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SYSTEMATIC REVISION

Carabelli's trait: Definition and review of a commonly used dental non-metric variable

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ABSTRACT

Carabelli's trait has been studied for more than 150 years. The use of this dental morphological trait in biodistance analyses, phylogenetic studies, kinship inference and forensic anthropology is broadly documented. Due to these and other anthropological and evolutionary applications of the trait, and to its variability, it is still a subject of interest in the anthropological literature. This work aims to briefly define and review the character and its research history. Known since 1827 and made popular by Georg Carabelli, an Austrian dentist, Carabelli's trait is usually considered to not present sexual dimorphism. It has been one of the main variables in establishing reliable recording methodology for dental non-metric traits. It presents distinctions in population frequencies and can be related with the expression of other traits besides being generally considered hereditary.

All of these issues will be presented and discussed, in order to establish the potential bibliographical foundations of future research approaches.

Keywords: Dental morphology; biodistance and phylogenetics; intertrait correlations; cusp of Carabelli; Carabelli's tubercle.

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RESUMO

O carácter de Carabelli é estudado há mais de 150 anos. O uso deste traço morfológico dentário em análises de distâncias biológicas, estudos filogenéticos, aferição de parentesco, e antropologia forense está amplamente documentado. Devido a estas e outras aplicações em Antropologia e Evolução, e à sua variabilidade, mantém-se um assunto de interesse na literatura antropológica. O presente trabalho tem como propósitos definir e rever brevemente este traço e a história da investigação que lhe é relativa. Conhecido desde 1827 e popularizado pelo dentista austríaco Georg Carabelli, o carácter de Carabelli é considerado normalmente como isento de dimorfismo sexual. Foi uma das principais variáveis usadas na criação de uma metodologia de registo de traços morfológicos dentários fiável. Apresenta distintas frequências populacionais. Pode estar relacionado com a expressão doutras características, além de ser geralmente considerado hereditário. Todos estes assuntos serão apresentados e discutidos, de modo a estabelecer potenciais bases bibliográficas de futuras abordagens científicas.

Palavras-chave: Morfologia dentária; distância biológica e filogenética; correlações de caracteres morfológicos; cúspide de Carabelli; tubérculo de Carabelli.

Introduction

The Morphology subfield of Dental Anthropology has the objective of recording, evaluating and interpreting metric and non-metric morphological crown and root traits (Scott and Turner, 1988; 1997; Jernvall and Jung, 2000; Aguirre *et al.*, 2006). In 1670, the Dutchman Kerkring was the first anatomist to describe the morphological variations of the skull (Silva, 2012). Then, these variations were seen as anomalies, and only by the mid-20th century were they first recognized not as anomalies, but as variables that allowed the evaluation of the degree of likeliness/divergence existing amongst the various human populations (Silva, 2012). Presently, these skeletal and dental variations are considered in kinship studies, which allow for socio-political understanding of population structures and can shed light on post-marital residence as well as other demographic processes (Larsen, 2002; Silva, 2012; Stojanowski and Schillaci, 2006).

Contrarily to osseous elements, teeth have the advantage of better preservation, since they are composed by hard and highly mineralized materials, such as enamel, dentine and cement, which can resist taphonomical changes in environments prone to fast diagenesis (Turner, 1967; Scott and Turner, 1988; Turp and Alt, 1998; Silva, 2012; Hillson, 2005; Aguirre *et al.*, 2006; Scott, 2008; Irish and Nelson, 2008). Another advantage is that teeth, once formed, do not undergo changes in morphology like bones; dental discrete traits, however, can disappear due to dental wear and certain oral pathologies like caries (Scott and Turner, 1988; Jernvall and Jung, 2000; Scott, 2008; Irish and Nelson, 2008).

