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Assessment of skeletal and dental fluctuating asymmetry in two historic Dutch populations

by

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Declaration

I declare that the dissertation, which I hereby submit for the degree Master of Science in Anatomy at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at another university.

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Alieske C. Hagg

This ____ day of _____ 2016

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In the end, all I can say is *Soli Deo Gloria*!

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Abstract

The study of human remains in terms of health and disease of past populations is of immense interest to physical anthropologists and bioarchaeologists. One method utilised for such an assessment is fluctuating asymmetry. Fluctuating asymmetry refers to the morphological inequality in bilateral anatomical structures and is considered an indicator of developmental stress. The purpose of this study was to assess and compare the magnitude of skeletal and dental fluctuating asymmetry between and within two populations and to correlate these findings with three other markers of skeletal stress, namely, enamel hypoplasia, cribra orbitalia/porotic hyperostosis and subperiosteal bone reactions. The sample comprised of two urban archaeological samples housed at the University of Amsterdam, the Grote Kerk sample (n=171), representing the general population of the 18th to early 19th century, and the psychiatric hospital sample from Meerenberg (n=106) of the 19th to early 20th century. Left and right measurements were recorded from various traits of the cranium, mandible, humerus, radius, femur, tibia and dentition, from which the fluctuating asymmetry values were calculated.

No statistically significant differences between the sexes or age categories were documented, although skeletal fluctuating asymmetry was slightly greater in adults. The Grote Kerk exhibited significantly greater frequencies of subperiosteal bone reactions, while the Meerenberg population exhibited greater frequencies of enamel hypoplasia. Individuals who exhibited one of the three pathological lesions were more asymmetrical than individuals without lesions. No significant differences existed in the level of asymmetry between the two populations. However, the Meerenberg population exhibited slightly greater asymmetry in the facial and vault region of the cranium, and the Grote Kerk population in the long bone lengths. Based on the frequencies and aetiologies of the pathological lesions, it is suggested that the two populations were probably subjected to similar levels of stress, even though the source, timing and duration of stress might have been different.

Despite the similar levels of stress, the Meerenberg population was expected to exhibit increased levels of fluctuating asymmetry due to the premise that individuals with mental disorders or deficiencies are developmentally less stable than the mentally healthy. Therefore, the possibility should also be considered that fluctuating asymmetry is not a highly sensitive indicator of developmental stress.

Keywords: bioarchaeology, canalisation, developmental instability, developmental stress, fluctuating asymmetry, Grote Kerk, Meerenberg, mental health, Netherlands, palaeopathology

Chapter 1: Introduction

"No human face is exactly the same in its lines on each side, no leaf perfect in its lobes, no branch in its symmetry. All admit irregularity as they imply change; and to banish imperfection is to destroy expression, to check exertion, to paralyze vitality. All things are literally better, lovelier, and more beloved for the imperfections which have been divinely appointed, that the law of human life may be Effort, and the law of human judgment, Mercy."

(Ruskin, 1867: 189)

Bioarchaeologists and physical anthropologists gain insight into the health and disease of present and past populations through the study of human remains (Armelagos, 2003; Larsen, 2002). One proposed manner in which to do so is by measuring the amount of fluctuating asymmetry (FA) among or between populations (DeLeon, 2007; Storm, 2007; Kujanová *et al.*, 2008). Fluctuating asymmetry is considered an indicator of developmental stress and, therefore, provides a means to assess the developmental stability of a population.

Defined as a morphological inequality of bilateral anatomical structures, FA strongly links to the internal developmental pathways of morphological traits. Bilateral structures are the product of a common gene complex with two identical pathways (Adams and Niswander, 1967; Ulijaszek and Mascie-Taylor, 1994; Møller and Swaddle, 1997; Palmer and Strobeck, 2003; Storm, 2008). In an ideal external and internal environment, the common gene complex will follow identical developmental pathways and lead to two morphologically identical traits, resulting in perfect symmetry. Such an ideal internal environment is dependent on developmental homeostasis, which mainly consists of two components: developmental stability and developmental canalisation (Møller and Swaddle, 1997).

Canalisation acts as a buffering agent against changes in the external and internal environments, reducing their effect on the developmental pathways, and ensuring that the intended genetic end-result is produced. A decrease in the canalisation capacity of a developmental pathway, or an increase in disturbance from internal and external factors, will divert a developing mass or material out of its developmental pathway and onto another pathway or trajectory (Waddington, 1942, 1957).

Developmental pathways are differentially canalised and therefore differ in their sensitivity to changes in the environment. This differential canalisation applies to both the so-called identical pathways of a trait, and the pathways of different traits. This is why the disturbance of developmental pathways will lead to the expression of FA, but it is also the reason why different traits within an organism will exhibit differential levels of FA. For example, if the maximum length of the femur displays FA due to altered developmental

pathways, it will likely exhibit a different magnitude of FA than the maximum length of the humerus or the breadth of the orbit (Møller and Swaddle, 1997; Wagner *et al.*, 1997).

The second aspect of developmental homeostasis, developmental stability, refers to the ability of an organism to resist random errors under specified internal and external conditions, perceived as the phenotypic expression of the genome. It follows that when an individual is developmentally unstable for a specific trait, the phenotypic expression of a bilateral trait will not be identical, but will express FA. Therefore, the lower the canalisation ability of a developmental pathway, or the greater the changes in the internal or external environment during development, the higher the expected expression of FA will be. That is to say, high levels of fluctuating asymmetry in a morphological trait are a reflection of the genetic capacity of an individual or organism to buffer extreme or adverse environmental influences during development (Waddington, 1957; Palmer and Strobeck, 1986; Møller and Swaddle, 1997; Wagner *et al.*, 1997). The changes in the external (environmental) and internal (genetic) environment, which adversely influence developmental homeostasis are generally referred to as developmental noise or stress, and increase the amount of developmental instability (Van Valen, 1962; Møller and Swaddle, 1997; Vøllestad *et al.*, 1999; Palmer and Strobeck, 2003). Some examples of factors within the genome that may cause distress to the internal cellular development include random mutations of a gene and disruptions to the interactions between and among genes (Clarke, 1993a; O'Neill, 2012). Environmental stressors are easier to quantify and identify, and include changes in temperature, economic hardship, environmental pollution, and nutritional stress, to name a few (Zakharov and Yablokov, 1990; Palmer, 1994; Storm, 2007).

A vast number of studies have investigated the relationship between external stressors, developmental instability and FA. Higher magnitudes of FA have been associated with a lower socio-economic status (Storm, 2009), infectious disease of the mother during pregnancy (Livshits *et al.*, 1988; Livshits and Kobyliansky, 1991), nutritional deficiencies (Harris and Nweeia, 1980), and environmental pollution and psychological stress during foetal development (Gawlikowska *et al.*, 2007a). Related studies have correlated indicators of nutritional stress on dry bone and teeth (such as enamel hypoplasia (EH), cribra orbitalia, and delayed growth or development) to the levels of FA. Higher levels of FA coincided with the presence of the aforementioned indicators (DeLeon, 2007; Hoover and Matsumura, 2008).

Another indicator of wellbeing that has been the subject of many asymmetry studies is mental health status (e.g. Markow and Gottesman, 1989; Shackelford and Larsen, 1997; Martin and Manning, 1999; Lalumière *et al.*, 2001; Reilly *et al.*, 2001). These studies

revealed that mental illnesses are associated with increased developmental instability. Therefore, it can be inferred that mentally ill individuals will exhibit higher levels of asymmetry as compared to mentally healthy individuals (Thornhill and Møller, 1997). For instance, Malina and Buschang (1984) assessed the levels of FA within the long bones of mentally healthy men as opposed to mentally ill men and noted greater levels of asymmetry within the mentally ill patients. Specific mental and neurological disorders that have been linked to greater magnitudes of FA include schizophrenia, depression and cerebral palsy (Malina and Buschang, 1984; Markow and Wandler, 1986; Martin et al., 1999; Reilly et al., 2001). While the term 'mental illness' was utilised throughout this study, it should be noted that it was used in a broad manner, and that it can refer to various other mental and neurological disorders or deficiencies, such as cognitive impairments as a result of developmental disorders.

In addition to differences in the level of FA due to environmental and genetic stressors, patterns of FA are also sometimes distinguishable between the sexes and at different ages or stages of skeletal maturity. Differences in the expression of FA levels between the sexes are not always evident. However, where differences do exist, the majority are statistically insignificant and are not considered as a general trend within the literature, although it is clear that differences between the sex differ between populations, between skeletal traits and between different teeth (e.g. Kujanová *et al.*, 2008; Storm, 2009; Bigoni *et al.*, 2013; Weisensee, 2013). While the literature reveals a stronger association between age and the magnitude of FA in skeletal material, this association is not unambiguous and seems to be less clear within the dentition (e.g. Hallgrímsson, 1999; Guatelli-Steinberg *et al.*, 2006; Kujanová *et al.*, 2008). A few studies have reported skeletal elements expressing greater magnitudes of asymmetry during late childhood and early adolescence, as well as with increasing age during adulthood (Saunders and Mayhall, 1982; Wilson and Manning, 1996; Storm, 2009). Even though general trends in the expression of FA across the skeleton exist, it seems to vary between populations and according to the degree of developmental stress, which coincides with the differential sensitivity of different traits to adverse external and internal stressors (Møller and Swaddle, 1997; Wagner *et al.*, 1997).

