# Fluctuating asymmetry in dental and mandibular nonmetric traits as evidence for childcare sex bias in 19th/20th century Portugal

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## Abstract

Fluctuating asymmetry, often considered a measure of developmental instability, was studied in the dental morphological traits of 600 individuals from among the poorest sectors of society in 19th-20th century Portugal. The aims are to identify and interpret any differences between: 1) males and females, and 2) patterns of distribution among teeth with different odontogenic timings, to assess if any sex bias existed in childcare.

Dental and mandibular morphological traits were recorded using the Arizona State University Dental Anthropology System. Z-ratios were used to compare summed absolute fluctuating asymmetry frequencies between sexes and age groups. Results from rank correlation coefficients ruled out directional asymmetry and antisymmetry, based on positive (>0.2) bilateral association of traits in larger samples. Sex differences were significant (z-ratio = 3.128; p = 0.0018), while age differences were not (z-ratio = -0.644; p = 0.5196). Teeth forming after infancy tended to be more asymmetric in females.

Potential reasons for the sex difference include: 1) greater female susceptibility to developmental instability, 2) greater male childhood mortality that yields lower fluctuating asymmetry in surviving males, and/or 3) cultural bias favoring male access to resources. Results suggest the latter hypothesis is most likely, as fluctuating asymmetry is enhanced during childhood, perhaps coinciding with gender role definitions. There seems to be no association between asymmetry and early mortality in males. A lack of parallels in prior research renders differential sex reaction to environmental stress dubious. This population may have favored male children in their access to appropriate conditions for development.

## Introduction

Bilateral asymmetry of structures in an organism can be divided into at least three kinds: 1) directional asymmetry, 2) antisymmetry and 3) fluctuating asymmetry. The directional form occurs when one side, or antimere, is consistently overdeveloped relative to the other across a population (Graham et al., 1993; Klingenberg and Nijhout, 1999; Markow, 1995; Palmer, 1996). In antisymmetry, asymmetry is present in the majority of a population though without a dominant side (Graham et al., 1993; Klingenberg and Nijhout, 1999; Markow, 1995; Palmer, 1996). Fluctuating asymmetry (FA) is characterized by slight deviations without side bias. Fluctuating asymmetry is measured as the difference from expression on the right side to the expression on the left. A population's average difference should be zero and all individual differences should yield a normal distribution. Variance of FA is considered a measure of

developmental instability (DI), or ‘noise’ (Bollini et al., 2009; DeLeon, 2007; Graham et al., 1993; Klingenberg and Nijhout, 1999; Markow, 1995; Palmer, 1996).

Although directional asymmetry and antisymmetry may be related to stress, those recurring phenotypes are more likely dependent on environmental stimuli and their degree or direction, alongside any given organism’s susceptibility at early development, rather than genetic input (Graham et al., 1993). When associating stress-induced asymmetry and dental nonmetric traits, FA is the perceived phenomenon.

Fluctuating asymmetry (FA) occurs in dental morphology, when a given character can be found on one side but not in its antimere, or be expressed differently (at a different grade) in each side (Bollini et al., 2009; Rizk et al., 2008; Scott and Turner, 1997). Decades of research have demonstrated that this phenomenon is a relatively constant occurrence with environmental, rather than genetic, origins. The expression of genes is affected by environmental factors during ontogeny (DeLeon, 2007; Rizk et al., 2008; Scott and Turner, 1997). In dental morphology, bilateral asymmetry is a form of qualitative FA (Bollini et al., 2009).

The patterning cascade model could explain FA in dental morphological variables (Salazar-Ciudad and Jernvall, 2002, 2010). This model posits a connection between genotype and phenotype, as mediated by morphology during development. Such a connection is possible because the occurrence of extra traits (i.e., formation of new enamel knots) depends on the relative distance among major cusps and tooth size. These variables can be limited by environmental variation affecting developmental paths (Salazar-Ciudad and Jernvall, 2002, 2010).

Fluctuating asymmetry (FA) can be used to measure developmental instability. Developmental instability is the relative reaction of developing structures to internal or external disturbances (Klingenberg and Nijhout, 1999), and is caused by either environmental factors or maladaptation (Van Dongen and Gangestad, 2011). The concept opposed to developmental instability is developmental precision; of equal importance, it is the ability of an organism to respond to genomic guidance during ontogeny and is subjected to opposing forces: 1) developmental noise, hindering precision; and 2) developmental homeostasis, redirecting the organism toward bilateral symmetry after perturbation. Developmental homeostasis can have genetically determined limitations (Palmer, 1996). So, FA appears to be the result of interplay between environmental stimuli and genetic responses (Klingenberg and Nijhout, 1999).

Although random asymmetry is most likely affected by environment and limited by paralleled (or bilateral) developmental genetic control (Baume and Crawford, 1980), the correlation between dental FA and environmental factors is not unquestioned (Bermúdez de Castro, 1989; Graham et al., 1993). However, further research is required to clarify the connection (Markow, 1995; Palmer, 1996; Van Dongen et al., 1999). The relationship between FA and developmental instability has rarely been studied in dental morphology studies, with only three published studies in the last 30 years (Bollini et al., 2009; Mayhall and Saunders, 1986; Noss et al., 1983).

In the 19$^{th}$ through mid-20$^{th}$ centuries, Portugal was a poor and underdeveloped country, dominated by a conservative attitude that helped maintain a technically traditional agriculture and weak industrial economy (Cardoso, 2005; Correia Pereira, 1912; Reis, 1987; Roque, 1982). One of the consequences was very high child mortality that particularly affected males (Miranda, 1999; Roque, 1988; Valério, 2001). At the time, child labor and neglect were common, since the Catholic Church did not permit fertility control, and the family economy and domestic management depended on all family members (Johansson, 1987; Lancaster and Lancaster, 1987; Lopes, 2002). Boys and girls had their social roles defined soon in life. For example, in the Portuguese Alentejo region, young males were allowed to play outside while females were taught to mind the house and their younger siblings (Dias, 1955). In cities, boys also had access to the outside world more than girls who, again, were taught domestic chores, infant care, and how to find a suitable husband from early on (Dias, 1955).