Currently, over 100 dental morphological traits are known (Aguirre *et al.*, 2006; for a recent example, see Cunha *et al.*, 2012). These elements are dependent on strong genetic control. They present slow and selectively neutral evolutionary changes and little sexual dimorphism (Tyrrell, 2000). They are phenotypically manifested at a precise genetically controlled position and morphological variation (Turner, 1967; Jernvall and Jung, 2000; Aguirre *et al.*, 2006). Despite this, they are also subject to some environmental influence (Biggerstaff, 1967; Townsend and Martin, 1992; Sperber, 2004; Rizk *et al.*, 2008). These traits can have negative or positive manifestations with different degrees of expression. A cusp is an example of a positive trait, while a pit can exemplify a negative one (Scott and Turner, 1997; Silva, 2012; Aguirre *et al.*, 2006).

Teeth, besides giving information about diet, can enlighten the phylogenetic and biological affinities among different human populations and different hominin species (Scott and Turner, 1988; 1997; 2008; Jernvall and Jung, 2000; Silva, 2012; Guatelli-Steinberg and Irish, 2005; Aguirre *et al.*, 2006). Consequently, dental morphology enables classification of different populations and species into taxonomies (Aguirre *et al.*, 2006). It also has an important role in Forensic Anthropology, since it can aid in identifying an individual or his/her ancestry (Pretty and Sweet, 2001; Aguirre *et al.*, 2006; Edgar, 2009a; 2013). Despite this, the use of one or few dental traits is limited, so the use of multiple characters, all degrees of expression and complex analysis is recommended (Edgar, 2009b).

The use of genetic analysis in inferring the degree of kinship or the biological affinities from skeletal material has undergone great development. Still, it requires uncontaminated material and its (at least partial) destruction. Besides this, costs inherent to such methodologies tend to be elevated. With the analysis of dental discrete variables, destruction of odontological material is not required and the study of kinship and population phylogenetic distance is also possible to carry out, although at a much lower cost (Silva, 2012; Marado, 2010; 2012; In prep.). Besides using skeletal material, dental morphological traits, such as Carabelli's trait, can be recorded *in vivo*, so that biological affinities between past and present populations can be addressed (Tsai *et al.*, 1996; Silva, 2012). Carabelli's trait is one of the most studied discrete traits (Joshi *et al.*, 1972). This article reviews its definition, types of classification, population frequencies, sexual dimorphism and intertrait correlations.

Carabelli's trait definition

This character was first observed in 1827 by Rousseau (Joshi *et al.*, 1972). However, it is most commonly known as Carabelli's trait, cusp or tubercle, due to the observations of Georg Carabelli, the dentist of Austrian Emperor Franz in 1842 (Carbonell, 1960; Joshi *et al.*, 1972; Hillson, 1996). This trait has also been designated *tuberculum anomalum*, *tuberculum impar*, fifth lobe, supplementary cusp, additional cusp, protostyle (see Kraus, 1951), mesiolingual/mesiopalatal elevation or prominence (Kraus, 1951; Meredith and Hixon, 1954; Carbonell, 1960; Sadatullah *et al.*, 2012).

Carabelli's trait (Figure 1) is expressed on the lingual surface of the mesiolingual cusp (the protocone, or cusp 1). It occurs on maxillary molars, with greater frequency in the upper first permanent molar, with decreased frequency in the second permanent molar and is rarely expressed on third permanent or second deciduous molars (Dietz, 1944; Meredith and Hixon, 1954; Carbonell, 1960; Turner, 1967; Biggerstaff, 1973; Alvesalo *et al.*, 1975; Kolakowski *et al.*, 1980; Scott, 1980; Turner *et al.*, 1991; Townsend and Martin, 1992; Hillson, 1996; Tsai *et al.*, 1996; Hsu *et al.*, 1999; Codinha, 2001; Silva, 2012; Kondo and Townsend, 2006; Sadatullah *et al.*, 2012). Dietz (1944), in his study of American soldiers, observed that the Carabelli's trait was present on the second molar only when the first molar presented it, and on the third molar (with a small expression) only if expressed on the second molar.

This variable is expressed in several forms, from a little groove (also known as negative cusp) to a large triangular cusp (Meredith and Hixon, 1954; Dahlberg, 1963; Alvesalo *et al.*, 1975; Laatikainen and Ranta, 1996; Hsu *et al.*, 1999).

Figure 1: Left maxilla. The upper first molar presents a small cuspal form of Carabelli's trait (ASUDAS grade 5). The upper second molar presents a smooth lingual surface (ASUDAS grade 0) of the protocone (cusp 1).