In comparison to other traits within the skeleton, higher levels of FA has previously been observed for the cranial vault and base (DeLeon, 2007; Gawlikowska *et al.*, 2007a), the lower limbs, and lengths of the long bones (Kujanová *et al.*, 2008), the height of the mandibular ramus and the temporal bone of the cranium (Storm, 2009). Lower levels of FA, on the other hand, have been observed in the facial area (DeLeon, 2007; Gawlikowska *et al.*,

2007a; Storm, 2009) and the breadth of the mandible (Storm, 2009). Within the dentition, the magnitude of FA seems to increase from mesial to distal within a tooth class. Furthermore, the permanent maxillary teeth tend to be more asymmetric than their mandibular counterparts, with the greatest magnitudes observed for the mesiodistal diameter of the maxillary tooth crowns (Garn *et al.*, 1966; Townsend and Brown, 1980; Khalaf *et al.*, 2005). In contrast, deciduous dentition has been shown to exhibit the most FA in the buccolingual diameter of mandibular tooth crowns (Townsend and Garcia-Godoy, 1984).

Although there has recently been a rise in the number of studies on FA or developmental instability in both past and modern populations (Guatelli-Steinberg *et al.*, 2006; Gawlikowska *et al.*, 2007; Storm, 2007, 2008; Kujanová *et al.*, 2008), much remains to be learned about its causes, development, and expression, specifically in skeletal remains. The assessment of FA levels within skeletal remains also provides an opportunity to test the premise that a mentally ill population is developmentally less stable than a mentally healthy population, and the assertion that teeth are developmentally more stable compared to the rest of the skeleton. For this reason, this study aims to assess the developmental stability of the skeletal remains and dentition of two historic Dutch populations.

1.1. Aims and Objectives

The aim of this study was to assess the levels of fluctuating asymmetry between and within the skeletal and dental remains of two archaeological Dutch samples, from the Grote Kerk and Meerenberg populations respectively. The samples date from the early 18th century to the early 20th century. The following objectives aided in the achievement of the aim of this study:

1. Standard physical anthropological analyses of the Dutch populations for a general assessment of the demographic profile of all individuals
2. The collection of osteometric and odontometric measurements from the cranium, mandible, humerus, radius, femur, tibia and teeth of the two Dutch skeletal populations in order to obtain fluctuating asymmetry values for each trait
3. The comparison of the overall mean or median level of fluctuating asymmetry between the skeleton and the dentition of the two populations
4. The assessment of mean and median fluctuating asymmetry levels within and between the Grote Kerk and Meerenberg populations, per sex and age category

5. The assessment of skeletal and dental material for pathological lesions, especially signs of stress, in order to assess whether a relationship exists between the occurrence of certain markers of stress (cribra orbitalia/porotic hyperostosis, enamel hypoplasia and subperiosteal bone reactions) and the magnitude of fluctuating asymmetry

Chapter 2: Literature Review

2.1. The path to symmetry

2.1.1. Developmental homeostasis, stability and canalisation

In order for an organism to be perfectly symmetrical, constant internal homeostasis during development is a necessity. Developmental homeostasis involves self-regulating mechanisms such as feedback systems to regulate the internal environment of an organism against an ever-changing external and internal environment during ontogeny. The maintenance of homeostasis (highly stabilised development) will produce the ideal or intended phenotype. Random developmental errors or the interruption of developmental processes, on the other hand, will result in imperfect growth (Palmer, 1994; Møller and Swaddle, 1997). Two important aspects of developmental homeostasis are developmental stability and the canalisation of developmental reactions or pathways. An organism can be regarded as developmentally stable when it is able to resist random errors under specific genetic and environmental conditions, yielding the intended phenotypic outcome of the genotype (Møller and Swaddle, 1997; DeLeon, 2007). Developmental canalisation, on the other hand, acts as a buffer or regulator to a range of changes in the internal and external environment during development, ensuring the intended genetic end-result of a developmental pathway. In other words, when the development of a mass or material, along a specific pathway, is forced from its path by some factor(s), and is then buffered or regulated to return to its intended pathway, it is considered canalised (Waddington, 1942, 1957; Møller and Swaddle, 1997).

Waddington (1957) illustrated the process of canalisation in terms of an epigenetic landscape, in which balls are placed on an inferiorly sloping surface with ridges and valleys (Figure 2.1; Waddington, 1957: 29). The slope represents a developmental pathway along which a trait or mass will develop, and ultimately ends in the phenotypic end-state at the bottom. During development, a disturbance, such as environmental stress, can push a ball out of a valley and over a ridge into another valley, resulting in a different end state; canalisation compensates for this disturbance by ensuring that the ball still reaches its intended end-state. Shallow valleys with gentle slopes depict a less canalised path of development while deep valleys with steep slopes represent a highly canalised pathway. If, however, genetic and/or environmental influences are greater than the threshold level for a trait, the steepness of the

ridges can be reduced, increasing the chances that the ball will not end in its intended phenotypic end-state.

Buffering capacity or canalisation can be described on two different levels: genetic canalisation and environmental canalisation. Genetic canalisation entails the buffering of internal factors that play an important role in the genetic variance of a trait or characteristic. The buffering of external changes refers to environmental canalisation, and is dependent upon two factors, namely the degree of variation in the environmental factor (such as temperature), and the reaction of the genotype and ultimately also the phenotype to this change in the environment (Wagner *et al.*, 1997).

Due to natural genetic predispositions, organisms do not possess equal levels of buffering or canalisation ability. In other words, certain genotypes encompass an enhanced ability to regulate or canalise a developmental pathway relative to other genotypes. The resultant phenotypic expression of a trait will emulate the differential canalisation abilities of the genotype (Waddington, 1957). Besides varying degrees of canalisation between organisms, canalisation, as well as developmental stability, also differs within organisms; for both different traits and stress factors. The differential buffering of distinct traits to an identical stress factor relate to their separate locations (loci) on a gene(s) while the differential buffering between stress factors are attributable to the differential response of identical traits (situated at the same locus) to different stress factors. That is to say, canalisation at a locus against a certain variation (such as temperature) does not imply canalisation against another variation (such as pollution) at the same locus (Møller and Swaddle, 1997; Wagner *et al.*, 1997).

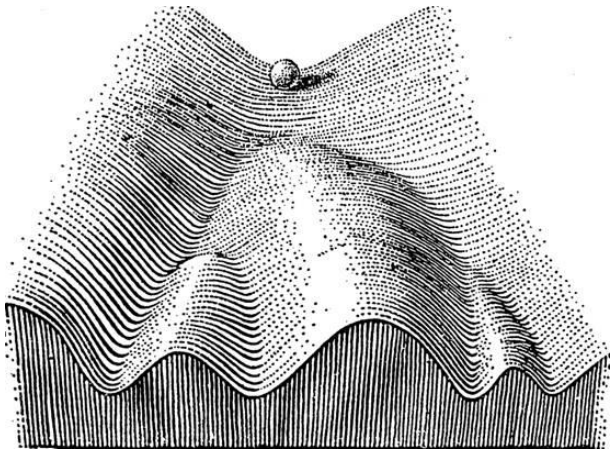

Figure 2.1. The process of canalisation as depicted by the epigenetic landscape (Waddington, 1957: 29).

Bilateral structures, such as the left and right humerus, are products of a common gene complex with identical developmental pathways. The ideal result of these identical pathways within an organism is two identical structures that are bilaterally symmetrical. Bilateral symmetry will occur when developmental homeostasis sufficiently buffers the developmental stresses during development, or in other words when the developmental pathways are highly canalised. When this occurs, an individual is said to be developmentally stable for that specific trait. However, developmental homeostasis cannot always be maintained, therefore, deviations from symmetry in bilateral structures are common. This deviation from symmetry in bilateral structures due to developmental instability is referred to as fluctuating asymmetry (FA) (Waddington, 1942; Adams and Niswander, 1967; Ulijaszek and Mascie-Taylor, 1994; Møller and Swaddle, 1997; Palmer and Strobeck, 2003; Storm, 2008).

2.1.2. Developmental noise or stress

The theoretical use of the phrase 'perfect bilateral symmetry' is erroneous in practice, as perfection hardly exists. All developmental processes possess some degree of randomness, even when their development is highly canalised and stable in a perfectly balanced environment. This inherent randomness, albeit very small, unpredictably generates developmental errors during development, disrupting developmental homeostasis (Van Valen, 1962; Møller and Swaddle, 1997). In addition, various internal (genetic) and external (environmental) conditions can additively and negatively affect developmental homeostasis, causing long-term changes to an organism's biological system. One such possible change is a decrease in the stability or canalisation of developmental pathways, leading to an increased chance of expressing an altered form of the intended phenotype. These genetic and environmental factors are collectively known as developmental noise or stress (Van Valen, 1962; Møller and Swaddle, 1997; Vøllestad *et al.*, 1999; Palmer and Strobeck, 2003).

Within the bioarchaeological and anthropological fields, 'stress' is defined around a series of skeletal indicators as '*disruptions to physiological homeostasis at particular points of development'* (Temple and Goodman, 2014: 190), caused by strain on an organism from various constraints or pressures (Reitsema and McIlvaine, 2014; Temple and Goodman, 2014). Fluctuating asymmetry, as a physical measure of developmental instability in bilateral traits, therefore inherently provides a means by which to measure the stress in past and present populations (Bailit *et al.*, 1970; Møller and Swaddle, 1997; Palmer and Strobeck, 2003).