In the present study, a large sample of 19$^{th}$-20$^{th}$ century individuals from Portugal is evaluated regarding the degree and possible causes of FA in dental discrete traits. The main goal of this investigation (Cuozzo et al., 2012) is to identify any differences by sex. Secondarily, such differences in FA will be interpreted through the analyses of: 1) pattern along odontogenic timings and 2) differences among age groups, i.e., non-adults and adults. Given the social differences between boys and girls in this population, these goals will be accomplished by testing two hypotheses. First, males should present less FA than females; the reason, noted, is that the former should have been less exposed to work and had greater access to outdoor physical exercise. Second, there should be no correlation between early death and FA, since the sex difference in FA should not have been caused by higher male child mortality.

## Materials and methods

The dental and mandibular morphology of 600 identified individuals (300 males and 300 females) was bilaterally scored. Ages at death range from 7 to 97 years (males: 11 to 84 years), with a mean of 35.8 years (109 non-adult individuals, up to 20 years of age; 491 adults, 21 years and older). These individuals were born in 1820-1924 in most districts of Portugal, though the majority are from Coimbra (n=402 individuals, 67.0%); a small subset (n=9, 1.5%) of immigrants that died in the country between 1896 and 1934 were also included. Figure 1, where the origins of this sample are indicated, illustrates Portugal and its geographical surroundings. Dental nonmetric traits were used to test for biological diversity within the present sample, comparing individuals from different regions of Portugal and born abroad (Marado, 2014); the sample was considered to be homogeneous and representative of the overall Portuguese population. Differences in FA between regions were also tested (Marado, 2014) and were found insignificant. All remains are curated at the Department of Life Sciences, University of Coimbra (Faculty of Sciences and Technology), in two collections: the Trocas Internacionais and Escolas Médicas.

**INSERT Table 1 ABOUT HERE**

The Trocas Internacionais collection (all 300 males and 269 females in the present sample) was acquired from the Conchada cemetery in Coimbra by Eusébio Tamagnini between 1932 and 1942, with the intent of trading the skulls with international institutions (Cunha and Wasterlain, 2007; Fernandes, 1985; Rocha, 1995; Santos, 2000; Wasterlain, 2006). The Escolas Médicas collection (31 females in the present sample) was formed by Bernardino Machado, who wanted to have every district in continental Portugal represented. Skeletal remains were gathered from the Medical Schools of Oporto and Lisbon, and the Anatomical Museum of the Faculty of Medicine of the University of Coimbra between 1886 and 1903 (Cunha and Wasterlain, 2007; Fernandes, 1985; Rocha, 1995; Santos, 2000; Wasterlain, 2006).

The Arizona State University Dental Anthropology System (ASUDAS) (Turner et al., 1991) was used in scoring 25 nonmetric traits, and Scott and Turner's (1997) guidelines were followed for another, i.e., UM1 mesial marginal accessory tubercles. A further trait, the mandibular molar pit tubercle (MMPT), was scored after Weets (2004, 2009). Lastly, two nonmetric mandibular variables (*foramina mentales* and mylohyoid bridge) were recorded (Hauser and De Stefano, 1989). In total, 58 nonmetric traits of the dentition and mandible were analyzed, since some were scored in more than one tooth. Graded results (or raw scores,

as opposed to data dichotomized into presence/absence) were considered when defining asymmetry. Dichotomized data were used to determine bilateral trait absence, not to calculate FA.

Measurement error and the possibility of directional asymmetry are the main obstacles to validate conclusions in the study of FA (Van Dongen and Gangestad, 2011). In the present study all observations were made by the first author. Intra-observer error was low and within the expected range, when compared to that found by Nichol and Turner (1986). To avoid biasing the results, the first author made two complete observations of the sample. The mean overall agreement (calculated on raw scores for the final 47 traits selected; see below) between scoring sessions was 90%, ranging from 57.4% to 100%. The mean agreement within one grade of error was 95.3%, ranging from 83.8% to 100%. Asymmetry was calculated during both recording sessions; when observations did not correspond (e.g., one was found to be asymmetric and the other not) they were removed from results and analyses.

Kendall's $\tau$-b rank correlation coefficient (SPSS 19.0) was used to determine the trend of antimere asymmetries; as such, directional asymmetry or antisymmetry could be ruled out, as moderate to very strong positive associations should occur only in cases of FA. Directional asymmetry should result in very weak to weak (positive or negative) correlations, as most of a population sample would present asymmetry with a typical direction (e.g,, the left side is larger than the right in 90% of the sample). Antisymmetry should present moderate to strong negative associations, since most individuals in the sample would present asymmetry in a random direction (e.g., 44% of individuals present larger left sides, 48% present larger right, and 8% are symmetric).

Frequencies of FA were then compared between the males and females and between non-adults and adults. Data were approached in three ways: 1) overall frequency, where the number of asymmetric traits was divided by the total number of bilaterally scored traits by sex; 2) frequencies excluding bilateral trait absences (whenever individuals presented trait absence on both sides, they were excluded from that trait's dataset), henceforth termed "comparable FA"; and 3) frequencies excluding bilateral trait absences and traits with small samples for either sex – subsequently called "comparable large sample FA". These small samples were defined as those with $n<30$, or $n<20$ for age group comparisons. Removal of bilateral absences diminishes the effect of different trait presence in overall asymmetry, making the sexes and age groups more easily comparable (Mayhall and Saunders, 1986). The minimum number of individuals allowing trait inclusion on the "comparable large sample FA" was determined to exclude very small samples in averaged or summed results. Only

traits with ≥30 observations were included when comparing sexes, with the intention of giving as much statistical power to the results as possible. The difference in minimum sample size for age (≥20) is justified by the much smaller number of non-adults in the younger age group.

Van Dongen and Gangestad (2011) suggested averaging all asymmetries when inferring developmental instability, but considered the use of traits from the same body area less informative. However, teeth have relatively wide ontogenic timings, which begin *in utero* and only cease in late adolescence or early adulthood (AlQahtani et al., 2010; Scheuer and Black, 2000). Another characteristic that benefits the aggregation of morphological traits is the generalized lack of intertrait correlations (Scott and Turner, 1997). The correlation of FA presence between traits was calculated (results not shown, but available from the first author). When two traits' FA were associated (here set as $\tau$-b > 0.3), the trait that was least informative -- showing little morphological variation in the sample, or involved in further correlations – having consistently moderate to high correlation with more than one variable, was removed. Eleven traits were removed from the results and subsequent analysis. Therefore, it was deemed appropriate to average FA frequencies per trait, and aggregate data to compare males and females. Proportions of asymmetry were compared from aggregated values, i.e., that summed all trait frequencies, using z-ratios to statistically test sexual differences in FA.

