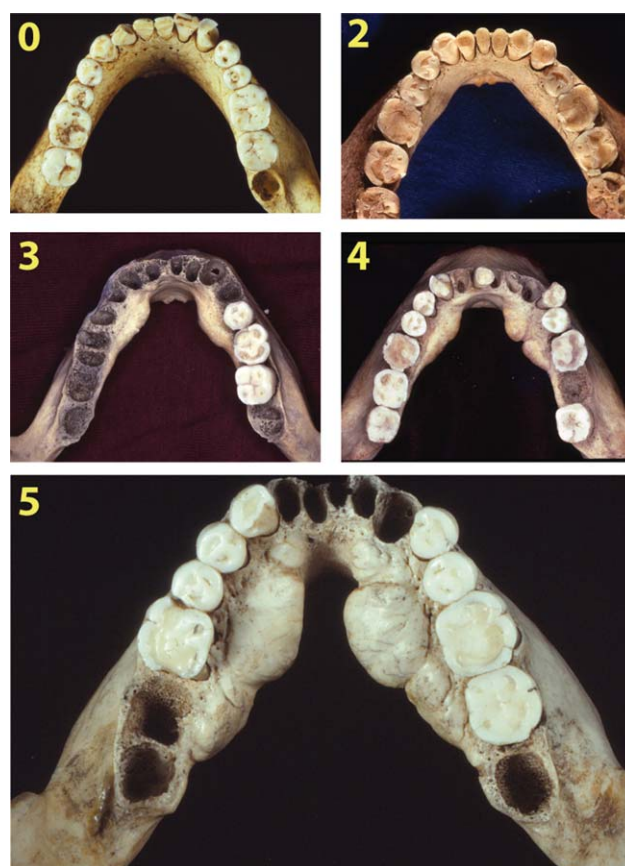


FIGURE 1 Six grade scale used to score mandibular torus expression in the Norse; grade 1 not shown as it is only evident through palpation

a focus on Greenlanders. Additionally, we want to determine how the pattern of torus variation among Europeans in this part of the world compares to populations in every environmental setting imaginable, from the Arctic to subarctic, temperate deciduous forests, grasslands, tropical rainforests, deserts, and Pacific islands. Excluding Antarctica, every continent is sampled.

2 | MATERIALS

All Greenlandic Norse skeletons excavated up to 1986 were examined in this study. The Eastern settlement sites of Herjolfsnes and Gardar along with the Western settlement sites of Sandnes and Anavik were excavated by P. Nørlund and A. Roussel between 1921 and 1932 (Nørlund, 1924, 1929; Roussel, 1936, 1941). The Benedictine Convent of the Eastern settlement was excavated by C.L. Vebæk from 1945 to 1948 (Vebæk, 1956). K. Krogh and J.B. Jørgensen excavated Thjodhild's Church during the 1960s (Krogh, 1967; Lynnerup, 1998).

Comparative data were collected from Icelandic, Norwegian, and Danish samples. The Icelandic sample, excavated in 1905 by V. Steffanson, dates around the 14th and 15th centuries and is comprised of remains excavated from Alftanes Island and Haffjordery (Hooton, 1918). C. Long excavated the Norwegian sample in the 1970s from the medieval church of St. Gregory's in Trondheim, Norway (Hanson,

TABLE 1 Expression of mandibular torus in Vikings, Norwegians, Icelanders, and Norse Greenlanders

Sample	Age Sex	Range	n	Grade of Expression						Total Frequency	χ^2 age	χ^2 sex	Mean trait score
				0	1	2	3	4	5				
Vikings	M	18-30	16	93.8	6.3	0.0	0.0	0.0	0.0	6.3			
	F		7	100.0	0.0	0.0	0.0	0.0	0.0	0.0	NA		
	M	30±	22	95.5	4.5	0.0	0.0	0.0	0.0	4.5		NA	
	F		19	78.9	15.8	5.3	0.0	0.0	0.0	21.1	NA		
	Total		64	90.6	7.8	1.6	0.0	0.0	0.0	9.4			0.109
Norwegians	M	18-30	15	73.3	13.3	13.3	0.0	0.0	0.0	26.7			
	F		16	43.8	31.3	25.0	0.0	0.0	0.0	56.2	0.036		
	M	30±	35	54.3	34.3	8.6	2.9	0.0	0.0	45.7		1.447	
	F		32	43.8	37.5	6.3	12.5	0.0	0.0	56.2	0.333		
	Total		98	52.0	31.6	11.2	5.0	0.0	0.0	47.8			0.694
Iceland	M	18-30	9	44.4	22.2	0.0	11.1	22.2	0.0	55.6			
	F		15	33.3	40.0	13.3	13.3	0.0	0.0	66.7	1.600		
	M	30±	15	26.7	13.3	26.7	6.7	26.7	0.0	73.3		2.105	
	F		43	25.6	39.5	20.9	14.0	0.0	0.0	74.4	0.333		
	Total		82	29.3	32.9	18.3	12.2	7.3	0.0	70.7			1.353
Greenland Eastern Early (EE)	M	18-30	2	0.0	50.0	50.0	0.0	0.0	0.0	100.0			
	F		5	0.0	40.0	40.0	20.0	0.0	0.0	100.0	NA		
	M	30±	20	5.0	40.0	25.0	15.0	15.0	0.0	95.0		1.210	
	F		7	0.0	14.3	0.0	28.6	28.6	28.6	100.0	NA		
	Total		34	2.9	35.3	23.5	17.6	14.7	5.9	97.0			2.235
Greenland Eastern Middle Late (EML)	M	18-30	1	0.0	0.0	100.0	0.0	0.0	0.0	100.0			
	F		10	40.0	40.0	10.0	10.0	0.0	0.0	60.0	NA		
	M	30±	10	0.0	20.0	40.0	30.0	10.0	0.0	100.0		7.410*	
	F		17	17.6	41.2	29.4	0.0	11.8	0.0	82.4	1.266		
	Total		38	18.4	34.2	28.9	10.5	7.9	0.0	81.5			1.553
Greenland Western Settlement (West)	M	18-30	2	0.0	100.0	0.0	0.0	0.0	0.0	100.0			
	F		10	30.0	50.0	10.0	0.0	10.0	0.0	70.0	NA		
	M	30±	6	33.3	0.0	16.7	33.3	0.0	16.7	66.7		1.009	
	F		19	42.1	21.1	15.8	10.5	10.5	0.0	57.9	0.862		
	Total		37	35.1	29.7	13.5	10.8	8.1	2.7	64.8			1.351