2.1.2.1. Genetic stress

In basic terminology, the genetic component of developmental noise refers to factors that cause distress in the internal cellular development (Møller and Swaddle, 1997). Genetic factors that may potentially cause this internal distress include high levels of inbreeding (decreased genetic variety), homozygosity (the two alleles of a gene are identical, coding for only one phenotypic expression of the genotype – AA or aa), random new mutations of a gene(s), and disruptions to the interaction of genes (co-adapted gene complexes) necessary for a developmental process (Clarke, 1993a; Møller and Swaddle, 1997; O'Neill, 2012).

While the effect of environmental or genetic stressors is rather simple to comprehend independently, some uncertainty exists pertaining to the combined influence of genetic and environmental stress on FA expression (Livshits *et al.*, 1988; Møller and Swaddle, 1997). In order to clarify the uncertainties surrounding this combined influence, Livshits and Kobyliansky (1989, 1991) measured eight bilateral traits in two independent nuclear families. They found that the environmental factors alone explained most of the variance for the individual FA traits, but that the combination of genetic components with environmental factors contributed significantly to mean FA values. The mean FA values also indicated a more or less consistent correlation with parent-child relations; an indication that genetic mechanisms do influence FA levels, likely due to differential sensitivity of different gene products to changes in the environment. In line with their latter observation, other researchers have argued that the probability for, and degree of, the expression of FA may be heritable (e.g. Palmer and Strobeck, 1986; Livshits and Kobyliansky, 1987; Thornhill and Sauer, 1992; Møller and Thornhill, 1997).

One main aspect in this regard is heterozygosity. Heterozygosity refers to a genotype consisting of two different alleles of a gene (Aa) at one or more locations for a particular trait (O'Neill, 2012). Heterozygous individuals are believed to have an increased resistance to pathogens or other environmental influences due to decreased phenotypic variability (increased canalised developmental pathways), limiting or decreasing the susceptibility to FA (Livshits and Kobyliansky, 1991). However, the issue of whether a decrease in heterozygosity causes an increase in FA levels has caused much debate over the years, mainly due to conflicting results. While some studies found a positive correlation between FA and heterozygosity (e.g., Livshits and Kobyliansky, 1984; Blanco *et al.*, 1990), several other studies found a weak to absent correlation between heterozygosity and the level of asymmetry (Bailit *et al.*, 1970; Clarke, 1993a; Vøllestad *et al.*, 1999; Gilligan *et al.*, 2000), rendering the relevance of hetero- or homozygosity for studies of FA uncertain.

2.1.2.2. Environmental stress

Developmental noise due to environmental factors includes extreme climate changes, economic hardship (related to socio-economic status), nutritional stress, high population density, and chemical-, noise-, and general environmental pollution (Zakharov and Yablokov, 1990; Palmer, 1994; Møller and Swaddle, 1997; Palmer and Strobeck, 2003; Storm, 2007; Özener, 2010). Increases in environmental stress compel organisms to allocate most of their energy to survive the extreme environment, leaving little energy for the maintenance of homeostasis and other important activities such as reproduction or growth (Møller and Swaddle, 1997). Consequently, in a demographical sense, environmental stress is frequently described in terms of fertility, mortality and morbidity (Bailit *et al.*, 1970). That is to say, the birth rate or reproductive success, life expectancy at birth, and changes in disease patterns within a population, are closely related to the economic, sociologic and demographic environment in which a population lives (Omran, 1971; Leke *et al.*, 1993). Examples of studies, which investigated the effect of environmental stressors of the human skeleton, are included in Section 2.3.1.

2.2. Deviation from symmetry

Besides FA, two other types of bilateral asymmetry exist, namely directional asymmetry (DA) and antisymmetry. Bilateral traits may exhibit all three types of asymmetry simultaneously, therefore, it is important to know how DA and antisymmetry differ from FA since DA and antisymmetry can significantly confound and obscure the evaluation and expression of FA. Antisymmetry and DA are both forms of adaptive asymmetry, meaning that the asymmetry of a trait is usually due to, or related to, some behavioural factor (Van Valen, 1962; Palmer, 1994; Møller and Swaddle, 1997). Figure 2.2 (Palmer, 1994: 337) illustrates the frequency distributions of the three types of bilateral asymmetry.

2.2.1. Fluctuating Asymmetry

Fluctuating or random asymmetry refers to a morphological inequality of bilateral (left and right sided) anatomical structures, induced by the inability to maintain developmental homeostasis against various internal and external stressors (Palmer and Strobeck, 1986; Møller and Swaddle, 1997). Bilateral structures exhibiting FA grow and develop simultaneously under identical genetic and environmental conditions, thereby controlling for both internal and external factors, FA is consequently considered an accurate

estimator of developmental instability (Møller and Swaddle, 1997). The main theoretical premise behind FA is that a disturbance in the stability of development will result in the lack of precision of development of a certain developmental pathway or genotype, resulting in an altered expression of the expected phenotype of a bilateral anatomical feature (Adams and Niswander, 1967). The resultant variation or asymmetry of a bilateral trait is usually slight and therefore not easily observed with the naked eye, but it can be detected anthropometrically (Ulijaszek and Mascie-Taylor, 1994). An increase in developmental instability, or the inability to withstand genetic and/or environmental disturbances during development, will increase the observed levels of asymmetry (Van Valen, 1962; Clarke, 1995; Storm, 2008).

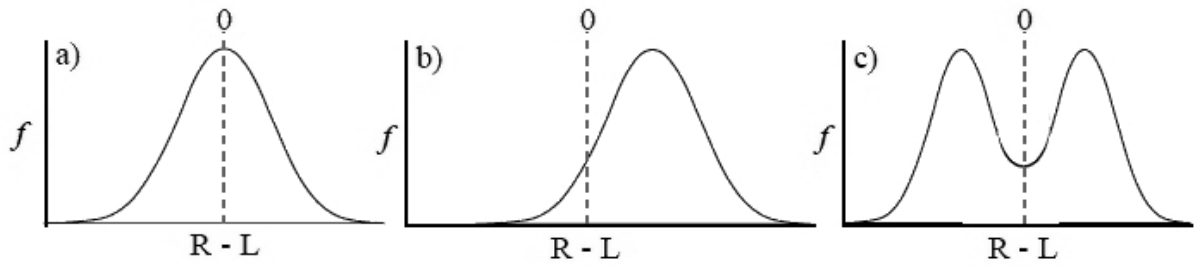

Figure 2.2. Frequency distributions of the three forms of bilateral asymmetry: a) Fluctuating asymmetry, b) directional asymmetry (depicted here as asymmetric to the right), and c) antisymmetry or bimodal symmetry (adapted from Palmer, 1994: 3).

While the expression of individual asymmetry for a specific trait may be asymmetrical to the right (positive) or to the left (negative), the average expression of the trait in a population will be symmetrical, resulting in a normal distribution around a mean of zero (for signed (raw) asymmetry scores: right - left; see Figure 2.2a). The level of developmental instability of the population as a whole can be seen by the deviation around the mean, or simply by the breadth of the normal distribution. Although FA is considered a population statistic, individual expressions of asymmetry can be utilised as a measure of the individual developmental instability against the FA levels of the population (Møller and Swaddle, 1997). Corresponding to the characteristics of developmental stability (see Section 2.1.1), or rather instability, the levels of FA differ for each trait within an organism - due to each trait's differential response to a type of developmental noise, as well as the differential canalisation ability of the different traits. This means that a certain trait, such as orbital breadth, may exhibit higher levels of FA than another trait, such as orbital height or the maximum length of the humerus. Despite the differential buffering capacity between traits, a general pattern in terms of buffering ability (as suggested by the FA levels) of traits within the human skeleton

and dentition is apparent from the literature and is described in Section 2.3.2.1 (DeLeon, 2007; Storm, 2009; Blackburn, 2011).

Studies on FA of bilateral human traits, especially on skeletal material, are sparse in relation to the amount of FA studies on various plant and animal species. Fluctuating asymmetry studies on non-human traits have, to name a few, been conducted on leaves (Albarrán-Lara *et al.*, 2010), shrews (Badyaev *et al.*, 2000), stalk-eyed flies (Bjorksten *et al.*, 2000), Alaskan moose (Bowyer *et al.*, 2001), chickens (Campo *et al.*, 2007), shrimp (Clarke, 1993b), blood worms (Clarke, 1993b), and macaques (Willmore *et al.*, 2005). Studies on FA within humans are discussed in Section 2.3.

2.2.2. Directional Asymmetry

Directional asymmetry is defined as a constant greater increase in the development of a trait on one side of the body or plane of symmetry (Van Valen, 1962; Palmer and Strobeck, 1986), such that the side of greater development is usually constant among the majority of individuals within a population. That is to say, the bilateral trait is, on average, larger to the right *or* to the left within a population, resulting in a skewed distribution with the mean either larger or smaller than zero - Figure 2.2b (Palmer, 1994; Møller and Swaddle, 1997). Although FA is traditionally regarded as the greatest estimator of developmental instability, DA has also been utilised for this purpose (Van Valen, 1962; Palmer, 1994; Vøllestad *et al.*, 1999). However, controversy exists regarding the reliability of DA as a measure of developmental stability, as DA (and antisymmetry) are believed to have a genetic component (Palmer, 1994). The presence of DA in a trait or individual may imply that some portion of the asymmetry has a genetic basis, and the measured asymmetry will therefore not be due to developmental noise or stress alone (Palmer and Strobeck, 1992; Palmer, 1994).