The function of Carabelli's trait is still uncertain (Guatelli-Steinberg and Irish, 2005). Some authors hypothesize that the trait evolved recently to make up for dental size reduction, a secular trend (Scott, 1979; Tsai *et al.*, 1996; Hsu *et al.*, 1999). An alternative, in opposition to the latter, was also suggested, stating that the trait is primitive and molar reduction is indeed causing its disappearance (Scott, 1979; Tsai *et al.*, 1996; Hsu *et al.*, 1999). A third supposition argues that Carabelli's trait can supply the first upper molar with greater resistance to biomechanical stress (Tsai *et al.*, 1996; Hsu *et al.*, 1999).

Bilateralism and symmetry

Generally, Carabelli's trait is seen as being bilateral and symmetrical in the expressed grades of each superior dental arch (Dietz, 1944; Meredith and Hixon, 1954; Carbonell, 1960; Joshi *et al.*, 1972; Alvesalo *et al.*, 1975; Townsend and Martin, 1992; Laatikainen and Ranta, 1996; Khamis *et al.*, 2006), but the degree of asymmetry varies with each population (Kolakowski *et al.*, 1980). However, despite the majority of research reporting large frequency of bilateral and symmetric expressions of the trait, there is also some percentage of asymmetry, either when presence/absence or expression grades are considered (Dietz, 1944; Meredith and Hixon, 1954; Carbonell, 1960; Joshi *et al.*, 1972; Alvesalo *et al.*, 1975; Townsend and Martin, 1992; Laatikainen and Ranta, 1996; Khamis *et al.*, 2006; Sadatullah *et al.*, 2012). Equal genetic information on both sides is assumed, with an expected consequence of symmetry in presence and expression. Asymmetry could be the result of environmental effects on individual odontogeny (Khamis *et al.*, 2006; Van Dongen and Gangestad, 2011).

Sexual dimorphism

There has been a lively debate on the existence of sexual dimorphism in Carabelli's trait (Tsai *et al.*, 1996). Some research corroborates (Hsu *et al.*, 1999; Khamis *et al.*, 2006; Kondo and Townsend, 2006) while other negates sexual dimorphism in the expression of Carabelli's trait in some analyzed populations (Biggerstaff, 1973; Alvesalo *et al.*, 1975; Scott, 1978; Scott, 1980; Kolakowski *et al.*, 1980; Townsend and Martin, 1992; Laatikainen and Ranta, 1996). According to Townsend and Martin (1992), this inconsistency is due to sexual dimorphism being a population-specific characteristic. Tsai and colleagues (1996) and Hsu and colleagues (1999) underline the difficulty in comparing results from different studies, since authors commonly apply different methodologies and sample sizes vary.

Meredith and Hixon (1954) observed 200 first molars from 50 boys and 50 girls. Boys (66 teeth) more often presented a greater expression of Carabelli's cusp than girls (53 teeth). Joshi and colleagues (1972) reported a quantitative difference between sexes, since 69.5% of 198 boys presented the trait, when compared to 61.2% of the girls. These differences remain unexplained. Possibly, it is related to odontogenic differences between the sexes or corresponds to a greater retention of a primitive cusp in males, since Carabelli's trait can diminish biomechanical stress, as previously referred (Tsai *et al.*, 1996; Hsu *et al.*, 1999). Some light was recently shed on this issue, since it can be related to the role of tooth size in the patterning cascade model (Salazar-Ciudad and Jernvall, 2002; see below).

Classification systems

There are several classificatory systems describing Carabelli's trait (Scott, 1980). This caused a lack of uniformity regarding the recording of the trait in different studies, complicating the comparison between different populations (Laatikainen and Ranta, 1996; Hsu *et al.*, 1999; Silva, 2012).

Many methodologies entail for some subjectivity (Laatikainen and Ranta, 1996). Besides the subjective descriptions and the attribution of different number of grades in each system, there are methods without illustrative images or photographs, which enhance confusion and subjectivity among researchers using the same system.