EE: Thjodhild's Church.

EML: Gardar, Herjolfnes, Benedictine Convent.

West: Sandnes, Anavik.

1986). This sample dates from the early 12th century to 1531. While the Norwegian and Icelandic samples are medieval in age, the Danish sample came from a variety of Viking age burials dating between A.D. 800 and 1000.

Although the dates of each burial location in Greenland are not precise, they can be placed in a broad temporal framework. Thjodhild's Church, dating to the early years of occupation (ca. A.D. 1000-1150), is referred to as the Early Eastern Settlement. Burials from the sites of Sandnes and Anavik make up the Western Settlement sample. Due to temporal complications and small sample sizes, Gardar, Herjolfnes, and the Benedictine Convent were combined to create a Middle Late Eastern Settlement sample that is roughly contemporaneous with the

Western settlement sample (ca. 13th-14th centuries). Radiocarbon dates on human bone corroborate these temporal assignments (Arneborg et al., 1999).

The above data were collected by the first author (GRS). However, to put the North Atlantic Norse into a broader world context, data were obtained from a wide variety of published sources. When geographic areas were underrepresented, we went through the original data sheets of Christy G. Turner II (CGT II) to fill in the blanks. This was particularly true for Southeast Asia, Australia and the Pacific, Mesoamerica, and South America. We report mandibular torus frequencies for 335 world populations. From the literature, data were obtained for 42,418 individuals from 202 samples; an additional 7,552 individuals

were tabulated from the CGT II database from 133 samples. The total number tabulated equals 49,970, with the North Atlantic samples bringing the total to over 50,000. Although there might be minor differences in how researchers score the lowest grades of mandibular torus, the large number of samples and individuals smooth out issues associated with interobserver error.

3 | METHODS

Mandibular torus is a bony growth expressed on the internal aspect of the mandible below the lower canine and extending back as far as the second molar. Trait expression varies among individuals who exhibit one continuous growth or have expression broken down into two or more distinct lobes. Determining the degree of torus expression does not lend itself to interval scale measurement as there are no consistent landmarks. However, the bony ridges and lumpy nodules that make up the torus vary considerably in size, both in terms of linear length along and projection away from the body of the mandible (Hasset, 2006). To accommodate this variation, a ranked scale was developed that includes grade 0 (absence) and grades 1 through 5 (increasingly pronounced degrees of expression). When a mandible lacks a torus altogether, this is determined through a combination of visual examination and palpation. When there are no visible signs of torus and no slight bony projection detectable by touch, the individual is scored as grade 0. A rank of 1 is assigned to a torus that cannot be visibly identified but is evident by palpation. Grades 2 and above are all visually observable and range from slight to pronounced protuberances (Figure 1).

4 | RESULTS

4.1 | Torus expression by age and sex

Table 1 shows the class frequency distributions for mandibular torus in the six Scandinavian samples broken down by two adult age categories and sex. Although age may be implicated in torus development, there is no significant difference between young adults and older adults in any sample. Torus was so rare in Vikings that a test of sex difference was not possible. For the remaining samples, four of five show no significant difference between males and females. There was a significant difference for the Eastern Middle Late sample but small sample sizes may be implicated in this finding. At least for the samples in this study, age and sex differences are minimal or nonexistent.

4.2 | Geographic variation

While the Scandinavian samples exhibit no patterned differences in age and sex, they show pronounced temporal and geographic variation. In the Viking age sample, mandibular torus is extremely rare. A few jaws exhibit palpable tori but only one shows a small grade 2 form. Over 90% of this sample fails to show any torus whatsoever and mean trait expression is 0.109. The closest sample to the Vikings is medieval Norwegians. For this group, about half (47.8%) of the sample exhibits some form of torus with palpable expressions the most common