Besides the genetic influence on the expression of DA, behavioural changes such as directional loading, or handedness, contribute significantly to its expression. Directional loading refers to continuous one-sided mechanical stimuli to the musculoskeletal system in such a manner that it affects the skeletal dimensions (Steele, 2000; Auerbach and Raxter, 2008; Blackburn, 2011). Directional asymmetry during growth seems to coincide with the locomotor behaviour of infants and young children. A study on the DA of the postnatal development of the humerus in 11 archaeological skeletal populations from England indicated a statistically significant difference in median DA values between the age groups. Both humeral length and combined measurements (humeral length, epicondylar breadth and maximum midshaft diameter) exhibited increased right-sided asymmetry per ‘increasing’ age

group, with the humeri being symmetrical only until about one year of age. This pattern of increasing DA coincides with an intensified mechanical loading due to advancing hand preference and the commencement of walking in infants (Blackburn, 2011). Auerbach and Raxter (2008) assessed the function of the clavicle (shoulder girdle) in response to directional loading of the humerus (upper limb). In their study, greater degrees of asymmetry in both humeral and clavicular diaphyseal breadths as compared to lengths suggest an increased sensitivity and responsiveness in diaphyseal breadths to directional loading. Additionally, significant positive correlations were noted for contralateral side-dominance in humeral (right-sided) and clavicular (left-sided) diaphyseal asymmetries, as well as in the majority of length measurements. Further evidence supporting the relationship between DA and directional loading may lie in the findings of Auerbach and Ruff (2006), who compared the long bone measurements of several populations from preindustrial and industrial periods. Preindustrial individuals exhibit increased levels of DA, consistent with a more active lifestyle that likely contributed to higher mechanical forces on their limbs.

Studies on human skeletal DA have mostly been conducted on the upper and lower limbs, and most frequently included the humerus, radius, femur and tibia (e.g., Čuk *et al.*, 2001; Auerbach and Ruff, 2006; Blackburn, 2011). Directional asymmetry within human populations seems to follow a general trend within the skeleton. Upper limb bones are generally larger on the right while lower limb bones tend to be larger on the left, albeit less so than the upper limb. This pattern of asymmetry is commonly referred to as crossed asymmetry. Overall the humerus has been shown to exhibit the most directional asymmetry. Furthermore, within the long bones and clavicle, diaphyseal breadth dimensions have the propensity to be more directionally asymmetric than lengths (Čuk *et al.*, 2001; Auerbach and Ruff, 2006; Auerbach and Raxter, 2008). Similar to the upper limb bones, the metacarpals and phalanges of the hand have also shown to be dominant to the right, although phalangeal asymmetry levels were lower than metacarpal asymmetry (Cashmore and Zakrzewski, 2009).

Directional asymmetry of the cranium has primarily been associated with natural lateral asymmetries of the cranium and is related to physiological, anatomical and behavioural expression of the brain and masticatory functions of the mandible and related cranial structures (Shah and Joshi, 1987; Pirttiniemi, 1998; Oertel-Knöchel and Linden, 2011). The left and right sides of the brain vary in their development, which may lead to natural asymmetry of the brain and overlying cranium. The relationship between the normal and abnormal function and shape of the brain in relation to asymmetry of the cranium are further discussed in Section 2.4. The vault and base of the cranium have generally been found

to be larger on the right (Woo, 1931; Storm, 2009), although a study by Gawlikowska *et al.* (2007b) found the cranial base to be dominant to the left. The upper and lower facial areas seem to differ in the directionality of asymmetry; the former has been shown to be left-side dominant, and the latter right-side dominant (Gawlikowska *et al.*, 2007b). Directional asymmetries of the face and base of the cranium are associated with mandibular and dental DA, which are mostly studied in relation to malocclusion or masticatory function. Possible causes for a naturally occurring asymmetry of the face and mandible are not clear, although the differential muscle action of the left and right sides are deemed to play an important role (Pirttiniemi, 1998). Dental occlusion and mastication has shown a propensity to be right-sided (Shah and Joshi, 1987; Pirttiniemi, 1998). Pirttiniemi (1998) suggested that the asymmetry in dental occlusion might be linked to asymmetry of the cranial base. The temporomandibular joint forms part of the cranial base. Therefore, structural or functional changes in the cranial base may be reflected in the shape of the mandible; or changes in the shape of the mandible (be it due to directional masticatory function) can affect the shape of the cranial base, if only the mandibular fossa. Somewhat dissimilar to the trends observed for occlusion and mastication, a study by Storm (2009) found the mandible to be asymmetric to the left in length, but dominant to the right in the height of the ramus.

2.2.3. Antisymmetry

Antisymmetry or bimodal symmetry is a unilateral departure from symmetry, but unlike DA, the side of greater development differs at random from individual to individual, such that the population frequency will exhibit two modes around a mean of zero (Figure 2.2c) (Van Valen, 1962; Palmer, 1994; Møller and Swaddle, 1997). The presence of antisymmetry in any one trait can greatly affect the degree of FA, especially when asymmetry is dependent upon size. Therefore, traits known to exhibit marked antisymmetry or size variability should not be included in the study of developmental instability, and the expression of antisymmetry should be assessed for all traits within the studied population by means of statistical tests before the analyses of FA results (Palmer, 1994; Rowe *et al.*, 1997). Bilateral traits exhibiting antisymmetry will markedly vary in size and structure. The simultaneous expression of FA and antisymmetry is collectively known as non-directional asymmetry (Guatelli-Steinberg *et al.*, 2006; Storm, 2008).

2.3. Fluctuating asymmetry in populations

2.3.1. Fluctuating asymmetry as a marker of developmental instability

While some researchers (e.g., Black, 1980; Bjorksten *et al.*, 2000) have questioned the reliability of FA as an indicator of developmental stability, the vast majority of asymmetry studies on the human skeleton indicate a strong correlation between external stressors and FA, supporting the use of FA as an indicator of developmental instability. For instance, Livshits *et al.* (1988) investigated a few aspects of the relationship between FA, developmental homeostasis and developmental instability. One aspect of their study considered the hypothesis that individuals with higher levels of morbidity (such as preterm births and individuals with developmental anomalies) will exhibit higher levels of developmental instability compared to healthy individuals. A comparison of several bilateral measurements in 216 newborn infants (preterm and term) and their parents revealed statistically significant differences between the FA values of the infants, with extremely preterm infants having the highest FA values. Fluctuating asymmetry values for the parents were similar to those of the infants, although less distinct. Additional analyses of each infant's mean FA value against several biological and social factors, such as infectious disease of the mother during pregnancy, gestational age and cardiovascular disease of the infant, indicated a linkage between increased levels of asymmetry and pathological factors that may bring about prematurity. They concluded that the use of FA is a practical method to predict possible developmental instabilities from an early age (Livshits *et al.*, 1988; Livshits and Kobyliansky, 1991).

In further support for the use of FA as an indicator of developmental instability, Storm (2007; 2008; 2009) found increased levels of FA in human archaeological remains from the Medieval to the Victorian periods in England that coincided with the environmental and social changes brought on by the British Industrial Revolution. Additional comparative analyses, based on the socio-economic status (SES) of a number of the archaeological populations, revealed higher levels of FA in the populations of lower SES, further supporting the premise that FA, and inherently developmental instability, increases with adverse external or environmental conditions.

The majority of studies on FA as an indicator of developmental instability focus on FA of the cranium (e.g. DeLeon, 2007; Gawlikowska *et al.*, 2007a; Hoover and Matsumura, 2008). For example, a study by DeLeon (2007) assessed nutritional and systemic stress in the craniofacial skeletons from two Christian cemeteries in Sudanese Nubia, by means of FA.

The two cemeteries were dated to the Early Christian (AD 550 – 850) and Late Christian (AD 550 – 1500) periods. The majority of traits in the Early group exhibited higher levels of FA. While only 11% of the measured traits were significantly different between the groups, the overall higher levels of FA in the Early group coincided with other indicators of developmental stress, such as higher frequencies of enamel hypoplasia (EH) and cribra orbitalia, retarded growth during late childhood and adolescence and higher mortality rates.

Hoover and Matsumura (2008) correlated the prevalence of EH (as an indicator of nutritional stress) with FA levels in 13 archaeological Japanese populations from various time periods. Enamel hypoplasia was recorded for mandibular and maxillary anterior dentition while FA was evaluated on only three traits: orbital height, orbital breadth and facial breadth (adapted to measure right and left sides with nasion as midline landmark). Even though individuals with EH exhibited higher levels of FA, only facial breadth showed a statistically significant correlation. The lack of a strong positive correlation between EH and FA may be attributed to a relatively small sample size (n=49) and a limited number of bilateral traits. Because traits may differ in their buffering capacity against stressors, more traits could possibly have given a better indication of FA levels within the sample (DeLeon, 2007).

Another recent study on FA in craniofacial skeletons was conducted on an identified skeletal sample from mid 19th to early 20th century Lisbon, Portugal (Weisensee, 2013). This sample is unique in the sense that the causes of death are known, which enabled the comparison of FA levels between individuals who suffered from infectious (tuberculosis, syphilis), degenerative (heart disease, diabetes), neoplastic (cancers and tumours) and 'other' (old age, senility, sudden death, gunshot) diseases or causes of death. Individuals who suffered from degenerative diseases exhibited higher FA levels than individuals who died from infectious diseases. No significant differences were indicated between the FA levels of the individuals with other groups of diseases or causes of death. The author concluded that the significant difference in FA levels provides a reasonable means with which to measure developmental instability, and may be linked to the Developmental Origins of Health and Disease hypothesis that *"developmental instability during the fetal [sic] and post-natal period has long-term consequences on adult health outcomes"* (Weisensee, 2013: 415).