In the late 1940s, Albert A. Dahlberg created a system for recording several characters, including Carabelli's trait, since he considered it would not suffice to record presence or absence (Turner *et al.*, 1991). That method introduced several plaques molding each expression of the traits, from minimal to maximal. It has been altered successively by Dahlberg and his students and followers (see Dahlberg [1963], for example), reaching its current status as one of the most used methodologies (Silva, 2012). This is known as the Arizona State University Dental Anthropology System, ASUDAS, or ASU standards. The plaque used to characterize Carabelli's cusp was originally conceived by Dahlberg in 1956. The current ASUDAS considers eight grades of expression, where the letters used by Dahlberg have been replaced by numbers (Turner *et al.*, 1991). The grades are exemplified in Figure 2. Those are:

0 – Absent (Fig. 2a);

1 – Presence of a groove (Fig. 2b);

2 – Presence of a pit (Fig. 2c);

3 – Small Y shaped depression (Fig. 2d);

4 – Large Y shaped depression (Fig. 2e);

5 – Small cusp without free apex, not contacting the lingual groove (Fig. 2f);

6 – Medium sized cusp (no free apex), contacting the lingual groove (Fig. 2g);

7 – Large free cusp (Fig. 2h).

Some authors only consider trait presence when dealing with grades 5 to 7, with a positive expression of Carabelli's cusp. This deems grades 0 and 1 to 4, respectively, its absence and negative expressions (Silva, 2012).

Despite the fact that ASUDAS is most commonly used, other classification systems were created, like those by Meredith and Hixon (1954) who constructed a four categories system and Alvesalo and colleagues (1975) who created a five class system to categorize the Carabelli's trait.

Population affinities and frequencies of Carabelli's trait

Carabelli's trait is not exclusive to *Homo sapiens*; despite its rarity in fossil forms, it exists in *Australopithecus* sp., *Paranthropus* sp., Neanderthals and great apes (Carbonell, 1960; Swindler *et al.*, 1998; Guatelli-Steinberg and Irish, 2005; Harris, 2007). It is phylogenetically very old (Kolakowski *et al.*, 1980). This means the trait is evolutionarily meaningful based on its development following the phylogenetic branch from which modern man originated (Carbonell, 1960). Despite this, Carabelli's trait in *Pan* sp., *Australopithecus* sp. and *Paranthropus* sp. can occur merely as a developmental anomaly (Ortiz *et al.*, 2012) and can be homoplastic, surfacing multiple times in diverse species due to the interplay between tooth size and intercuspal distances (Hunter *et al.*, 2010; Moormann *et al.*, 2013).

In *Homo sapiens*, Carabelli's trait frequencies vary depending on the population (Laatikainen and Ranta, 1996). It is one of the most used traits in biodistance studies (Joshi *et al.*, 1972).