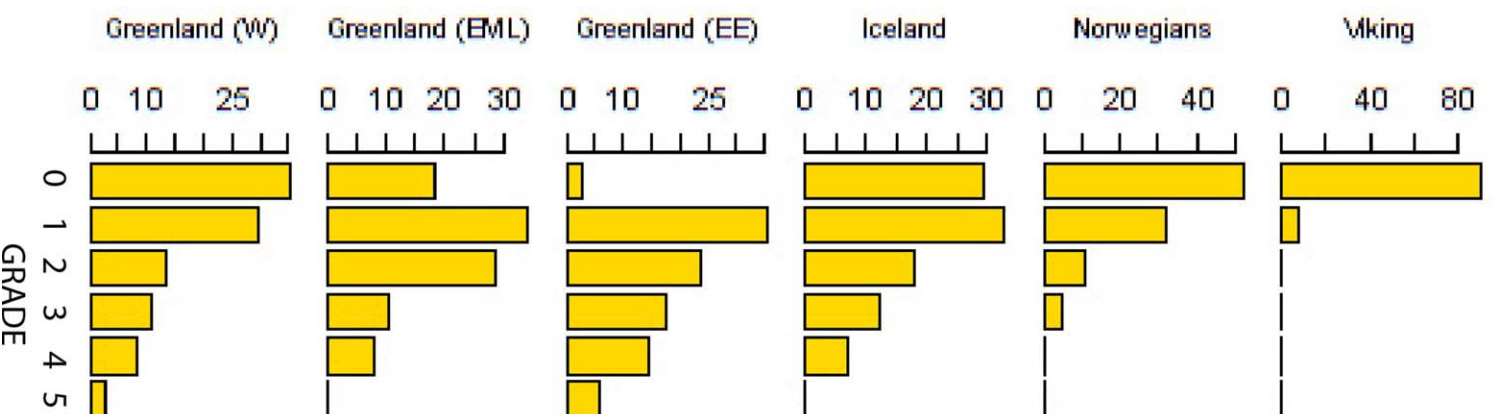


FIGURE 2 Class frequency distributions for mandibular torus in the Greenlandic Norse, along with Vikings and medieval Norwegians and Icelanders

(31.6%). Mean trait expression is 0.694. The Icelanders and Greenlanders differ dramatically from the Vikings and Norwegians. The most pronounced tori are found in the Eastern Early sample, which has a total frequency of 97% and a mean trait score of 2.235. These values are significantly higher than those for Icelanders (70.7%; $mts = 1.353$)

TABLE 2 Mean frequencies of mandibular torus for 15 regional groups

Regional group	k	Mean %	S.D.	95% confidence limits	References
Greenland and Iceland	11	0.512	0.2036	0.375–0.649	(Axelsson & Hedegård, 1981; Drenann, 1937; Fischer-Møller, 1942; Igarashi, Ohzeki, Uesu, Nakabayashi, & Kanazawa, 2008; Oschinsky, 1964; Steffensen, 1969)
Northern Europe	15	0.177	0.1418	0.098–0.255	(Alvesalo & Kari, 1972; Axelsson & Hedegård, 1981; Drenann, 1937; Furst & Hansen, 1915; Haugen, 1992; Howells, 1941; Kolas et al., 1953; McLoughlin, 1950; Mellquist & Sandberg, 1939; Oschinsky, 1964; Schreiner, 1935; Sognaes, 1954) (CGT 6)
Southern Europe	10	0.147	0.1633	0.030–0.264	(Cunha, 1994; Czarnetzki, 1975; Galera, Garralda, Casas, Cleuve-not, & Rocha, 1995; Hrdlička, 1940; Reichart, Neuhaus, & Sookasem, 1988; Rouas & Midy, 1997; Witkop & Barros, 1963)
North Africa and Middle East	17	0.030	0.0635	0.003–0.062	(Irish, 1993; Khaki, 2000; Salem, Holm, Fattah, Basset, & Nasser, 1987; Sawair, Shayyab, Al-Rabab'ah, & Saku, 2009) (CGT 1)
South Asia	8	0.163	0.1277	0.056–0.270	(Kaul & Anand, 1979; Ohno, Sakai, & Mizutani, 1988; Shah, Sanghavi, Chawda, & Shah, 1992; Zoubov, 1973) (CGT 1)
Sub-Saharan Africa	27	0.039	0.0692	0.012–0.067	(Adeyemo, Emeka, Taiwo, & Adeyemi, 2009; Agbaje, Arowojolu, Kolude, & Lawoyin, 2005; Bruce, Ndanu, & Addo, 2004; de Villiers, 1968; Dosum, Arotiba, & Ogunyinka, 1998; Drenann, 1937; Ihunwo & Phukubye, 2006; Irish & Konigsberg, 2007; Rightmire, 1972; Shaw, 1931) (CGT 2)
North Asia	56	0.408	0.1894	0.357–0.458	(Akabori, 1939; Dodo, 1974; Dodo & Ishida, 1987; Djurić-Srejić & Nikolić, 1995; Hrdlička, 1940; Igarashi, in press; Igarashi et al., 2008; Miyashita, 1935; Ohno, Sakai, & Mizutani, 1988; Pechenkina & Benfer, 2002; Rouas & Midy, 1997; Sakai, 1954; Sugihara et al., 2003; Tamaki, Marzola, & Tamaki, 1970; Zoubov, 1973) (CGT 29)
Southeast Asia	31	0.097	0.0989	0.061–0.134	(Hashim, Haidar, & Kalsom, 1983; Jainkittivong, Apinhasmit, & Swasdison, 2007; Kerdpon & Sirirungrojying, 1999; Nair, Samar-anayake, Philipsen, & Itthagaran, 1996; Reichart et al. 1988; Van den Broek, 1941; Zoubov, 1973) (CGT 24)
Australia-Melanesia	31	0.018	0.0344	0.006–0.031	(Campbell & 1925; Fenner, 1939; Hrdlička, 1940) (CGT 27)
Polynesia and Micronesia	15	0.030	0.0492	0.002–0.057	(Turner & Scott, 1977; Witkop & Barros, 1963) (CGT 12)
Circumpolar (Eskimo-Aleuts)	38	0.596	0.1825	0.536–0.656	(Dodo & Ishida, 1987; Furst & Hansen, 1915; Hrdlička, 1940; Jarvis & Gorlin, 1972; Jorgensen, 1953; Mayhall, 1970; Mayhall, Dahlberg, & Owen, 1970; Mayhall & Mayhall, 1971; Moorrees, 1957; Moorrees et al., 1952; Oschinsky, 1964; Ossenberg, 1978; Russell & Huxley, 1899; Schreiner, 1935; Scott, 1991; Steffensen, 1969; 85)
Native North America (North)	14	0.290	0.2000	0.174–0.405	(Cybulski, 1975; Ossenberg, 1978) (CGT 3)
Native North America (South)	31	0.233	0.1882	0.164–0.302	(Birkby, 1973; Blakely, 1973; Buikstra, 1972; El-Najja, 1974; Hooton, 1918; Hooton, 1930; Hrdlička, 1940; Ossenberg, 1978; Sublett, 1970; Wiltschke-Schrotta, 1988) (CGT 9)
Mesoamerica	13	0.053	0.0854	0.001–0.104	(Escobar, Conneally, & Lopez, 1977) (CGT 10)
South America	18	0.053	0.0592	0.024–0.083	(Balaz, Diaz, & Perez, 1983; Bernaba, 1977; Hrdlička, 1940; Sawyer et al., 1979; Yaacob, Tirmzi, & Ismail, 1983; 85) (CGT 9)
World total	335	0.224	0.2425		Literature (202); CGT (133)