However, not all studies found a clear positive relationship between environmental stress and FA. For example, radiographic analyses of modern and Medieval male Polish crania (Gawlikowska *et al.*, 2007a) revealed higher levels of FA in the modern population even though general socio-economic conditions, such as nutrition, were expected to be better in the modern population than in the Medieval population. The greater FA levels in the

modern populations were attributed to increased levels of developmental stress as a result of environmental pollution and psychological stress during foetal development. These authors speculated that the 20th century modern population could have lived in worse socio-economic circumstances than expected and as compared to current 21st century living populations.

While dental FA has readily been assessed, asymmetry studies on the human mandible are limited, and are usually conducted in relation to malocclusions and crossbite (Schmid *et al.*, 1991; Melnik, 1992; Rose *et al.*, 1994; O'Byrn *et al.*, 1995). Dental development is generally accepted to be under greater genetic control and, therefore, less sensitive to developmental stress as compared to skeletal development (Bogin, 1988; Cardoso, 2007). However, studies of various populations under different levels of environmental and genetic stress (Bailit *et al.*, 1970; Guatelli-Steinberg *et al.*, 2006) suggest that FA in the dentition can also be utilised as a measure of developmental instability. Similar to findings on skeletal material, dental FA tends to increase with a general increase in environmental and genetic stress (Bailit *et al.*, 1970; Perzigian, 1977; Harris and Nweeia, 1980; Guatelli-Steinberg *et al.*, 2006). For example, mesiodistal diameters from dental casts of four populations subjected to different amounts of genetic and environmental stress revealed mean asymmetry values that correlated with the expected rankings in stress levels. The four populations were ranked in decreasing order based on ethnographic and medical data: Tristanites, Kwaio, Nasioi and Boston whites. The Kwaio and Nasioi populations were subjected to relatively severe environmental conditions, but with relatively low genetic stress. The Tristanites, to the contrary, endured high levels of both genetic and environmental stressors, while, in comparison, the Boston whites lived under the most favourable conditions (Bailit *et al.*, 1970). This provides further evidence that the degree of asymmetry in bilateral traits corresponds to the amount and intensity of stress factors, both environmental and genetic.

Similarly, Harris and Nweeia (1980) compared dental FA values of a horticultural Indian group, the Tunica, to modern American whites, prehistoric Hopi Indians (agriculturalists) and prehistoric Alaskan Eskimo (hunters) populations. Overall, the rankings of FA magnitudes in mesiodistal and buccolingual crown diameters of the four populations concur with the differing food sources and subsequent nutritional intake of each population. The American whites exhibited the least amount of FA (much less than the other three populations), followed by the Tunica, and the Alaskan Eskimo and Hopi Indian populations. In yet another study, Guatelli-Steinberg *et al.* (2006) demonstrated higher levels of FA in the dentition of a 20th century American population compared to an Archaic and Late Prehistoric

Ohio Valley Native American population. Historical and archaeological evidence suggests that this 20th century population was subjected to higher levels of stress than the Native Americans.

Instead of a comparison between FA and general stress indicators, Hoover *et al.* (2005) directly evaluated the relationship between a single indicator of stress, EH, and dental FA. This sample comprised of 72 individuals from the Isola Sacra necropolis (ancient Rome). Due to possible additive stress effects in teeth exhibiting both FA and EH (which will result in false-positive interactions), incisors and canines were evaluated for EH only while first and second premolars were evaluated for asymmetry. An additional rationale for the aforementioned selection is based on the general postulation that anterior teeth are more susceptible to EH, and posterior teeth to fluctuating asymmetry. Only a few correlations indicated a statistically significant relationship between the frequency of EH and level of FA. Considering that the individuals in the sample were all subjected to the same level of stress and the comparison between EH and FA was between different teeth of the same individual, this is not surprising. Therefore, Hoover *et al.* (2005) suggested that a comparison between hypoplastic and non-hypoplastic teeth may provide a better indication of stress within and between populations.

2.3.2. Expressing fluctuating asymmetry

Due to differing levels of resistance or buffering of causative agents or noise, FA usually does not occur uniformly throughout an individual and differs among individuals, at different ages, and between males and females (Van Valen, 1962; Ruff and Jones, 1981; Palmer, 1994; Storm, 2009). Therefore, it is important to consider each of these variables separately.

2.3.2.1. Trends in the skeleton

Unlike the relatively consistent DA trends in skeletal elements, FA trends within the skeleton seem to be more variable or even conflicting, although some general trends can be discerned. Within the cranium, most studies reported the levels of FA to be least in magnitude in the facial area and greatest in either the vault or base of the cranium. Gawlikowski *et al.* (2007a) studied the male crania in a modern and Medieval population, and observed the greatest levels of FA in the cranial vault and base within the modern population, while the Medieval skulls exhibited an opposite trend, with high levels of FA in the facial area and the lowest FA levels in the cranial vaults. Similar to Gawlikowska *et al.*'s

(2007a) modern population, DeLeon (2007) observed the highest FA levels around the neurocranium and the least within the facial area. In this study on Nubian crania from early and late Christian periods, several bilateral traits on the skulls from the early period, believed to be from times of greater levels of stress, exhibited the most asymmetry. These bilateral measurements (traits) included the following cranial landmarks: pterion posterior, nasion, lambda, dacryon and the greater palatine foramen. The authors suggested that the latter landmarks might be more sensitive indicators of stress than other landmarks. A study on Medieval crania from central Europe also found comparable trends in FA magnitude: the cranial base exhibited the greatest amount of asymmetry and the upper facial area the least. The cranial vault FA levels fell in between those of the base and upper face (Bigoni *et al.*, 2013).

Most FA studies involving the mandible have been studied in relation to the dental arch and the dentition, and not on the bone itself. However, a study by Storm and Knüsel (2005) observed the degree of asymmetry in 17 cranial and mandibular traits in two Medieval populations from England, where mandibular ramus height, together with mastoid length, mastoid breadth, bregma-porion length and orbital breadth exhibited the most asymmetry. Mandibular ramus breadth, orbital height, zygomatic height and diagonal orbital breadth expressed the lowest degree of asymmetry. Mandibular condyles have also been shown to exhibit FA, with no significant differences in the degree of FA between the sexes or with advancing age (Costa, 1986).

While the focus of the literature on bilateral asymmetry within the long bones and appendicular skeleton is mainly on the expression of DA (e.g., Mays *et al.*, 1999; Plochocki, 2002; Auerbach and Ruff, 2006; Auerbach and Raxter, 2008; Blackburn, 2011), several studies have revealed a slight trend in FA expression within the long bones and appendicular skeleton (e.g., Kujanová *et al.*, 2008; Storm, 2009). For example, lower limb bones in modern and Medieval Central European populations exhibited a higher prevalence of FA compared to upper limb bones, even though the levels of FA were very low in magnitude. The highest degree of FA was observed in length dimensions, although the values became negligible when corrected for size differences (Kujanová *et al.*, 2008). A study on an English archaeological population by Storm (2009) indicated a higher magnitude of asymmetry within the adult upper limb than in the lower limb, with humeral length and the maximum midshaft diameter of the radius being the most asymmetric traits. When the asymmetry levels of the upper limb were compared by index, such as the humeral index that included all the

humeral traits, the clavicular bone exhibited the most FA and the metacarpals the least. The lower limb not only exhibited a smaller magnitude of median FA compared to the upper limb but also compared to the cranium and pelvis. Within the lower limb, the diaphyses exhibited the highest levels of FA, while the lengths of the femur, tibia and metatarsals exhibited the least asymmetry. In the aforementioned study, the FA levels within the sacrum were the second highest compared to all other skeletal elements, surpassed only by clavicular FA. Left-right differences in the height and breadth of the os coxae were almost symmetrical. Similar to the abovementioned findings in adult skeletal material, smaller magnitudes of FA were observed in the lower limbs as opposed to the upper limbs in living subadults (five to 11 years of age) from Jamaica (Trivers *et al.*, 1999).

Taking the results from all the above mentioned studies into account, the following general trend within the skeleton is evident: the base and vault of the cranium, the height of the mandibular ramus and the upper limb bones generally exhibit more asymmetry than the facial region of the cranium, the breadth of the mandibular ramus and the lower limbs.

2.3.2.2. Trends in the dentition

Within the dentition, FA seems to increase within each tooth class from mesial to distal, such that, for example, the second maxillary premolars exhibit higher levels of FA than the first maxillary premolars (Garn *et al.*, 1966; Perzigian, 1977; Harris and Nweeia, 1980; Townsend and Brown, 1980; Khalaf *et al.*, 2005). Furthermore, maxillary teeth not only appear to exhibit greater FA levels than corresponding mandibular teeth (Harris and Nweeia, 1980; Townsend and Brown, 1980; Hoover *et al.*, 2005; Hoover, 2007), but they also tend to show greater FA magnitudes within mesiodistal crown dimensions as opposed to buccolingual crown dimensions (Harris and Nweeia, 1980). However, other studies found the latter pattern within both the maxillary and mandibular dentition (Townsend and Brown, 1980; Khalaf *et al.*, 2005). A study on deciduous teeth found the buccolingual diameters of mandibular canines to exhibit the most asymmetry, and both crown dimensions in the molar teeth the least asymmetry. Yet, none of the differences were statistically significant (Townsend and Garcia-Godoy, 1984). From the above information, it seems that the pattern of fluctuating asymmetry within the dentition tends to be less variable than in the skeleton.