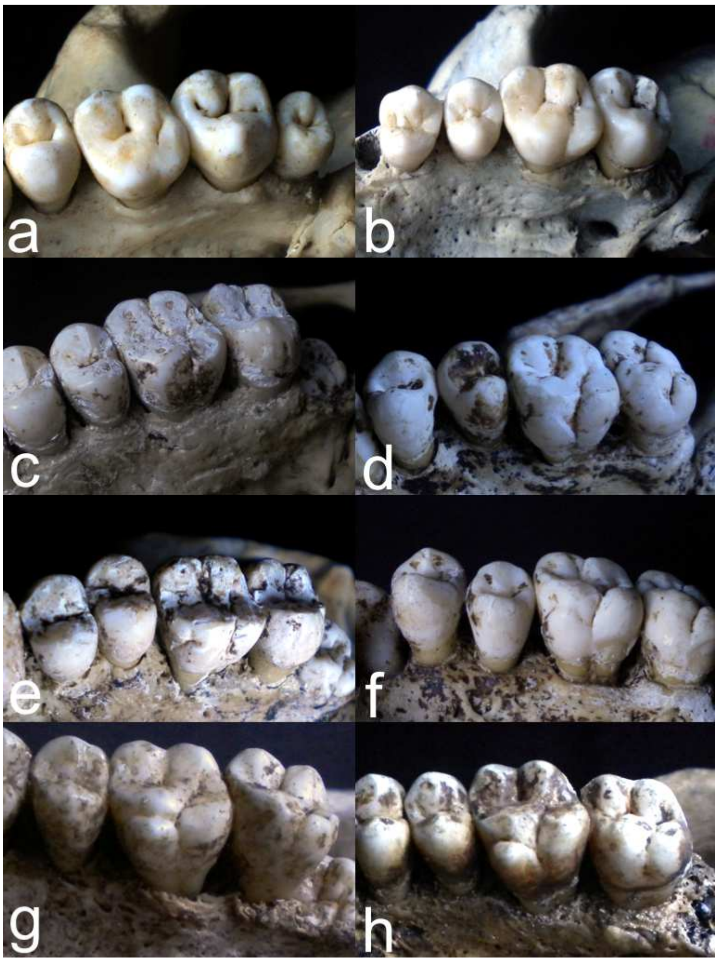

Figure 2. Different expressions of Carabelli's trait, according to ASUDAS: a) smooth mesiopalatal surfaces on the first (UM1) and second upper molars (grade 0; note also the reduced third molar); b) slight diagonal groove on the palatal surface of the mesiolingual cusp of UM1 (grade 1); c) mesiolingual cusp of UM1 indentation on the most occlusal and mesial corner of the lingual facet (grade 2, darkened *post mortem*; note forming third molar) ; d) ASU grade 3 (small Y shaped groove); e) grade 4 (deeper and larger Y shaped groove); f) grade 5 (small mesiolingual cusp; g) grade 6; h) grade 7. Images d, e, g and h are from the right side of the upper dental arcade. Images a, b, c and f are from the left side.

Several studies suggested it is predominant in Europe or peoples derived from European populations (Carbonell, 1960; Turner, 1967; Joshi *et al.*, 1972; Alvesalo *et al.*, 1975; Scott, 1980; Laatikainen and Ranta, 1996; Tsai *et al.*, 1996).

The trait was also present in Portuguese populations of several historic contexts (Codinha, 2001; Trinkaus *et al.*, 2001; Correia and Pina, 2002; Silva, 2012). For example, Trinkaus and colleagues (2001) observed this trait in an individual from the Upper Paleolithic. Silva (2012) reported frequencies for several Neolithic individuals, Codinha (2001) found it in three Medieval individuals and in 1921, Corrêa found that 13.5% of his Portuguese contemporary sample had Carabelli's trait (according to Correia and Pina, 2002).

Several researchers testified to an intermediate frequency among African populations and lower frequencies in Asian ones (Carbonell, 1960; Turner, 1967; Alvesalo *et al*., 1975; Scott, 1980; Tsai *et al*., 1996). Carabelli's trait was also rarely found in Inuit and Bushmen (Joshi *et al.*, 1972). Low Carabelli's trait frequency and high presence of shoveling was found to be characteristic of Asian populations, distinguishing them from European ones (Tsai *et al*., 1996; Hsu *et al*., 1999).

In order to further clarify the world-wide and Portuguese diachronic distributions of frequencies in *Homo sapiens* samples, Tables 1 and 2 were projected. It shows the wide diversity of this trait frequency, whatever the breakpoint selected, and counters some of the cited research.

The higher frequency for West Asian samples (32%), from Mediterranean, Near and Middle Eastern populations, and the equivalence of European (22.6%) and North African (22.7%) frequencies in Hanihara's (2008) data suggest that population differences can be diluted when dealing with large, geographically wide samples (see Table 1).

Scott and Turner (1997) reports put Western Europe on top as having the greatest frequency for Carabelli's trait (27.3%; Table 2). However, lower frequencies were documented for Northern Europe (18.1%) than for North Africa (20.0%), West Africa (21.3%) and Southeast Asia (20.8%).

Portuguese Late Neolithic/Chalcolithic samples (Silva, 2012) showed the variability that relatively close samples can present. As for Coimbra, its frequency was in line with other European samples (24.2%).

Intertrait correlations

Intertrait correlations have been a point of interest in dental morphology for a long time, since some statistical tests depend on trait independence (Scott and Turner, 1997) and taxonomical considerations should be derived only from independent morphological variables (Kangas *et al.*, 2004; Salazar-Ciudad and Jernvall, 2010; Skinner and Gunz, 2010).