and the two medieval Greenlandic samples (81.5 and 64.8%; mts = 1.553 and 1.351). This dramatic difference is illustrated in Figure 2 that shows the distribution of torus expression in the two European samples and the four North Atlantic samples.

5 | DISCUSSION

The Greenlandic Norse were exposed to an inhospitable climate where wood was scarce and agriculture impossible due to short growing seasons and the presence of permafrost. During the 500 year Norse occupation of Greenland, expression of mandibular torus was at a maximum in the settlement period population (see Table 1 and Figure 2). It is difficult to determine the extent to which environ-

mental factors in Greenland contributed to this pattern because the settlement period population came directly from Iceland. Although we examined medieval Icelanders, we do not know how settlement period populations from Iceland exhibited mandibular torus. Medieval Greenlanders show dramatic torus frequencies and expressions consistent with observations of medieval Icelanders, but these are less pronounced than what we see in the earliest colonizers of Greenland. All three Greenlandic samples and the Icelanders exhibit more mandibular torus than related populations from Denmark and Norway. Given the presumably similar genetic backgrounds of Scandinavian populations in Europe and the Norse colonists in the North Atlantic, it seems that environmental pressures trump genetic background in determining mandibular torus expression in these

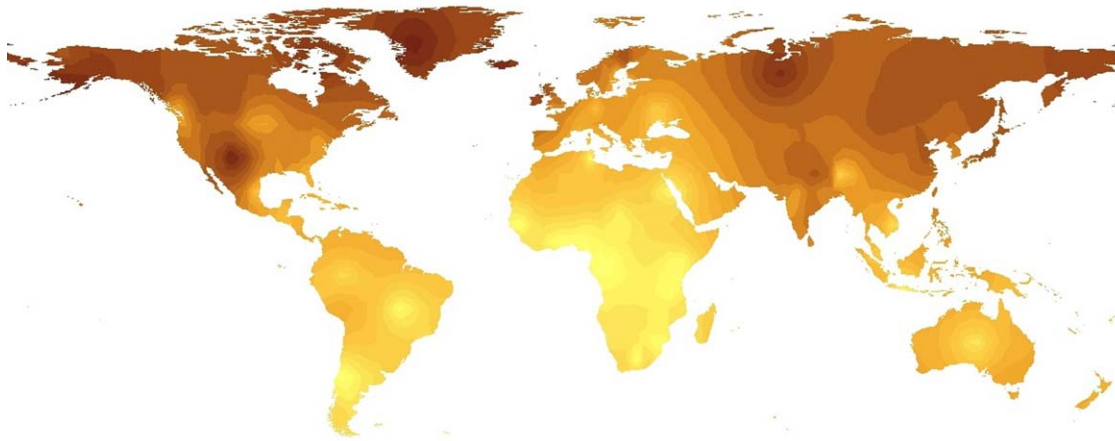


FIGURE 3 World map showing clinal variation in mandibular torus frequencies; the highest frequencies are shown as dark gold with the lowest frequencies as light gold

colonizing populations. To evaluate this question further, these six Scandinavian samples are viewed in the context of torus expression around the world.

5.1 | World variation

The 335 samples tabulated for total mandibular torus frequencies were broken down into 15 major geographic areas (see Table 2). The first group, representing the Norse colonists of Greenland and Iceland, does not include the samples reported in this study. Those were independent observations provided by other researchers. Western Eurasia is broken down into four regions, including Northern and Southern Europe, North Africa-Middle East, and South Asia. Africa has been less intensively studied for torus than other regions so there is only a single Sub-Saharan Africa category. Asia and the Pacific are more complex. Asia is divided into North Asia and Southeast Asia. The Pacific is broken down into Australia-Melanesia and Polynesia-Micronesia. Over a third of the world samples come from the Americas which are divided into five regions: Circumpolar, North America (North), North America (South), Mesoamerica, and South America.

In terms of percentages, the geographic pattern of mandibular torus variation is clear if regions are broken down into high (40%+), moderate (20–39%), low (10–19%), and very low frequency (<10%) groupings. Not surprisingly the high frequency group is headed by Circumpolar populations (Eskimo-Aleuts) with a mean frequency of 59.6%. Greenland and Iceland have the next highest average frequency (51.2%), followed by North Asians (40.8%). The high frequencies in Circumpolar and North Asian populations likely reflect genetic relationships to some extent. The same cannot be said for Greenland and Iceland where convergence rather than similar genetic backgrounds is indicated. Only two regions fall in the moderate frequency category: American Indians in the northern reaches of North America and those found at lower latitudes as far south as the U.S.-Mexican border. Populations in the northern and southern parts of Europe, along with Asiatic Indians, fall in the low frequency grouping. Almost half of all world samples fall in the very low frequency group. Southeast Asia is close to

10% (i.e., 9.7%) but the remaining six groups are at or below 5%. Frequencies are very low in Sub-Saharan Africans along with North Africans-Middle Easterners. The world's lowest frequencies are in the Pacific, especially Australia and Melanesia, although Polynesia and Micronesia are not far behind. In marked contrast to their neighbors to the north, American Indians in Mesoamerica and South America have low mean torus frequencies that are exactly the same at 5.3%.