2.3.2.3. Sex differences

Reports on the expression of FA in males and females are conflicting and vary between populations, skeletal elements and the dentition. In a comparison between the sexes,

Storm (2009) showed females to exhibit more asymmetry within long bone lengths than males, while males showed greater asymmetry in midshaft dimensions. Results from another study comparing modern and Medieval individuals from Central Europe indicated only a small subset of the traits to be statistically significant between the sexes. Asymmetry values of the sexes differed between the two time-periods, with higher levels of FA observed in male postcranial traits from the modern sample, while the corresponding postcranial traits in the Medieval sample revealed higher FA levels in females (Kujanová *et al.*, 2008). Similarly, a study of Medieval crania from central Europe showed greater magnitudes of FA within the higher socio-economic status group, while males were more asymmetrical within the group of lower socio-economic status (Bigoni *et al.*, 2013). However, other studies indicated no statistically significant differences in the magnitude of FA between the sexes. One such study was that of Hallgrímsson (1999) on the crania, dentition, long bones, metacarpals and metatarsals of 236 individuals from the Hamann-Todd Osteological Collection. Similarly, no sex differences in FA levels were apparent in a study of mandibular condyles in Haida Indians (Costa, 1986). While no significant differences existed between the sexes concerning the craniofacial skeletons of 392 adult individuals from Lisbon (Portugal), males demonstrated slightly higher FA levels than females (Weisensee, 2013).

Within the dentition, most studies found male teeth to be more asymmetrical than female teeth, although the differences were not always statistically significant (Townsend and Brown, 1980; Saunders and Mayhall, 1982; Hoover, 2007). However, Harris and Nweeia (1980) found females to exhibit more asymmetry in mesiodistal diameters. Guatelli-Steinberg *et al.* (2006) documented greater FA in the buccolingual diameter of the female mandibular canine, although significantly greater FA levels were exhibited by the male maxillary first premolar. Khalaf *et al.* (2005) conducted a study on various crown dimensions of permanent teeth and found no sex difference in the magnitude of FA. A study by Townsend and Garcia-Godoy (1984) indicated no significant sex differences in the FA levels of deciduous teeth and Perzigian (1977) found more in deciduous and young adult dentitions.

2.3.2.4. Age differences

Most studies on the change in FA with advancing age focused on either adult or subadult individuals (e.g. Wilson and Manning, 1996; Kujanová *et al.*, 2008; Bigoni *et al.*, 2013). Only a few studies have considered the difference between adult and subadult asymmetry values, especially within the skeleton (Saunders and Mayhall, 1982; Hallgrímsson, 1999; Guatelli-Steinberg *et al.*, 2006; Storm, 2009). For example, in her study

of archaeological British individuals, Storm (2009) noted that levels of asymmetry were greater in subadults than in adults. She also noted that FA increased in late childhood and adolescence, as well as with increasing age during adulthood. Similarly, Wilson and Manning (1996) found FA in several measurements of the face, ears and hands of living children (2-18 years of age) to decrease with increasing age in childhood until 10 years of age, to increase during the end of late childhood to the first part of adolescence (11 to 15 years of age), and to decrease again during the second part of adolescence up to 18 years of age. Comparable to the trend observed by Storm (2009), a study on craniofacial asymmetries by Rossi *et al.* (2003) found decreasing levels in ZA (a measurement from the spinous foramen to the zygomatic arch, on the zygomaticotemporal suture) asymmetry from infants to adults, while three other craniofacial distances showed no age differences in the level of FA. A study on subadult and adult cranial and postcranial elements, found FA to increase with increasing age in the craniometric and postcranial traits up to 20 years of age, but not in the postcranial traits after 20 years of age (Hallgrímsson, 1999).

Patterns within the dentition seem to differ between studies. For example, Saunders and Mayhall (1982) found deciduous molar teeth to be less asymmetrical than permanent molars (for the morphological traits protostylid and Carabelli's cusp), while a study by Guatelli-Steinberg *et al.* (2006) revealed only three (out of twelve) tooth pairs to be statistically significant between the permanent and deciduous dentitions. Out of the three significant differences, only one exhibited higher FA values in the permanent dentition. Hallgrímsson (1999), on the other hand, found no correlation between FA and age in the dentition.

2.4. Mental health and fluctuating asymmetry

Besides anticipated differences in the level of FA due to sex, age and differences in developmental stress, positive correlations between FA and mental illness, as well as health and learning disabilities, have been established in the biological and anthropological fields (Galaburda and Kemper, 1979; Thornhill and Møller, 1997; Miller and Clarren, 2000; Bates, 2007). Functional asymmetries between right and left hemispheres of the brain usually go together with morphological asymmetries of the brain. As skull shape tends to mirror the shape of the underlying brain, functional asymmetries of the brain can manifest as asymmetry of the cranium (Woo, 1931; Ulijaszek and Mascie-Taylor, 1994). However, functional asymmetries of the brain and cranium also occur due to natural physiological or functional

differences in the right and left hemispheres, such as differences in language areas (Ulijaszek and Mascie-Taylor, 1994). Asymmetry due to functional or morphological changes of the brain can manifest in the neurocranial and craniofacial structures as well as the base of the cranium (Pirttiniemi, 1998). Furthermore, a study by Thoma *et al.*(2002) demonstrated that the asymmetry of the brain, both anatomically and physiologically, can be predicted by FA of the body, indicating that developmental noise affects the development of the brain and therefore, also the cranium and the rest of the body in a similar manner.

A vast number of studies (Malina and Buschang, 1984; Markow and Wandler, 1986; Markow and Gottesman, 1989; Shackelford and Larsen, 1997; Martin *et al.*, 1999; Lalumière *et al.*, 2001; Reilly *et al.*, 2001) have associated various mental illnesses in living individuals with an increase in developmental instability, and henceforth also with increased levels of asymmetry. However, a search of the literature revealed no previous studies between FA and mental illness or deficiencies in skeletal samples.

Perhaps the most relevant asymmetry study on the relationship between mental illness and FA was conducted by Malina and Buschang (1984) on living adult males. Eleven bilateral measurements were collected on 202 mentally deficient (or mentally ill) males, and on about 200 mentally healthy males ranging from five to 52 years of age. The mentally deficient males were divided into four aetiological categories of mental condition: Down's syndrome, non-specific, mental disorders with cerebral palsy, and 'other'. The 'other' category included cases with rubella, anoxia, prematurity, encephalitis, and meningitis, to name a few. Overall, higher magnitudes of asymmetry were observed in the mentally deficient group, with significant differences primarily for upper limb measurements. Left – right differences between the four aetiological groups were statistically significantly greater for the 'mental disorder with cerebral palsy' and 'other' categories. They concluded that the significantly higher asymmetry levels of the cerebral palsy group might be an indication that individuals exhibiting a mental illness or disorder with a neurological impairment have a greater tendency to be more developmentally unstable than individuals suffering from other categories of mental illness or deficiency.

Individuals diagnosed with schizophrenia also exhibit higher levels of FA as compared to mentally healthy individuals. A study on dermatoglyphic characters of sets of twins indicated the highest FA values for individuals where the twin was also schizophrenic, followed by schizophrenic individuals with a twin diagnosed with another mental illness (such as psychopathy), and individuals with a mentally healthy twin (Markow and Gottesman, 1989). Their findings corroborate the results of other dermatoglyphic studies on

schizophrenic individuals. Not only were the FA levels greater in the schizophrenic group (Markow and Wandler, 1986; Reilly *et al.*, 2001), but the degree of FA increased with the degree of severity of the disease (Markow and Wandler, 1986). The aforementioned findings suggest that a greater genetic vulnerability to schizophrenia is likely associated with higher levels of FA (Markow and Wandler, 1986; Markow and Gottesman, 1989). A review of the literature on schizophrenia and brain laterality indicated a trend towards decreased or reversed functional and structural asymmetry of certain areas of the brain, such as the planum temporale and the cerebral halves (Oertel-Knöchel and Linden, 2011). Another common mental illness, depression, has been linked to increased FA levels in men, but no correlation was observed in women (Shackelford and Larsen, 1997; Martin *et al.*, 1999). Similarly, a study of male and female university students showed stronger correlations between FA and overall poor psychological, emotional and physiological health in men than in women (Shackelford and Larsen, 1997).

In line with the abovementioned positive correlations between FA and mental disease, an association between FA as an indicator of developmental instability and psychopathy seems reasonable. However, a study found FA results of psychopathic offenders to be higher than those of non-offenders, but lower than the FA values for non-psychopathic offenders (Lalumière *et al.*, 2001). Additionally, offenders with the highest psychopathy scores exhibited the lowest levels of FA as compared to the rest of the offenders. Interestingly, some of the most common characteristics of psychopathic individuals, such as high mating effort and aggression, have also been correlated with low levels of FA, although FA on soft tissues have been argued to be correlated with the secretion levels of hormones such as cortisol (Manning and Wood, 1998; Lalumière *et al.*, 2001).