## Results

Forty of the 47 traits provide significant rank coefficients (Kendall's $\tau$-b) for trait expression between the left and right sides, with $p < 0.01$ (Table 1). Statistically insignificant results display either no trait presence (UP3 tricuspid premolars, LP3 odontome) or minimal presence (UP3 accessory cusps, UP4 tricuspid premolars, LM1 MMPT, LM3 protostylid and LM3 C7); these traits, therefore, did not allow correlation calculations or produced unreliably low correlations with $p>0.05$.

Of the 40 significant rank order correlations, only four traits yielded moderately low coefficients (i.e., 0.2-0.3): *foramina mentales* presented values near 0.3 ($\tau$-b = 0.296), while UI1 interruption grooves, UM1 mesial marginal accessory tubercles, and LM3 MMPT probably owe their low coefficients to very small sample sizes (Table 2). All other traits have correlation coefficients of >0.3 (Table 1).

**INSERT Table 1 ABOUT HERE**

Twenty-four traits (of 47: 51.1%) display greater overall fluctuating asymmetry (FA) frequencies in females (Table 2). Females are more asymmetric relative to males for: LP4 lingual cusp number (F: 26.8%; M: 19.7%), LM2 groove pattern (F: 13.8%; M: 7.7%), and LM3 MMPT (F: 30.0%; M: 15.7%) and C6 (F: 16.3%; M: 4.1%). When bilateral absences are removed, and asymmetry only considers individuals with at least unilateral trait presence (i.e., "comparable FA"; sample sizes correspond to denominators in the two last columns of Table 2), females have greater FA frequencies for 22 traits (of 47: 46.8%). If only large samples (≥30 at least unilateral trait presences: "comparable large sample FA") are compared, females have greater FA frequencies in eight out of the 10 traits considered (or 80%; Table 2).

**INSERT Table 2 ABOUT HERE**

The average overall asymmetry is 7.4% for females and 6.3% for males. Summed overall FA frequencies (F: 431/6335 = 6.8%; M: 372/6449 = 5.8%) yield a z-ratio of 2.412 (p = 0.016), which supports higher female FA. "Comparable FA" yields an average of 56.8% for females and 52.5% for males. Aggregated frequencies for "comparable FA" (F: 420/1102 = 38.1%; M: 360/1132= 31.8%) display a z-ratio of 3.128 (P = 0.0018). The average "comparable large sample FA" is 34.7% and 30.8% for females and males, respectively. Summed "comparable large sample FA" also demonstrates independent proportions (F: 217/767 = 28.3%; M: 197/831 = 23.7%), through a z-ratio of 2.09 (P = 0.0366).

**INSERT Fig. 2 ABOUT HERE**

The FA proportion differences between sexes are distributed differently along tooth types (Fig. 2). Timings of crown formation were consulted (AlQahtani et al., 2010; Scheuer and Black, 2000) to determine if tooth type FA differences establish a trend. The earliest forming crowns are the first molars and incisors that mineralize around 3-4 years of age. These teeth have low average FA frequency differences between sexes (Fig. 2). However, incisors are few in number in this sample and represented only by upper teeth, (incisors are absent from "comparable large sample FA" Fig. 2C), so results should be viewed with caution. Canine and premolar crowns are formed between 1 and 6.5 years. Canines, which form at the low end of this range, have consistently higher FA averages in males (Fig. 2). Premolars show mixed results, and yet again small sample sizes of UP3 and UP4 may bias results. Later-forming LP4

and UP4 are the first crowns to appear consistently more asymmetric in females, with the exception only of "comparable FA" on the LP4 (Fig. 2B); the latter observation is higher for males, perhaps because of odontome absence. Second molar crowns, formed between 3.5 and 9-10 years, show clearly greater FA in females, particularly the LM2 (Fig. 2B). Lastly, third molars, with mineralization between 9 and 16 years, yield mixed results; once again sample size may be a factor, but the lower teeth show higher FA averages for females and the upper teeth have slightly higher FA averages for males (Fig. 2A and 2B).

Non-adults (N), comprising 109 individuals 7 to 20 years old (18.2% of the sample; 54 females and 55 males), were compared to 491 adults (A) aged 21 to 97 years (81.8% of the sample; 246 females and 245 males) for all types of summed FA. For overall FA (N: 194/2942 = 6.6%; A: 599/9842 = 6.1%), the calculation of the independence of proportions resulted in a z-ratio of 1.002 with a low statistical degree of confidence ($p = 0.3163$). "Comparable FA" frequencies were identical (N: 192/568 = 33.8%; A: 588/1666 = 35.3%) and statistically very similar (z-ratio: -0.644; $P = 0.5196$). "Comparable large sample FA" frequencies (N: 97/386 = 25.1%; A: 216/990 = 21.8%) yielded a z-ratio of 1.316 with a low confidence level ($p = 0.1882$). These results suggest individuals of different ages at death were not differently affected by FA.

## Discussion

Sex differences in FA have been found for some populations; females exhibited greater frequencies without apparent environmental or cultural differentiation, suggesting greater female susceptibility to developmental instability (Harris and Nweeia, 1980; Noss et al., 1983). There are also differences in FA where males show greater asymmetry (Buchwald and Grubska, 2012; Hope et al., 2013). Additionally, some studies report no evidence of sexual differentiation in FA (Peiris et al., 2013; Perzigian, 1977; Pirilä-Parkinnen et al., 2001).

The discovery of significant FA differences between the sexes should not be overlooked. Both biological and socio-cultural factors may be potential causes (Noss et al., 1983). The FA differences between male and female Portuguese individuals could be explained by: 1) biological distinctions between the sexes, which caused more successful developmental homeostasis in males; 2) exposure of females to greater indices of developmental instability; and/or 3) differential childhood mortality, effectively removing potentially at-risk boys affected by developmental instability from analysis.