In addition to the broad regional characterizations, individual sample frequencies were plotted on a world map to illustrate the pattern of variation for mandibular torus. Figure 3 shows that mandibular torus is strongly correlated with latitude. High latitude populations of both Asian and European descent show the highest torus frequencies in the world. Torus frequencies are markedly reduced in populations approaching the equator. The clinal maps are basically blank in Africa, Australia, the Pacific, Mesoamerica, and South America despite being represented by dozens of samples and thousands of individuals. The contrast in the Americas is especially telling. North American Indians differ to some extent from Mesoamerican and South American Indians, but the distinction between these areas for mandibular torus is far more dramatic than we see in genetic or dental markers (cf., Cavalli-Sforza, Menozzi, & Piazza, 1994; Scott & Turner, 1997).

The suggestion that mandibular torus development might be associated with wear is without foundation for a very basic reason. Northern populations have no monopoly on tooth crown wear. Researchers who have not worked with Eskimo-Aleut samples often assume they show an extraordinarily high degree of wear, but this is not the case. They show pronounced wear but no more than countless other groups who live at or near the equator and rarely express mandibular torus (e.g., Australian aboriginals). If bruxism impacts mandibular torus, occlusal stress may play a small role in its development but only a small role. What is it about northern latitudes that trigger unusually large tori? Beyond stress, cold and a high protein diet are two major factors that might be involved in torus formation. Until a test is devised to tease out divergent proximate causes, we can only conclude that genetics plays a small role but environmental agencies play the predominant

role in the manifestation of frequent and pronounced mandibular tori in northern populations from disparate genetic backgrounds.

ACKNOWLEDGMENTS

Remarkably, the late Christy G. Turner II collected more data on mandibular torus than any other single individual but, to the authors knowledge, he never did anything with these data. He published extensively, but his efforts were devoted primarily to how tooth crown and root morphology could be used to address anthropological issues (e.g., peopling of New World and Pacific). Going through his original data sheets allowed us to evaluate populations from geographic regions largely unknown for mandibular torus frequencies (e.g., Australia, New Guinea, Mesoamerica). Although the picture that emerged from a consideration of 202 sample frequencies taken from the literature pointed strongly in the direction of latitudinal clines in torus frequencies, the addition of 133 samples from the CGT collection solidified the point considerably, especially for equatorial populations.