2.5. Pathological skeletal lesions as indicators of stress

Chronic environmental stressors such as nutritional deficiencies, infection and illnesses can manifest as pathological lesions on dry bone and provide useful information on the health or level of stress of past populations (Mann and Murphy, 1990; Reitsema and McIlvaine, 2014). The manifestation of pathological lesions on dry bone forms the basis for any palaeopathological examination due to bone's limited response to stressors - bony tissues continuously resorb and form by means of osteoclastic and osteoblastic activity. When healthy or 'normal' conditions are disturbed, bone reacts in one of three ways; it is either resorbed, deposited (formed) or include a combination of resorption and deposition. Bony

responses to many diseases or stressors are characterised by specific marks or lesions on the bone. However, the interpretation of the main process of a reaction is fundamental to the identification of the possible pathology responsible for a particular lesion (Goodman and Armelagos, 1989; Mann and Murphy, 1990). Additionally, factors such as age, sex, ancestry and geographic habitat may affect the onset and development of a condition. Similarly, genetics (heritability) and environmental conditions may also alter the expression of a disease (Brickley and Ives, 2008).

According to Mann and Murphy (1990), pathological lesions on bone can be divided into seven broad categories: congenital, infectious, traumatic, toxic, metabolic, neoplastic or neuro-mechanical, and systemic. For the purpose of this study, a brief overview is given of three types of pathological lesions that are considered general indicators of stress in a population: cribra orbitalia and porotic hyperostosis, subperiosteal bone reactions, and enamel hypoplasia, which all fall under the category of infectious and metabolic diseases of dry bone.

2.5.1. Cribra orbitalia and porotic hyperostosis

Porotic hyperostosis and cribra orbitalia manifest in similar ways, and it is believed that a relationship between the two lesions may exist (Mann and Murphy, 1990). For this reason, the descriptions of the two lesions are combined. Porotic hyperostosis refers to the simultaneous occurrence of porosity and thickening of the outer table, and expansion of the diploe of the skull vault. The expansion of the skull vault is a response to hypertrophic bone marrow between the inner and outer skull tables. In severe cases, the outer cortical layer of the cranium thins and may disappear to expose the underlying trabecular bone (Goodman and Armelagos, 1989; Mann and Murphy, 1990; Walker *et al.*, 2009). Porosity, pitting and/or thickening of the orbital roof, on the other hand, is generally referred to as cribra orbitalia. Cribra is usually observed in both orbits and is more apparent in children, where lesions are more often active at the time of death while adults usually present with pitting only (Mann and Murphy, 1990; Walker *et al.*, 2009).

Slightly different aetiologies for the two lesions are presented in the literature. Mutual aetiologies include scurvy (vitamin C deficiency), parasitic infections (El-Najjar *et al.*, 1975; Fairgrieve and Molto, 2000; Brickley and Ives, 2008), and haemolytic or megaloblastic anaemias (Ortner, 2003; Walker *et al.*, 2009). One of the effects of scurvy is iron-deficiency anaemia. While iron-deficiency anaemia is believed to be sufficient to result in cribra orbitalia, recent research indicated that this form of anaemia likely does not produce enough

compensatory red blood cells (in response to an accelerated loss of mature red blood cells) to result in the marrow expansion of the skull vault in porotic hyperostosis. Haemolytic or megaloblastic anaemias seem to be a more likely cause of porotic hyperostosis (Walker *et al.*, 2009). A lack of vitamin C has been linked to haemorrhage, decreased collagen synthesis, and an increased vulnerability to infectious diseases. Anaemia due to a vitamin C deficiency may result from blood loss due to haemorrhage, in combination with a lack of blood formation, and insufficient metabolism of iron and folate. Haemorrhage beneath the periosteum of bones can cause the periosteum to be stripped from the bone, subsequently leading to subperiosteal inflammation. The inflammation may cause pitting or porosity in various skeletal areas, such as in the orbit or skull vault. Because the periosteum of a child is more loosely attached to the bone, children are more prone to subperiosteal haemorrhage (Brickley and Ives, 2008).

Malaria, gastroenteritis, infectious diseases and genetic anaemia have also been hypothesized to cause cribra (Fairgrieve and Molto, 2000; Ortner, 2003), while another possible cause for porotic hyperostosis includes chronic scalp infections.

A study by Meyer *et al.* (2013) on male Chinese mine labourers in the Witwatersrand mines (South Africa) supports the use of cribra orbitalia and porotic hyperostosis as general indicators of stress. The Chinese labourers were believed to have lived in poverty-stricken communities in China before their departure to South Africa, after which the harsh living and working conditions of the mining industry created new stresses. A high prevalence of porotic hyperostosis, cribra orbitalia and subperiosteal new bone growth was observed on the skeletons of the miners, as well as EH on the dentition, which concurred with the historical information on poverty, malnutrition and illness. However, indications of healing of the lesions suggested an improved nutritional intake during their stay in the Witwatersrand.

2.5.2. Subperiosteal bone reactions

Subperiosteal bone reactions, often referred to as ‘periostitis’ in palaeopathological literature, mostly occurs on the long bones but it can be observed on all skeletal elements, and results from inflammation or lifting of the periosteum. Active periostitis gives the impression of newly formed bone that is loosely attached to the cortical bone surface. It is usually gray in colour, porous or pitted, striated and with well-defined raised margins, similar to the bark of a tree (Mann and Murphy, 1990; Ribot and Roberts, 1996; Ortner, 2003). As the periostitis starts to heal, its colour and texture will be similar to that of the rest of the bone and the margins will be less clearly defined, becoming vague or sloped. Although the affected

area may be smoother in appearance, pitting may remain. The tibia is the most often affected bone, followed by the femur and fibula (Perriman and Uthman, 1972; Mann and Murphy, 1990; Meyer *et al.*, 2013).

The inflammation and subsequent subperiosteal bone deposition can be due to a vast number of factors, such as trauma to the bone, the spreading of infection through the blood (such as bacterial infections), subperiosteal bleeding (as a result of scurvy), neoplastic disorders, and venous insufficiency (varicose veins) (Friedman, 1958; Perriman and Uthman, 1972; Goodman and Armelagos, 1989; Mann and Murphy, 1990; Ribot and Roberts, 1996; Nicholls, 2005; Brickley and Ives, 2008). The chronic administration of drugs into the body via injection has also been linked to periostitis and osteomyelitis, through the direct injection into the periosteum or injection through infected skin (Taylor and Lawson, 1986).

In the study by Meyer *et al.* (2013), mentioned in Section 2.5.1 above, periostitis was observed bilaterally in more than 20% of the femurs and more than 40% of the tibias of Chinese mine labourers. Although specific diagnoses from subperiosteal bone reactions are difficult, the involvement of periostitis in both the left and right elements suggested their likely cause to be related to non-specific infectious diseases, rather than trauma. Zukeran *et al.* (2002) studied the skeletal remains of 33 individuals from Medieval and early modern Japan, in which high frequencies of not only cribra orbitalia and EH were present, but also of periostitis. Periostitis occurred more frequently in the lower than in the upper limbs. The high prevalence of periostitis within the sample, together with two cases of osteomyelitis, led the authors to believe that a specific infection, namely treponematosis, could likely have been responsible for these lesions.

2.5.3. Enamel hypoplasia

Linear horizontal lines/grooves or pitting of the enamel of tooth crowns characterise enamel hypoplasia (EH). The cessation of enamel matrix apposition or ameloblast activity during crown formation leads to imperfections in the thickness of the enamel, depicted by lines or pits on a normally smooth enamel surface (Goodman *et al.*, 1980; Mann and Murphy, 1990; Goodman, 1991; Ogden *et al.*, 2007). Enamel hypoplasia can occur on deciduous and permanent teeth, as the enamel of both the deciduous and permanent dentition is formed during important developmental periods, namely from the second trimester to early childhood (about 10 years of age) (Goodman and Rose, 1990; Brook, 2009; Schuurs, 2013). The hypoplastic defect within the tooth enamel is not specific to the type of insult, but rather the

duration and severity of the insult as well as the stage of tooth development (Goodman and Rose, 1990; Brook, 2009).

Enamel hypoplasia is regarded as a quantitative developmental defect and a nonspecific physiological stress indicator of nutritional deficiencies and illnesses that occur during tooth development (Goodman and Rose, 1990; Goodman, 1991; Wright, 1997; Schuurs, 2013). While undernutrition and infection have been regarded as the basic underlying components to cause EH, the hypoplastic defects within the enamel can more likely be attributed to a combination of factors and physiological processes (Goodman and Rose, 1990). A vast number of factors have been shown to cause structural defects in human tooth enamel. These factors can be local, systemic or congenital/inherited (Goodman and Rose, 1990; Schuurs, 2013).

Systemic factors are closely associated with chronic or acute malnutrition and can affect dental development pre-, peri- and postnatally. The systemic illnesses and abnormal vitamin or mineral concentrations, noted to have caused EH, include severe cases of untreated galactosaemia (insufficient galactose metabolism), vitamin D deficiency, extremely low levels of calcium at birth, maternal diabetes, deficient thyroid hormone (cretinism) or growth hormone concentrations, and metabolic disorders, to name a few. Exanthematous (skin) diseases, jaundice, common cold, pneumonia, neonatal asphyxia, asthma during early childhood, and treatment of anaemic mothers during pregnancy have also been noted to cause EH. Mechanical trauma to the deciduous teeth causing injury to the tooth germ of the permanent successor, and infection of the deciduous tooth affecting the development of the permanent successor are local factors that can result in EH of the permanent dentition. Inherited and congenital factors include coeliac disease, Type I diabetes, pseudohypoparathyroidism, congenital syphilis, spina bifida, phenylketonuria, and congenital cardiovascular disorders (Nozaka *et al.*, 1990; Seow, 1997; Brook, 2009; Schuurs, 2013). Some of the more commonly noted causes for EH formation in the literature include low birth weight or prematurity, and severe or chronic malnutrition.