The first two hypotheses are difficult to demonstrate or disprove, since they require clear historical ethnographic information to understand how the socioeconomic environment affected male and female childrearing differently. The hypothesis regarding better male developmental homeostasis seems unlikely, because it would imply biological distinctions between the sexes. Previous data on diachronic burials from the same site (DeLeon, 2007) and twin research (Corruccini et al., 1986) have shown biological continuity does not correlate with continuity in FA frequencies. These findings suggest that environment plays a role with developmental instability and, consequently, fluctuating asymmetry. Due to its functional relevance in mastication, dental symmetry could be prioritized. If so, FA in dental and mandibular discrete traits would not be differently affected by sex, despite the fact that different homeostatic devices can result from sexual selection (DeLeon, 2007). The second hypothesis, sex differences in FA caused by greater female exposure to developmental instability, seems to be supported by the existing historical information. The Portuguese population of the 19$^{th}$ and 20$^{th}$ centuries was affected by poverty and under-nutrition, since most people relied on subsistence agriculture (Cardoso, 2005; Correia Pereira, 1912). High mortality rates and low life expectancy were the norm. Women comprised the higher portion of a pyramidal demographic structure, and childhood mortality varied between 500‰ (mid-19$^{th}$ century) and 100‰ (first decades of the 20$^{th}$ century) (Roque, 1988; Valério, 2001).

One key factor in undermining Portuguese economic, social, and political development was the conservative attitude that prevailed (Cardoso, 2005; Correia Pereira, 1912; Reis, 1987). Agricultural activities were adversely affected by socioeconomic factors (Roque, 1982) and the resulting cycles of shortage and abundance caused the price of foodstuffs to fluctuate (Bocquet-Appel, 1984).

Marrying a daughter was costly -- due to dowries (Johansson, 1987; Lancaster and Lancaster, 1987), used by a groom for tools or shelter (Lopes, 2002). Marriages were also difficult to arrange, mainly due to male emigration (Veiga, 2004). It was not socially acceptable for unmarried women to be employed outside the home, so they became a financial burden (Dias, 1955; Lopes, 2002). The financial difficulties of the Portuguese families are demonstrated by the use of child labor during the period of intense male emigration and industrial increase (Lopes, 2002). Unmarried women (20% in Portugal, which is high relative to other countries: Veiga, 2004) largely became prostitutes, indigents, or lived with a family member who supported them in exchange for house work (Dias, 1955; Lopes, 2002).

Parental negligence was enabled by the Christian faith (Johansson, 1987; Lopes, 2002), and children with the least economic value were likely to be more neglected and abused

(Lancaster and Lancaster, 1987; Voland et al., 1997). The development and education of children was not considered in Portugal until the late 19th century onward (Gomes Ferreira, 2010). So, the greater economic costs of females to their families likely have justified greater negligence and abuse of girls during the difficult times of the 19th to mid-20th centuries; women could not work and children were evaluated according to their economic value.

In this period it was common for male children to have outside access and be allowed playtime; female children were expected to perform household chores and take care of infants and younger children (Dias, 1955; Miranda, 1999). Daughters had to justify their cost for the family since very early on.

The subsample with the least stress may have been affected by high childhood mortality, in opposition to the one with greater developmental instability that survived into adulthood despite evidence of stress (King et al., 2005). In 20th century Portugal, greater infant male mortality was typical, but when causes of death were reported (1970's and 80's) the difference was of an endogenous origin (e.g., birth defects) (Miranda, 1999). On the other hand, child mortality did not seem to affect either sex more. For example, in Barcelos, a "*concelho*" (administrative division) in the Minho region (Northern Portugal), until the early 20th century child mortality (between 1 and 7 years) was higher and showed greater balance between deaths of each sex than infant mortality (between 0-1 year) (Miranda, 1999).

Differences between non-adult and adult fluctuating asymmetry (FA) in the Portuguese sample are rare and statistically null. Therefore, greater FA was likely not correlated with early death, which reduces the possibility of greater male infant mortality biasing comparison of FA frequencies between the sexes.

Despite greater male susceptibility to mortality, morbidity, vulnerability and risk taking (factors that usually are not evident until adolescence: Kruger and Nesse, 2006), females in the past have been reported to be particularly susceptible to mortality, morbidity and stress due to the socio-cultural preferential treatment of males (Bigoni et al., 2013; Goodman et al., 1987; Guatelli-Steinberg et al., 2006; May et al., 1993; Šlaus, 2000). Such male preferential treatment is particularly prevalent in poverty-ridden underdeveloped countries (Goodman et al., 1987; May et al., 1993) like Portugal in the 19th and early 20th centuries. Portuguese female children were less valued and socio-culturally undermined in terms of access to health, nutrition, and proper living conditions; this resulted in greater evidence of developmental instability.

Fluctuating asymmetry (FA) in dental nonmetric traits should reflect the relative degree of developmental instability affecting an individual during development that occurred around the

time of tooth mineralization. The odontogenic timing of FA can be dependent on the process affected by stress. Tooth buds can be affected *in utero*, to mineralize after birth; mineralization itself can also be affected (Noss et al., 1983). An example of differences in FA timings (which potentially denote either different buffering of developmental instability or different exposure to environmental stress) is reported in a comparison between Neandertals and modern humans (Barrett et al., 2012).

Fluctuating asymmetry differences throughout ontogeny are most likely caused by different levels of environmental stress, as enhanced or diminished by socio-cultural biases. Contrary to that found by Harris and Nweeia (1980), FA differences between Portuguese males and females are clearer at a period when gender roles could be defined, and even when childcare bias may be introduced (after birth). In support, teeth mineralizing during childhood are mostly more asymmetric in females in the present sample. It should be noted that the comparisons using "overall FA" and "comparable FA" represent averages of differing numbers of traits between teeth. This can bias results, if FA differs greatly in traits within the same teeth, or if a particularly asymmetric trait is the only representative of a given tooth. In "comparative large sample FA" (Fig. 2C) all teeth are represented by one trait except LM1 (two traits) (see Table 2 for list of large samples: bold denominators in "comparable FA"). Females were integrated in household and childcare tasks by late childhood, and were thus exposed to more mature physical demands early on (Dias, 1955; Miranda, 1999). Males on the other hand, with evidence of preferential treatment, could have realized such health benefits as greater playtime exposure to sunlight, and probably better nutrition and superior treatment of disease, as suggested by these results.