There is a trend indicating that larger sized Carabelli cusps are correlated with larger molars, while molars with negative expressions of the trait are smaller (Tsai *et* *al.*, 1996; Hsu *et al.*, 1999; Kondo and Townsend, 2006). Kondo and Townsend (2006) report that mesiodistal and buccolingual measures of the dental crown are enhanced in the presence of Carabelli's cusp. Longer time of formation for larger molars may allow for the fifth enamel knot to produce the infolding of the inner enamel epithelium, thus forming the cusp. Smaller teeth may present only the reduced form of the trait, such as pits or grooves. This may explain the previously reported difference in frequencies and expression between male and female individuals of the same population (Kondo and Townsend, 2006).

Tsai and colleagues (1996), and Hsu and colleagues (1999) only describe differences related to the cusp presence in the bucco-lingual dimension.

Dietz (1944) noted that Carabelli's trait frequency is related to the shape of upper central incisors. The ones with more quadrangular shape were more likely to be correlated with the presence of Carabelli's trait on the first molars, and with larger such cusps, than upper central incisors with different shapes.

Chinese populations tend to have relatively small molars, which could be related to lower frequencies of this trait (Hsu *et al.*, 1999). Hsu and colleagues (1999) noted a positive correlation between shoveling and Carabelli's trait in Asian populations, which is to say there was an increase in the likeliness of occurrence of Carabelli when there was shoveling presence in incisors. This suggests the two traits could be developmentally connected, despite what was stated above (their aptitude in distinguishing Asian and European populations). Carabelli's trait is also positively correlated with hypocone (Scott, 1979) and protostylid (Scott, 1980). The hypocone is also known as C4 (cusp 4) or disto-lingual cusp, occurring in upper molars (Turner *et al.*, 1991; Scott and Turner, 1997; Silva, 2012). The protostylid is a tubercle emanating from the cingular region of lower molars, namely in the buccal surface of the mesiobuccal cusp (Scott, 1978). Associations between Carabelli's cusp and protostylid are also suggested by Townsend and colleagues (1990), who hypothesize that this set of variables could be evolutionarily advantageous.

This covariation (and the relation between molar size and Carabelli's traits mentioned above) could, however, be related to a morphodynamic process, the patterning cascade model. Tooth size and intercuspal distances seem to be correlated to the presence of some traits, since when the tooth is large enough, and given an appropriately small mean intercuspal distance, other enamel knots can be formed, in addition to the ones corresponding to the main cusps. This seems to be due to each enamel knot disabling the possibility of the formation of another knot along an area surrounding it. The patterning cascade model interconnects genotype, environment and phenotype, since the guidelines provided by genetics, given its environmental framing, contribute in producing phenotype (Salazar-Ciudad and Jernvall, 2002; 2010). Some traits have been demonstrated to corroborate this model, most importantly Carabelli's trait

(Hunter *et al.*, 2010; Moormann *et al.*, 2013), but also C6 on chimpanzee lower molars (Skinner and Gunz, 2010), the hypocone and upper molar additional cups (Moormann *et al.*, 2013).

Table 1: Distribution of the frequencies of the Carabelli's trait (sex-pooled) in six samples from contemporary world-wide populations.

Source (and breakpoint)	Sample origin	Frequency (%)	*n*
Hanihara, 2008 (+ = ASU 3-7)	East/Northeast Asia	9.1	367
	Southeast Asia	15.1	919
	West Asia	32.0	228
	Europe	22.6	738
	North Africa	22.7	286
	Sub-Saharan Africa	17.1	831

Carabelli's trait revealed slight correlation with intercuspal distances in upper first molars (Hunter *et al.*, 2010; Moormann *et al.*, 2013) and an indication of the same trend on upper second molars (Moormann *et al.*, 2013). In the latter tooth, correlations could be hindered by tooth size and shape. Carabelli's trait on the first molar also correlates with the hypocone, since larger expressions of this latter cusp are associated with enhanced expressions of Carabelli. Finally, Carabelli's trait on upper molars correlates to upper molar accessory cusps, when a moderate number of these are present. These associations are explained by the patterning cascade model: the cusps ontogeny is possible due to an approximation of enamel knots, but the formation of a greater number of new knots can hinder the formation of Carabelli's trait; on the other hand, the latter may be associated with a few number of accessory cusps or with large hypocone expressions if their development still allows the formation of that mesiolingual enamel knot (Moormann *et al.*, 2013).