REFERENCES

- Adeyemo, W. L., Emeka, C. I., Taiwo, O. A., & Adeyemi, M. O. (2009). Prevalence and pattern of presentation of mandibular and palatine tori in a Nigerian population. *The Nigerian Dental Journal*, 17, 16–18.
- Agbaje, J. O., Arowojolu, M. O., Kolude, B., & Lawoyin, J. O. (2005). Torus palatinus and torus mandibularis in a Nigerian population. *African Journal of Oral Health*, 2, 30–36.
- Akabori, E. (1939). Torus mandibularis. *Journal of the Shanghai Science Institute, Section IV*, 4, 239–257.
- Alvesalo, L., & Kari, M. (1972). Dental survey in hailuoto. V. Torus mandibularis: Incidence and some viewpoints connected with inheritance. *Proceedings of the Finnish Dental Society*, 68, 307–314.
- Arneborg, J., Heinemeier, J., Lynnerup, N., Nielsen, H. L., Rud, N., & Sveinbjörnsdóttir, A. E. (1999). Change of diet of the Greenland Vikings determined from stable carbon isotope analysis and ¹⁴C dating of their bones. *Radiocarbon*, 41, 157–168.
- Auskalnis, A., Rutkunas, V., Bernhardt, O., Sidlauskas, M., Salomskienė, L., & Basevičienė, N. (2015). Multifactorial etiology of torus mandibularis: Study of twins. *Stomatologija*, 17, 35–40.
- Axelsson, G., & Hedegård, B. (1981). Torus mandibularis among the Icelanders. *American Journal of Physical Anthropology*, 54, 383–389.
- Balaez, A. B., Diaz, E. M., & Perez, I. R. (1983). Prevalencia de torus palatinus y mandibulares en ciudad de la Habana. *Rev Cubana Estomatol*, 20, 126–132.
- Baumann, M., Lynnerup, N., & Scott, G. R. Stable isotopes and oral tori in Greenlandic Norse and Inuit. *International Journal of Osteoarchaeology*, online. DOI:10.1002/oa.2537.
- Bernaba, J. M. (1977). Morphology and incidence of torus palatinus and mandibularis in Brazilian Indians. *Journal of Dental Research*, 56, 499–501.
- Birkby, W. H. (1973). *Discontinuous morphological traits of the skull as population markers in the prehistoric Southwest* (PhD dissertation). University of Arizona, Tucson.
- Blakely, R. (1973). *Biological variability among and between two prehistoric Indian populations at Dickson mounds* (PhD dissertation). Indiana University, Bloomington.
- Bruce, I., Ndanu, T. A., & Addo, M. E. (2004). Epidemiological aspects of oral tori in a Ghanaian community. *International Dental Journal*, 54, 78–82.
- Buikstra, J. E. (1972). *Hopewell in the lower Illinois River valley: A regional approach to the study of biological variability and mortuary activity* (PhD dissertation). University of Chicago, Chicago.
- Campbell, T. D. (1925). *Dentition and palate of the Australian aboriginal*. Adelaide: Hassell Press.
- Carson, E. A. (2006). Maximum-likelihood variance components analysis of heritabilities of cranial nonmetric traits. *Human Biology*, 78, 383–402.
- Cavalli-Sforza, L. L., Menozzi, P., & Piazza, A. (1994). *The history and geography of human genes*. Princeton: Princeton University Press.
- Cunha, E. M. G. P. A. (1994). *Paleobiologia das populações medievais portuguesas. Os casos de fão e S. João de Almedina*. Diss Coimbra.
- Cybulski, J. S. (1975). *Skeletal variability in British Columbia coastal populations*. Ottawa: National Museum of Man, Mercury Series, Archaeological Survey of Canada, Paper 30.
- Czarnetzki, A. (1975). On the question of correlation between the size of the epigenetic distance and the degree of allometry in different populations. *Journal of Human Evolution*, 4, 483–489.
- de Villiers, H. (1968). *The skull of the South African Negro*. Johannesburg: Witwatersrand University Press.
- Djurić-Srejić, M., & Nikolić, V. (1995). Characteristics of skulls of ancient skeletons from the province of Xinjiang in China. *Srpski Arhiv Za Celokupno Lekarstvo*, 124, 124–129.
- Dodo, Y. (1974). Non-metrical cranial traits in the Hokkaido Ainu and the northern Japanese of recent times. *Journal of the Anthropological Society of Nippon*, 82, 31–51.
- Dodo, Y., & Ishida, H. (1987). Incidences of nonmetric cranial variations in several population samples from East Asia and North America. *Journal of the Anthropological Society of Nippon*, 95, 161–177.
- Dosum, O. O., Arotiba, J. T., & Ogunyinka, A. O. (1998). The prevalence of palatine and mandibular tori in a Nigerian population. *Odonto-Stomatologie Tropicale*, 20, 6–8.
- Drenann, M. R. (1937). The torus mandibularis in the Bushman. *Journal of Anatomy*, 72, 66–71.
- Eggen, S. (1989). Torus mandibularis: An estimation of the degree of genetic determination. *Acta Odontologica Scandinavica*, 47, 409–415.
- Eggen, S. (1993). *Torus mandibularis and torus palatinus in Norway: A study on factors influencing their variation* (PhD Dissertation). Eget forlag.
- Eggen, S., & Natvig, B. (1991). Variation in torus mandibularis prevalence in Norway. *Community Dentistry and Oral Epidemiology*, 19, 32–35.
- El-Najji, M. Y. (1974). *People of Canyon de Chelly: A study of their biology and culture* (PhD dissertation). Arizona State University, Tempe.
- Escobar, V., Conneally, P. M., & Lopez, C. (1977). The dentition of the Quechchi Indians. Anthropological aspects. *American Journal of Physical Anthropology*, 47, 443–452.
- Fenner, F. (1939). Observations on the mandibular torus. *Transactions of the Royal Society of South Australia*, 63, 224–229.
- Fischer-Møller, K. (1942). The mediaeval Norse settlements in Greenland: Anthropological investigations. *Meddelelser Om Grønland*, 89, 1–82.
- Furst, C. M., & Hansen, C. C. (1915). *Crania groenlandica*. Copenhagen: Høst.
- Galera, V., Garralda, M. D., Casas, M. J., Cleuvenot, E., & Rocha, M. A. (1995). Variabilidad de los tori orales en la población de Coimbra (portugal) a principios del siglo XX. *Antropologia Portuguesa*, 13, 121–138.