Wasterlain (2006) recorded the linear enamel hypoplasia (LEH) on a historic Portuguese sample, including a number of individuals in the present sample. This author found higher LEH in the LI1, LI2, UI1, LP4, UP4, UM2 and LM3 of females. She detected higher male LEH on the remaining teeth (UI2, LC, UC, LP3, UP3, LM1, UM1, LM2 and UM3). Still, LEH was found to have affected women most frequently, and significantly more female teeth displayed LEH (Wasterlain, 2006). Male children were less affected by LEH, as would be expected in the case of preferential care in a group of very poor socioeconomic status.

Dental morphology FA may be a long term measure of developmental instability or developmental stress, in opposition to episodic stress markers like LEH (Barrett et al., 2012). Despite these etiological differences, LEH supports potential childcare sex difference that apparently benefited males in the dental FA results. It cannot be ruled out, however, that the LEH findings are biased due to the osteological paradox if, unlike FA, high LEH frequencies

are related to age at death. Such a relationship could not be tested by Wasterlain (2006), as only individuals 20 years of age and older were used in her study.

Reports of greater female exposure to developmental instability and to episodic stress (linear enamel hypoplasiae) through socio-cultural biases have originated from historic (Bigoni et al., 2013; Šlaus, 2000) and contemporary populations (Goodman et al., 1987; Guatelli-Steinberg et al., 2006; May et al., 1993). These studies support the idea that socio-cultural differences in gender roles and childcare of males and females can produce a greater susceptibility to developmental instability, which may be detected by FA in dental and mandibular morphology of the Portuguese sample. Mixed results across the literature reiterate the need for caution when interpreting the origin of FA differences between sexes, but in the present case fluctuating asymmetry is likely environmental; there are no indications of a biological origin.

Exogenous causes (socioeconomic, accidental and weather-related deaths), including excessive work, poor nutrition and physical abuse, were associated with most infant and childhood deaths (Lopes, 2002; Miranda, 1999). This indicates the relevance of social negligence in childhood mortality. Independently of ending in early death or not, these stressful conditions disrupted developmental paths, causing developmental instability and, subsequently, fluctuating asymmetry. Biological differences should not have been the cause of sexual differences in FA, since prior research has not demonstrated any such case and there is low dental sexual dimorphism in the Portuguese (Galera and Cunha, 1993). Despite reports of high adult and childhood mortality, particularly in younger men (Miranda, 1999; Veiga, 2004), lack of distinctions between age groups suggests FA was not linked to early death. So a greater developmental instability may not have caused greater mortality in boys (i.e., to result in the removal of the most affected individuals from comparison). Exogenous causes, however, affected females more. They were subject to a greater deal of stress, since it was demonstrated girls a) were kept at home, away from sunlight and fresh air and taught to work from an early age, b) were economically less valuable (due to female overpopulation, related to male emigration and greater young male mortality) and more expensive (because of the need for dowries to get them married, or a family member's resources to keep them if they did not marry).

Higher dental and mandibular discrete trait fluctuating asymmetry frequencies in females suggest either biological distinctions between the sexes, or that females experienced greater environmental stress. The latter hypothesis seems better substantiated by parallels in the literature and a lack of clear association between different FA frequencies – as interpreted as

measures of developmental instability and biological distinctions. Greater susceptibility of females to environmental stress seems to have been culturally mediated, through early gender role definition and/or higher social status of males -- at least during growth and development.

The likelihood that higher male childhood mortality removed the most affected individuals from the present sample was tested indirectly. The lack of a significant difference between non-adults and adults suggests that FA is not correlated with early death.

The Catholic Church promoted high fertility policies and guaranteed that God would decide the fate of infants and children. The higher strata of society and the Portuguese state were on the brink of understanding the needs and development of children, as well as the importance of increasing the country's population for development. Yet, neglect and abuse were still socially acceptable. The wave of emigration (which affected males most) created lack of manpower and reduced marriage opportunity for females. Both consequences reduced the relative economic value of daughters, who were not employed outside the home, yet needed resources for their demanding dowries; otherwise they would be dependent on their families for life. Girls were therefore exploited from early on, mainly through domestic chores, which kept them away from the outdoors and social play. The differential treatment of male and female children has been seemingly related to greater FA in the latter, which suggests an expected greater developmental instability. Timing of the FA differences, as determined from expected odontogenic ages, also suggests exposure to physiological stress that is associated with the minimum age of gender role definitions.

The present results support the use of dental fluctuating asymmetry as a measure of developmental instability. These differences found for girls and boys in a socioeconomically poor population appear to be proportional to the economic value of each sex and with the way children, mainly girls, were treated at the time.

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## Legends to figures

**Fig. 1.** Map of southwest Europe and western Mediterranean. Portugal is shown in detail to the right; the present sample comes from the cities indicated and their districts.

**Fig. 2.** Line graphs comparing fluctuating asymmetry (FA) between female and male individuals. A - Overall FA; B - Comparable FA; C - Comparable large sample FA. X axis: teeth with available data ordered by time of crown formation; Y axis: FA percentage.