A single protein can affect several dental morphological traits, relating to intercuspal distance and exuberance in tooth morphology. Kangas and colleagues (2004), however, recognized the potential for individual traits to be independently affected by other gene activities, and merely advise caution in assuming independence of traits when comparing different species.

Table 2. Distribution of the frequencies of the Carabelli's trait (sex-pooled) in world-wide and Portuguese samples.

Source (and breakpoint)	Sample origin	Frequency (%)	*n*
Scott and Turner, 1997 (+ = ASU 5-7) Samples of widespread timeframe	Western Europe	27.3	249
	Northern Europe	18.1	138
	North Africa	20.0	200
	West Africa	21.3	61
	South Africa	11.4	246
	North and South American Natives	5.6	2054
	Southeast Asia (Recent)	20.8	701
Silva, 2012 (+ = ASU 5-7) Late Neolithic/Chalcolithic samples (except Coimbra)	Cova da Moura	20.0	15
	Dólmen de Ansião	16.7	30
	Paimogo	8.0	75
	São Paulo	12.0	25
	Serra da Roupa	0.0	14
	Monte Canelas I	0.0	17
	Coimbra (Modern)	24.2	198

Morphological variability in the mesiolingual cusp of humans and chimpanzees was compared in the outer enamel surface (OES) and enamel-dentine junction (EDJ) by Ortiz and colleagues (2012). Despite the occasional occurrence of Carabelli's trait in chimpanzees (which could be a developmental anomaly in *Pan*), the trait present on the mesiolingual cusp of these primates is different from the variability measured by ASUDAS, either on the OES or the EDJ. It is a shelf-like structure with no cusp development, called lingual cingulum. This analysis, besides clarifying the distinction between traits in the same *locus* in *Homo sapiens* and *Pan* sp., suggests the same distinction can divide *Australopithecus* sp. and *Paranthropus* sp. from *Homo* sp. The morphology of the *membrana praeformativa*, which later is mineralized as the EDJ, seems to be very important in determining OES morphology, mainly in chimpanzees, since human greater enamel thickness hinders association between grade classification of EDJ and OES morphology (Ortiz *et al.*, 2012).

The work of Ortiz and colleagues (2012) redirected focus towards the EDJ, and its baseline membrane, *membrana praeformativa*, a proto-structure which contributes to determine dental shape. The previously reviewed studies analyzing intercuspal distances and tooth size relations with Carabelli's cusp seem to overlook the odontogenic importance of this structure, assuming enamel knots (which correspond to dentine horns formed in the *membrana praeformativa*) independently predict the number and presence of accessory cusps. The complex interplay involving dental development needs to be further tested before the independence of dental morphological variables (such as Carabelli's trait) can be undoubtedly questioned.

Primary dental morphology is not generally correlated to permanent dental morphology, but one of the exceptions found is Carabelli's trait (between the upper second deciduous molar and the upper first permanent molar: Edgar and Lease, 2007).

Heredity

Another question without consensus regarding Carabelli's trait is its heredity. Some investigators report heredity in the character (Dietz, 1944; Turner, 1967; Kondo and Townsend, 2006), while others describe low degree of heredity (Biggerstaff, 1973; Alvesalo *et al.*, 1975).

Generally, studies inferring heredity are developed using monozygotic or dizygotic sets of twins. If Carabelli's trait is mostly influenced by genetic factors, a smaller variation is expected among homozygotic twins. If, however, environmental factors are the main force behind this trait variation, both sets of twins should present equal variation (Biggerstaff, 1973).