- Gould, A. W. (1964). An investigation of the inheritance of torus palatinus and torus mandibularis. *Journal of Dental Research*, 43, 159–167.
- Halfman, C. M., Scott, G. R., & Pedersen, P. O. (1992). Palatine torus in the Greenlandic Norse. *American Journal of Physical Anthropology*, 88, 145–161.
- Hanson, C. L. (1986). *Biological distance in medieval Western Scandinavia based on craniometrics* (PhD dissertation). Arizona State University, Tempe.
- Hashim, Y., Haidar, T., & Kalsom, I. (1983). The prevalence of oral tori in Malaysians. *Journal of Oral Medicine*, 38, 40–42.
- Hassett, B. (2006). Torus mandibularis: Etiology and bioarchaeological utility. *Dental Anthropology*, 19, 1–14.
- Haugen, L. K. (1992). Palatine and mandibular tori: A morphologic study in the current Norwegian population. *Acta Odontologica Scandinavica*, 50, 65–77.
- Hooton, E. A. (1918). On certain eskimoid characters in Icelandic skulls. *American Journal of Physical Anthropology*, 1, 53–76.
- Hooton, E. A. (1930). *The Indians of Pecos Pueblo*. New Haven: Yale University Press.
- Howells, W. W. (1941). The early Christian Irish: The skeletons at Gallen Priory. *Proceedings of the Royal Irish Academy*, 46, 103–219.
- Hrdlička, A. (1940). Mandibular and maxillary hyperostoses. *American Journal of Physical Anthropology*, 27, 1–67.
- Igarashi, Y. Frequency of mandibular tori in prehistoric and historic Japanese island populations. *Quaternary International*, in press.
- Igarashi, Y., Ohzeki, S., Uesu, K., Nakabayashi, T., & Kanazawa, E. (2008). Frequency of mandibular tori in the present-day Japanese. *Anthropological Science*, 116, 17–32.
- Ihunwo, A. O., & Phukubye, P. (2006). The frequency and anatomical features of torus mandibularis in a black South African population. *HOMO—Journal of Comparative Human Biology*, 57, 253–262.
- Irish, J. D. (1993). *Biological affinities of late Pleistocene through modern African aboriginal populations* (PhD dissertation), Arizona State University, Tempe.
- Irish, J. D., & Konigsberg, L. (2007). The ancient inhabitants of Jebel Moya redux: Measures of population affinity based on dental morphology. *International Journal of Osteoarchaeology*, 17, 138–156.
- Jainkittivong, A., Apinhasmit, W., & Swasdison, S. (2007). Prevalence and clinical characteristics of oral tori and 1,520 Chulalongkorn University dental school patients. *Surgical and Radiologic Anatomy*, 29, 125–131.
- Jainkittivong, A., & Langlais, R. P. (2000). Buccal and palatal exostoses: Prevalence and concurrence with tori. *Oral Surgery, Oral Medicine, Oral Pathology, Oral Radiology, and Endodontology*, 90, 48–53.
- Jarvis, A., & Gorlin, R. J. (1972). Minor orofacial abnormalities in an Eskimo population. *Oral Surgery*, 33, 417–427.
- Johnson, C. C., Gorlin, R. J., & Anderson, V. E. (1965). Torus mandibularis: A genetic study. *American Journal of Human Genetics*, 17, 433–442.
- Johnson, O. M. (1959). The tori and masticatory stress. *J Prosthet Dent*, 9, 975–977.
- Jorgensen, J. B. (1953). *The Eskimo skeleton*. Copenhagen: CA Reitzel.
- Kaul, S., & Anand, V. (1979). Non-metric variation of the skull in samples of four Indian populations. *Journal of Human Evolution*, 8, 693–697.
- Kerdpon, D., & Sirirungrojying, S. (1999). A clinical study of oral tori in Southern Thailand: Prevalence and the relation to parafunctional activity. *European Journal of Oral Science*, 107, 9–13.
- Khaki, M. N. (2000). Investigation of the prevalence of torus mandibularis and torus palatinus in attendants of Rafsanjan Dental School. *Journal of Kerman University of Medical Sciences*, 7, 182–187.
- Kolas, S., Halperin, V., Jefferies, K., Huddleston, S., & Robinson, H. B. G. (1953). The occurrence of torus palatinus and torus mandibularis in 2,478 dental patients. *Oral Surgery, Oral Medicine, Oral Pathology*, 6, 1134–1141.
- Krahl, V. E. (1949). A familial study of the palatine and mandibular tori. *Anatomical Record*, 103, 477.
- Krogh, K. (1967). *Viking Greenland*. Copenhagen: National Museum.
- Lynnerup, N. (1998). *The Greenland Norse—A biological-anthropological study* (Vol. 24). The Commission for Scientific Research in Greenland, Copenhagen, Denmark.
- Mayhall, J. T. (1970). The effect of culture change upon the Eskimo dentition. *Arctic Anthropology*, 7, 117–121.
- Mayhall, J. T., & Mayhall, M. F. (1971). Torus mandibularis in two northwest territories villages. *American Journal of Physical Anthropology*, 34, 143–148.
- Mayhall, J. T., Dahlberg, A. A., & Owen, D. G. (1970). Torus mandibularis in an Alaskan Eskimo population. *American Journal of Physical Anthropology*, 33, 57–60.
- McLoughlin, E. P. (1950). *Report on the anatomical investigation of the skeletal remains unearthed at Castleknock in the excavation of an early Christian cemetery in the summer of 1938*. Dublin: National Museum of Science and Art.
- Mellquist, C., & Sandberg, T. (1939). Odontological studies of about 1400 medieval skulls from Halland and Scania in Sweden and from Norse colony in Greenland, and a contribution to the knowledge of their anthropology. *Odontologisk Tidskrift*, 47, 1e83.
- Miyashita, K. (1935). The mandibles of Chinese. *Journal of Oriental Medicine*, 22, 617–624.
- Moorrees, C. F. A. (1957). *The Aleut dentition*. Cambridge: Harvard University Press.
- Moorrees, C. F. A., Osborne, R. H., & Wilde, E. (1952). Torus mandibularis: Its occurrence in Aleut children and its genetic determinants. *American Journal of Physical Anthropology*, 10, 319–330.
- Nair, R. G., Samaranayake, L. P., Philipsen, R. G. B., & Itthagarun, A. (1996). Prevalence of oral lesions in a selected Vietnamese population. *International Dental Journal* 46, 48–51.
- Nørlund, P. (1924). Buried Norsemen at Herjolfsnes. *Meddelelser Om Grønland*, 67, 1–267.
- Nørlund, P. (1929). Norse ruins at Gardar. *Meddelelser Om Grønland*, 76, 1–170.
- Ohno, N., Sakai, T., & Mizutani, T. (1988). Prevalence of torus palatinus and torus mandibularis in five Asian populations. *Aichi-Gakuin Dental Science*, 1, 1–8.
- Oschinsky, L. (1964). *The most ancient Eskimos*. Ottawa: The Canadian Research Centre for Anthropology, University of Ottawa.
- Ossenberg, N. S. (1978). Mandibular torus: A synthesis of new and previously reported data and a discussion of its causes. In Cybulsky JS (Ed.), *Contributions to physical anthropology* (pp. 1–52). Ottawa: National Museum of Canada.
- Pechenkina, E. A., & Benfer, R. A. Jr. (2002). The role of occlusal stress and gingival infection in the formation of exostoses on mandible and maxilla from Neolithic China. *HOMO*, 53, 112–130.
- Reichart, P. A., Neuhaus, F., & Sookasem, M. (1988). Prevalence of torus palatinus and torus mandibularis in Germans and Thai. *Community Dentistry and Oral Epidemiology*, 16, 61–64.
- Rightmire, G. P. (1972). Cranial measurements and discrete traits compared in distance studies of African Negro skulls. *Human Biology*, 44, 263–276.
- Rouas, A., & Midy, D. (1997). About a mandibular hyperostosis: The torus mandibularis. *Surgical and Radiologic Anatomy*, 19, 41–43.