**Table 1.** Kendall's *tau*-b rank correlation coefficients of left and right side expressions (male and female individuals aggregated).

| Trait (and tooth) | Kendall's *tau*-b | Trait (and tooth) | Kendall's *tau*-b |
|---|---|---|---|
| Double shoveling (UI1) | 0.737 | Anterior fovea (LM1) | 0.832 |
| Interruption grooves (UI1) | 0.268 | Groove pattern (LM1) | 0.545 |
| Interruption grooves (UI2) | 0.337 | Protostylid (LM1) | 0.606 |
| Peg incisors (UI2) | 0.785 | MMPT (LM1) | -0.014 |
| Distal accessory ridge (UC) | 0.662 | C5 (LM1) | 0.859 |
| Accessory cusps (UP3) | N/A | C6 (LM1) | 0.890 |
| Accessory crests (UP3) | 0.393 | C7 (LM1) | 0.639 |
| Tricuspid premolars (UP3) | N/A | Groove pattern (LM2) | 0.610 |
| Accessory cusps (UP4) | 0.345 | Distal trigonid crest (LM2) | 0.565 |
| Accessory crests (UP4) | 0.440 | Protostylid (LM2) | 0.448 |
| Tricuspid premolars (UP4) | N/A | MMPT (LM2) | 0.456 |
| Carabelli's trait (UM1) | 0.742 | C5 (LM2) | 0.713 |
| Metaconule (UM1) | 0.638 | C6 (LM2) | 0.815 |
| Mesial marginal accessory tubercles (UM1) | 0.235 | C7 (LM2) | 1.000 |
| Enamel extensions (UM1) | 0.760 | Groove pattern (LM3) | 0.356 |
| Hypocone (UM2) | 0.707 | Distal trigonid crest (LM3) | 0.485 |
| Enamel extensions (UM2) | 0.720 | Protostylid (LM3) | 0.065 |
| Enamel extensions (UM3) | 0.680 | MMPT (LM3) | 0.285 |
| Distal accessory ridge (LC) | 0.675 | C5 (LM3) | 0.635 |
| Odontome (LP3) | N/A | C6 (LM3) | 0.413 |
| Lingual cusp number (LP3) | 0.617 | C7 (LM3) | -0.011 |
| Odontome (LP4) | 1.000 | *Foramina mentales* | 0.296 |
| Lingual cusp number (LP4) | 0.572 | Mylohyoid bridge | 0.529 |
| Deflecting wrinkle (LM1) | 0.519 | | |

Underlined – $p < 0.01$; N/A – not available; MMPT – mandibular molar pit-tubercle; C – cusp.

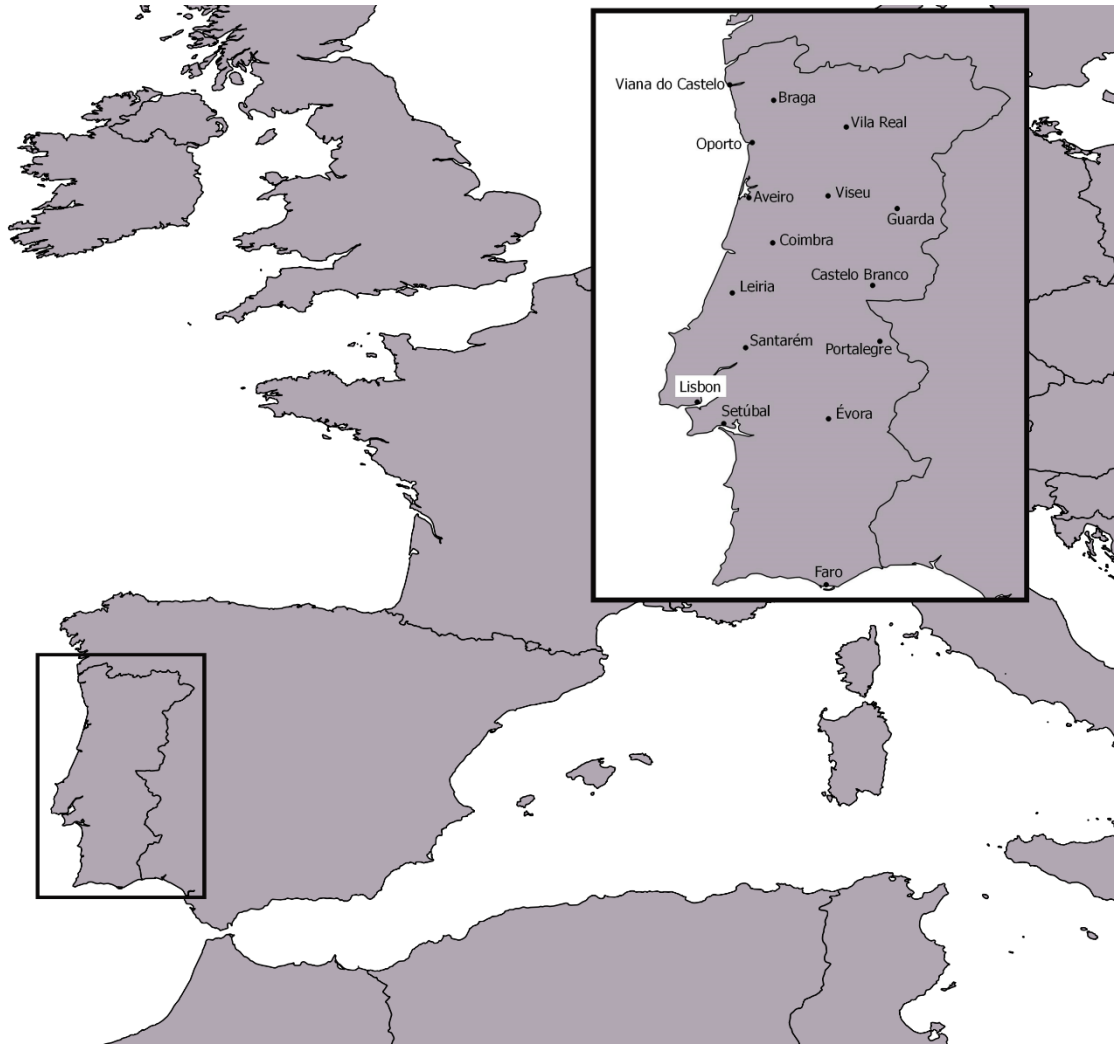
**Table 2.** Female and male overall FA and "comparable FA" frequencies for each scored nonmetric trait. Breakpoints used to exclude bilateral absences in "comparable FA" are stated for each trait.