Despite reports of low heredity, genetic transmission of the trait has been accepted since early on (Kraus, 1951). There is also great debate about the model of hereditary transmission of the trait (Alvesalo *et al.*, 1975). Dietz (1944) considered Carabelli as being the result of a single gene despite its great variability. Kraus (1951), who studied the trait distribution in eight Mexican and Papago native families, proposed a biallelic model. In summary, a "normal" homozygotic individual (cc) would present a smooth mesiolingual molar surface while a homozygotic individual with alleles for trait presence (CC) would present an exuberant Carabelli cusp. A heterozygotic individual (Cc) would present intermediate grades of expression. Goose and Lee (1971 *in* Alvesalo *et al.*, 1975) argued in their study that Kraus's (1951) model did not correspond to results, suggesting a polygenic model. Biggerstaff (1973) stated the trait is determined by different genes for each side of the dental arcade, while in 1980 Baume and Crawford referred genetic information to be equal along each side and asymmetry to be determined by environmental factors (Townsend and Martin, 1992). The models tested for inheritance of this trait could not be fitted for all samples tested, which could be due to the irregular influence of environmental factors and the uncertain genetic influence of a major locus (Kolakowski *et al.*, 1980). As pointed out above, the proportion to which Carabelli's trait is influenced by genetic or environmental factors is not known (Townsend and Martin, 1992). Carabelli's trait may be more frequently present on the deciduous dentition, which can be caused by reduced penetrance on the secondary dentition. The longer developmental period of permanent tooth formation may cause this difference (Bermúdez de Castro, 1989).

Final thoughts

Carabelli's trait is one of the most studied dental traits. It is expressed through several grades of quasicontinuous variation in the palatal surface of the mesiolingual cusp of upper molars. It is most prevalent on first molars. It occurs less frequently on the second upper molar (on both permanent and temporary dentitions) and on the third upper molar. It is generally a bilateral, symmetric trait. There is no consensus on its degrees of heredity and sexual dimorphism. Generally, men present greater frequencies of the trait than women (although this difference could statistically be the result of random sampling, in most studies). The function of the trait function is uncertain. It has been suggested that it enhances molar size, it is correlated with greater biomechanical stress, and it compensates for an evolutionary trend towards diminishing molar size.

Some authors claim Carabelli's trait to be primitive, due to its appearance in the dentition of hominins and great apes (Carbonell, 1960; Kolakowski *et al.*, 1980; Tsai *et al.*, 1996; Swindler *et al.*, 1998; Hsu *et al.*, 1999; Harris, 2007), while others suggest it is a homoplasy (Tsai *et al.*, 1996; Hsu *et al.*, 1999; Guatelli-Steinberg and Irish, 2005). *Homo sapiens* shows high variability in the frequencies found for each ancestry. Previous studies demonstrate that European populations tend to present greater frequencies, African communities present intermediate percentages, while Asians, Inuit and Bushmen rarely express it (Carbonell, 1960; Turner, 1967; Joshi *et al.*, 1972; Alvesalo *et al.*, 1975; Scott, 1980; Laatikainen and Ranta, 1996; Tsai *et al.*, 1996; Hsu *et al.*, 1999). Wider surveys on dental morphology indicate that these relations are not as simple – as seen before and evidenced by Tables 1 and 2 – since variation between samples can be diluted in large scale comparisons. In fact, Asian populations vary between 9.1% and 32.0%, encompassing African variation (between 17.1% and 22.7%) and European frequency (22.6%) when the breakpoint includes grades 3 to 7 (Hanihara, 2008; see Table 1). European range of frequencies (between 18.1% and 27.3%) also comprises the frequencies for African samples (between 11.4% and 21.3%) and the sample from Southeast Asia (20.8%) when only grades 5 to 7 are considered (Scott and Turner, 1997; Silva, 2012; see Table 2). There seems to be a positive increase in the frequency of Carabelli's trait in the presence of shoveling, protostylid, accessory cusps and hypocone, and when incisors present quadrangular shape.

Carabelli's trait evolutionary roots, intertrait correlations and odontogeny should be further clarified. Despite the very large amount of scientific research on the trait, only recently has its association with the morphology of main cusps and the morphology of the enamel-dentine junction been addressed, illustrating the usefulness of continuous focus and of future research on the subject(s).

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