- Roussell, A. (1936). Sandnes and neighboring farms. *Meddelelser Om Grønland*, 8, 1–219.
- Roussell, A. (1941). Farms and churches in the mediaeval Norse settlements of Greenland. *Meddelelser Om Grønland*, 9, 1–354.
- Russell, F., & Huxley, H. M. (1899). A comparative study of the physical structure of the Labrador eskimos and of the New England Indians. In Proceedings of the American Association for the Advancement of Science, 48th meeting (pp. 365–379), Columbus, Ohio.
- Sakai, T. (1954). Kougai ryuki oyobi kagakuryuki no seitai kansatsu. *The Shinshu Medical Journal*, 3, 303–307.
- Salem, G., Holm, S. A., Fattah, R., Basset, S., & Nasser, C. (1987). Developmental oral anomalies among schoolchildren in Gizan region, Saudi Arabia. *Community Dentistry and Oral Epidemiology*, 15, 150–151.
- Sawair, F. A., Shayyab, M. H., Al-Rabab'ah, M. A., & Saku, T. (2009). Prevalence and clinical characteristics of tori and jaw exostoses in a teaching hospital in Jordan. *Saudi Medical Journal*, 30, 1557–1562.
- Sawyer, D. A., Allison, M. J., Elzay, R. P., & Rezzia, A. (1979). A study of torus palatinus and torus mandibularis in pre-columbian Peruvians. *American Journal of Physical Anthropology*, 50, 525–526.
- Schreiner, K. E. (1935). *Zur osteologie der lappen*. Oslo: H. Aschehoug & Co.
- Scott, G. R., & Turner, C. G., II. (1997). *The anthropology of modern human teeth: Dental morphology and its variation in recent human populations*. Cambridge: Cambridge University Press.
- Scott, G. R. (1991). Continuity or replacement at the Uyak site, Kodiak Island, Alaska: A physical anthropological analysis of population relationships. In University of Oregon Anthropological Papers, No. 44, pp. 1–56, Eugene, Oregon.
- Scott, G. R., Halffman, C. M., & Pedersen, P. O. (1992). Dental conditions of mediieval norsemen in the north Atlantic. *Acta Archaeologica*, 62, 183–207.
- Sellevoid, B. J. (1980). Mandibular torus morphology. *American Journal of Physical Anthropology*, 53, 569–572.
- Shah, D. S., Sanghavi, S. J., Chawda, J. D., & Shah, R. M. (1992). Prevalence of torus palatinus and torus mandibularis in 1000 patients. *Indian Journal of Dental Research*, 3, 107–110.
- Shaw, J. C. M. (1931). *The teeth, the bony palate and the mandible in Bantu races of south Africa*. London: John Bale, Sons & Danielsson.
- Sognnaes, R. F. (1954). *Oral health survey of tristan da Cunha. Results of the Norwegian Scientific Expedition to Tristan da Cunha, 1937–1938*. Oslo.
- Steffensen, J. (1969). Thaettir ur líffraedi Islendinga. *Laeknaneminn*, 22, 5–18.
- Sublett, A. J. (1970). *Seneca physical type and changes through time* (PhD dissertation). State University of New York, Buffalo.
- Sugihara, N., Maki, Y., Matsukubo, T., Nakazawa, A., Kurokawa, A., & Musha, Y. (2003). Distribution of oral torus and the associated factors. *Japanese Journal of Gerontology*, 18, 258–259.
- Summers, C. J. (1968). Prevalence of tori. *Journal of Oral Surgery*, 26, 718–720.
- Suzuki, M., & Sakai, T. (1960). A familial study of torus palatinus and torus mandibularis. *American Journal of Physical Anthropology*, 18, 263–272.
- Tamaki, S. T., Marzola, C., & Tamaki, T. (1970). Incidence of torus palatinus and mandibularis. *Arquivos do Centro de Estudos da Faculdade de Odontologia da UFM G* 8, 153–164.
- Topazian, D. S., & Mullen, F. R. (1977). Continued growth of a torus palatinus. *Journal of Oral Surgery*, 35, 845–846.
- Turner, C. G., II, & Scott, G. R. (1977). Dentition of Easter Islanders. In Dahlberg AA, Graber TM (Eds.), *Orofacial growth and development* (pp. 229–249). The Hague: Mouton.
- Van den Broek, A. J. P. (1941). On exostoses in the human skull. *Acta Nederland Morphology*, 5, 95–118.
- Vebæk, C. L. (1956). Ten years of topographical and archaeological investigations in the mediaeval Norse settlements in Greenland. In *Proceedings of the 32nd international congress of Americanists*, Copenhagen.
- Wiltshcke-Schrotta, K. (1988). *Das frühbronzezeitliche gräberfeld von franzhausen I. Analyse der morphologischen merkmale mit besonderer berücksichtigung der epigenetischen merkmale*. Nat Diss Wien, Vienna, Austria.
- Witkop, C. J Jr., & Barros, L. (1963). Oral and genetic studies of Chileans 1960. I. Oral anomalies. *American Journal of Physical Anthropology*, 21, 15–24.
- Yaacob, H., Tirmzi, H., & Ismail, K. (1983). The prevalence of oral tori in Malaysians. *Journal of Oral Medicine*, 38, 40–42.
- Zoubov, A. A. (1973). *Etničeskaja odontologija (ethnic odontology)*. Moscow: Nauka (in Russian).