| Trait (and tooth) | Female overall FA | Male overall FA | Female "comparable FA" | Male "comparable FA" |
|---|---|---|---|---|
| Double shoveling (UI1)<br>+ = ASU 2-6 | 2.9%<br>(2/68) | 0.0%<br>(0/67) | 100%<br>(2/2) | N/A |
| Interruption grooves (UI1)<br>+ = ASU 1 | 4.7%<br>(4/85) | 5.0%<br>(5/101) | 100%<br>(4/4) | 100%<br>(5/5) |
| Interruption grooves (UI2)<br>+ = ASU 1 | 12.9%<br>(15/116) | 12.2%<br>(14/115) | 83.3%<br>(15/18) | 87.5%<br>(14/16) |
| Peg incisors (UI2)<br>+ = ASU 1-2 | 2.7%<br>(4/146) | 0.7%<br>(1/148) | 57.1%<br>(4/7) | 50.0%<br>(1/2) |
| Distal accessory ridge (UC)<br>+ = ASU 1-5 | 15.0%<br>(15/100) | 26.3%<br>(25/95) | 21.1%<br>(15/**71**) | 41.7%<br>(25/**60**) |
| Accessory cusps (UP3)<br>+ = ASU 1 | 0.7%<br>(1/144) | 0.7%<br>(1/143) | 100%<br>(1/1) | 100%<br>(1/1) |
| Accessory crests (UP3)<br>+ = ASU 1 | 1.4%<br>(2/141) | 2.8%<br>(4/145) | 50.0%<br>(2/4) | 100%<br>(4/4) |
| Tricuspid premolars (UP3)<br>+ = ASU 1 | 0.0%<br>(0/157) | 0.0%<br>(0/189) | N/A | N/A |
| Accessory cusps (UP4)<br>+ = ASU 1 | 3.1%<br>(4/129) | 3.2%<br>(4/125) | 100%<br>(4/4) | 66.7%<br>(4/6) |
| Accessory crests (UP4)<br>+ = ASU 1 | 14.0%<br>(17/121) | 9.8%<br>(10/102) | 73.9%<br>(17/23) | 50.0%<br>(10/20) |
| Tricuspid premolars (UP4)<br>+ = ASU 1 | 0.0%<br>(0/152) | 0.0%<br>(0/158) | N/A | N/A |
| Carabelli's trait (UM1)<br>+ = ASU 2-7 | 18.1%<br>(28/155) | 14.5%<br>(19/131) | 58.8%<br>(20/34) | 43.5%<br>(10/23) |
| Metaconule (UM1)<br>+ = ASU 2-5 | 6.0%<br>(10/167) | 2.7%<br>(4/148) | 77.8%<br>(7/9) | 50.0%<br>(1/2) |
| Mesial marginal accessory tubercles (UM1)<br>+ = Scott and Turner (1997) 1 | 2.6%<br>(4/152) | 2.2%<br>(3/137) | 100%<br>(4/4) | 60.0%<br>(3/5) |
| Enamel extensions (UM1)<br>+ = ASU 1-3 | 1.7%<br>(2/118) | 0.0%<br>(0/86) | 33.3%<br>(2/6) | N/A |
| Hypocone (UM2)<br>+ = ASU 1-5 | 30.9%<br>(47/152) | 27.3%<br>(42/154) | 35.9%<br>(47/**131**) | 30.4%<br>(42/**138**) |
| Enamel extensions (UM2)<br>+ = ASU 1-3 | 7.6%<br>(9/119) | 5.3%<br>(5/94) | 47.4%<br>(9/19) | 38.5%<br>(5/13) |
| Enamel extensions (UM3)<br>+ = ASU 1-3 | 2.0%<br>(1/49) | 3.9%<br>(2/51) | 33.3%<br>(1/3) | 66.7%<br>(2/3) |
| Distal accessory ridge (LC)<br>+ = ASU 1-5 | 5.8%<br>(8/139) | 11.8%<br>(14/119) | 21.1%<br>(8/**38**) | 34.1%<br>(14/**41**) |
| Odontome (LP3)<br>+ = ASU 1 | 0.0%<br>(0/195) | 0.0%<br>(0/196) | N/A | N/A |
| Lingual cusp number (LP3)<br>+ = ASU 2-9 | 14.8%<br>(24/162) | 11.6%<br>(19/164) | 64.9%<br>(24/**37**) | 51.4%<br>(19/**37**) |
| Odontome (LP4)<br>+ = ASU 1 | 0.0%<br>(0/165) | 0.0%<br>(0/192) | 0.0%<br>(0/1) | N/A |
| Lingual cusp number (LP4)<br>+ = ASU 2-9 | 26.8%<br>(33/123) | 19.7%<br>(27/137) | 42.3%<br>(33/**78**) | 31.8%<br>(27/**85**) |
| Deflecting wrinkle (LM1)<br>+ = ASU 1-3 | 1.9%<br>(2/108) | 2.2%<br>(3/135) | 50.0%<br>(2/4) | 75.0%<br>(3/4) |
| Anterior fovea (LM1)<br>+ = ASU 1-4 | 5.3%<br>(6/114) | 1.6%<br>(2/129) | 27.3%<br>(6/22) | 9.5%<br>(2/21) |
| Groove pattern (LM1)<br>+ = ASU Y | 4.7%<br>(6/127) | 3.5%<br>(5/144) | 5.0%<br>(6/**119**) | 3.6%<br>(5/**138**) |
| Protostylid (LM1)<br>+ = ASU 1-7 | 4.8%<br>(6/124) | 6.2%<br>(8/129) | 28.6%<br>(6/21) | 42.1%<br>(8/19) |
| MMPT (LM1)<br>+ = Weets (2009) [adpt.] 1-3+ | 0.8%<br>(1/132) | 0.7%<br>(1/148) | 100%<br>(1/1) | 100%<br>(1/1) |

**Table 2. Continued.**

| Trait (and tooth) | Female overall FA | Male overall FA | Female "comparable FA" | Male "comparable FA" |
|---|---|---|---|---|
| C5 (LM1) | 12.0% | 7.5% | 13.3% | 8.5% |
| + = ASU 1-5 | (13/108) | (10/134) | (13/**98**) | (10/**118**) |
| C6 (LM1) | 0.0% | 1.3% | 0.0% | 66.7% |
| + = ASU 1-5 | (0/130) | (2/159) | (0/1) | (2/3) |
| C7 (LM1) | 0.8% | 2.7% | 33.3% | 40.0% |
| + = ASU 1a-4 | (1/129) | (4/148) | (1/3) | (4/10) |
| Groove pattern (LM2) | 13.8% | 7.7% | 18.3% | 9.6% |
| + = ASU + and X | (21/152) | (12/156) | (21/**115**) | (12/**125**) |
| Distal trigonid crest (LM2) | 2.5% | 0.0% | 50.0% | 0.0% |
| + = ASU 1 | (4/163) | (0/170) | (4/8) | (0/2) |
| Protostylid (LM2) | 5.3% | 7.7% | 61.5% | 57.9% |
| + = ASU 1-7 | (8/151) | (11/142) | (8/13) | (11/19) |
| MMPT (LM2) | 3.5% | 0.6% | 85.7% | 33.3% |
| + = Weets (2009) [adpt.] 1-3+ | (6/173) | (1/169) | (6/7) | (1/3) |
| C5 (LM2) | 7.8% | 9.0% | 56.5% | 51.7% |
| + = ASU 1-5 | (13/166) | (15/166) | (13/23) | (15/29) |
| C6 (LM2) | 0.6% | 0.0% | 100% | 0.0% |
| + = ASU 1-5 | (1/176) | (0/181) | (1/1) | (0/2) |
| C7 (LM2) | 0.0% | 0.0% | N/A | N/A |
| + = ASU 1a-4 | (0/180) | (0/177) | | |
| Groove pattern (LM3) | 15.1% | 17.0% | 57.9% | 59.3% |
| + = ASU Y | (11/73) | (16/94) | (11/19) | (16/27) |
| Distal trigonid crest (LM3) | 4.8% | 5.6% | 28.6% | 33.3% |
| + = ASU 1 | (4/84) | (5/90) | (4/14) | (5/15) |
| Protostylid (LM3) | 2.4% | 7.1% | 66.7% | 100% |
| + = ASU 1-7 | (2/85) | (6/85) | (2/3) | (6/6) |
| MMPT (LM3) | 30.0% | 15.7% | 80.0% | 70.0% |
| + = Weets (2009) [adpt.] 1-3+ | (24/80) | (14/89) | (24/30) | (14/20) |
| C5 (LM3) | 26.7% | 22.6% | 60.5% | 42.2% |
| + = ASU 1-5 | (23/86) | (19/84) | (23/**38**) | (19/**45**) |
| C6 (LM3) | 16.3% | 4.1% | 94.1% | 57.1% |
| + = ASU 1-5 | (16/98) | (4/98) | (16/17) | (4/7) |
| C7 (LM3) | 1.1% | 0.9% | 100% | 100% |
| + = ASU 1a-4 | (1/95) | (1/114) | (1/1) | (1/1) |
| *Foramina mentales* | 1.7% | 3.4% | 62.5% | 83.3% |
| + = >1 | (5/292) | (10/291) | (5/8) | (10/12) |
| Mylohyoid bridge | 10.6% | 10.9% | 64.3% | 54.5% |
| + = >0 | (27/254) | (24/220) | (27/**42**) | (24/**44**) |

MMPT - mandibular molar pit-tubercle; C - cusp; N/A - data not available; **bold** - large samples with ≥30 trait presences.


Viana do Castelo
Braga
Vila Real
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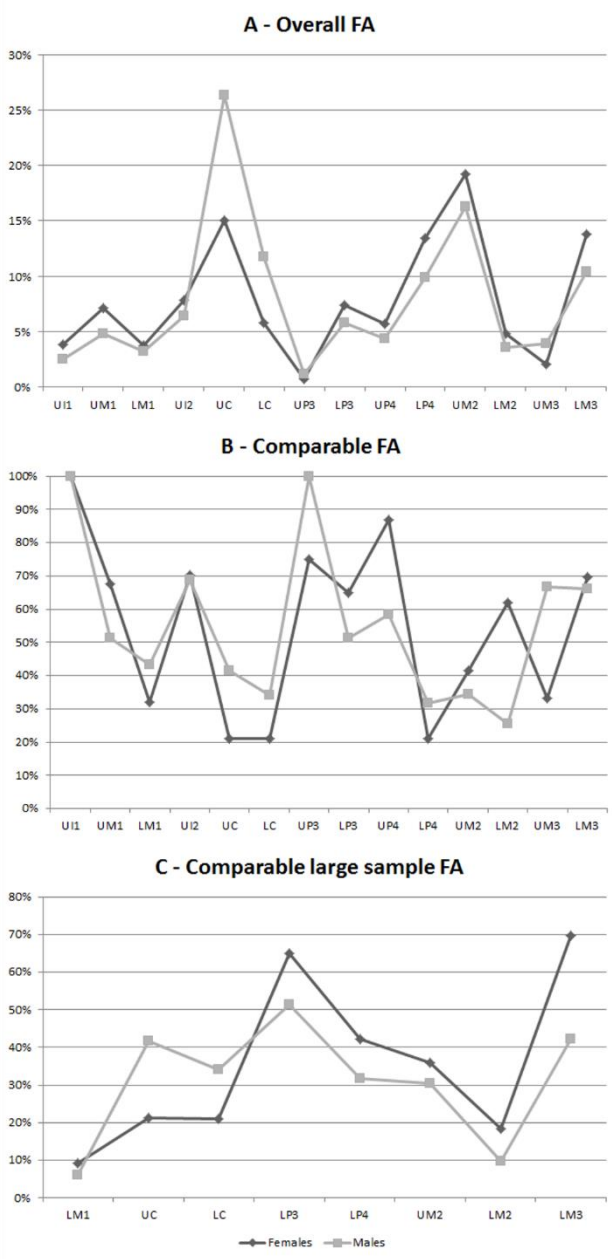
Aveiro
Viseu
Guarda
Coimbra
Castelo Branco
Leiria
Santarém
Portalegre
Lisbon
Setúbal
Évora
Faro

**Fig. 1**


A - Overall FA
30%
25%
20%
15%
10%
5%
0%
UI1 UM1 LM1 UI2 UC LC UP3 LP3 UP4 LP4 UM2 LM2 UM3 LM3
B - Comparable FA
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
UI1 UM1 LM1 UI2 UC LC UP3 LP3 UP4 LP4 UM2 LM2 UM3 LM3
C - Comparable large sample FA
80%
70%
60%
50%
40%
30%
20%
10%
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LM1 UC LC LP3 LP4 UM2 LM2 LM3
Females
Males

**Fig. 2**