Several syndromes have also been associated with the presence of EH and can be attributed to the mutation of several developmental regulatory genes, which are also active in odontogenesis. Therefore, the mutation(s) can lead to syndromes of which dental anomalies, such as EH, are a part of (Brook, 2009). Some of these syndromes include ectodermal dysplasia (x-linked), Down's syndrome (x-linked), congenital rubella, tricho-dento-osseous syndrome (TDO), tuberous sclerosis, epidermolysis bullosis, autoimmune polyendocrinopathy-candidiasis-ectodermal dystrophy (APECED), and otodental

dysplasia/syndrome (Brook, 2009; Schuurs, 2013). In addition to the presence of EH, some of these syndromes are associated with mental disability or underdeveloped brains. The syndromes mentioned above that are (to a greater or lesser extent) associated with mental disabilities and EH include Down's syndrome, congenital rubella, and tuberous sclerosis (Webb *et al.*, 1991; Määttä *et al.*, 2006; Bhatia *et al.*, 2012). Additionally, other causes of EH, such as phenylketonuria and cretinism, are also known to cause brain damage and ultimately mental disabilities (Schuurs, 2013).

The stage of dental development at which an insult occurred can be inferred from the distribution or position of the hypoplastic defect(s) on the teeth (Brook, 2009). Because it is possible to estimate the age at which a line or imperfection occurred on each tooth, EH, in essence, provides a longitudinal record of stress within an individual or population (Goodman *et al.*, 1980; Wright, 1997). The estimated time of disturbance and the distribution of the defects over the dentition can also be utilised to predict the cause of EH (Schuurs, 2013).

The susceptibility to stress seems to differ between the types of teeth, both in general and at different age intervals. Anterior teeth are generally considered to exhibit a higher prevalence of EH than posterior teeth, although exceptions exist (Goodman *et al.*, 1980; Wright, 1997; Ogden *et al.*, 2007). In a study of 111 adults by Goodman *et al.* (1980), the mandibular canines exhibited 70% of the total EH, followed by the maxillary central incisors. Estimated age of EH formation indicated that the susceptibility to stress shifted from the incisors (especially the maxillary incisors) at birth to 3 years of age, to the canines at 3 – 6.5 years of age, and to the mandibular premolars at 6.5 to 7 years of age. Similarly, the mandibular canine was the most frequently affected tooth in an adult population from Guatemala (Wright, 1997).

In contrast, a study of 45 archaeological subadults from London revealed the highest prevalence and extensive EH on the first molars as compared to the incisors and canines (Ogden *et al.*, 2007). The apparent higher sensitivity of the first molars were attributed to the shorter time of molar crown development (approximately half that of the canines). Based on the unique and complex pattern of EH observed on these subadult molars, a new term was developed to better specify the observed enamel defects, namely 'Cuspal Enamel Hypoplasia'. The latter term refers to the simultaneous presence of nonlinear pitting and irregular plane-form defects in the enamel, as well as additional cusps on the occlusal surface together with a disruption of normal cusp development. Cuspal Enamel Hypoplasia is believed to develop during the onset of molar development and cusp pattern formation.

2.6. Dutch socio-economic environment: 1700 – 1914

While it is difficult to ascertain the internal or genetic stress of the two Dutch populations, some records of their general external environment, such as their socio-economic history, are available. Developmental stressors (genetic and environmental) can increase the observed magnitude of FA within a population (Van Valen, 1962; Palmer and Strobeck, 1986). Therefore, information on the possible differences in the socio-economic environment of the two populations is necessary for the interpretation of the differences in asymmetry. Figure 2.3 provides a timeline of the major socio-economic trends during the time periods in which the GRK and MeB individuals lived.

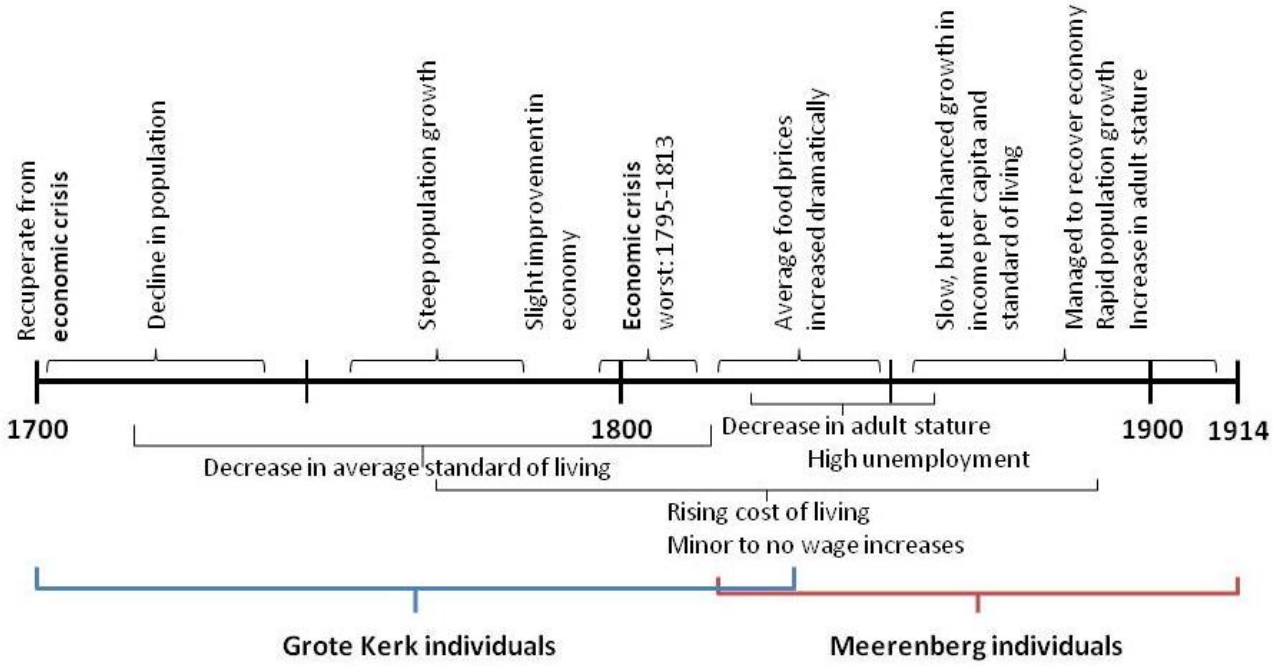

Figure 2.3. Timeline of the major socio-economic trends during the time periods in which the GRK and MeB individuals lived.

In the beginning of the 18th century, the Netherlands was characterised by an endeavour to recuperate from the economic crisis of the late 17th century. The last quarter of the 17th century represented a decline and the end of the economic Golden Age, which epitomised the first three quarters of the 17th century (De Vries and Van der Woude, 1997). The aforementioned economic crisis of the late 17th century caused a diminished rural demand for urban goods and services as well as a stagnation of a great number of industrial endeavours, which led the way to de-urbanisation and chronic unemployment, and ultimately to increased poverty of the lower class in particular (Van den Eerenbeemt, 1962; De Vries

and Van der Woude, 1997). The smaller cities such as Alkmaar, Dordrecht, Leeuwarden, Groningen and Utrecht were detrimentally affected (De Vries and Van der Woude, 1997).

The Dutch population declined until the 1740's, but steep population growth again occurred during the second half of the 18th century, despite the still rather precarious state of the economy (Van den Eerenbeemt, 1962; De Vries and Van der Woude, 1997; Allen, 2000). Between 1740 and 1780 the economy improved slightly, but in spite of the rising costs of living wage increases were minor and infrequent; some wages did not increase for 200 years (Van den Eerenbeemt, 1962; De Vries and Van der Woude, 1997; Allen, 2001a). Differences in average wages between urban and rural areas and between large and small cities were insignificant. Both rural and urban people had access to a variety of occupations/services from the mid-18th century. The services were scarcer in the rural areas, especially those of doctors and surgeons. The most promising and beneficial economic growth of the 18th century was the colonial trade market (De Vries and Van der Woude, 1997).

While the Dutch economy had improved by 1780, especially in terms of a highly productive agricultural economy, it lacked credit-creating institutions to effectively buffer another economic crisis. Therefore, it is no surprise that the declaration of war by the British in 1780 and the subsequent French rule over the Netherlands in 1795 (imposing an enormous tax burden) knocked the Netherlands into yet another economic crisis. This economic recession was at its worst between 1795 and 1813 (De Vries, 1968; De Vries and Van der Woude, 1997). During this time, de-urbanisation and re-agriculturalisation occurred, which is evident by the population decline of 10% in the cities of Holland and Zeeland (Figure 2.4; Provinces of the Netherlands, 2015) and the population growth that increased by 10% in the rural areas and the provincial cities (combined). The end of this period (1795 – 1813) was characterised by a nation in poverty (De Vries and Van der Woude, 1997).

Despite the economic recession, various cities in the northern parts of Holland were provided with several specialised services in 1811, which included religious, economic, judicial, medicinal, social, cultural and educational services. Alkmaar was one on these cities. The smaller cities mostly possessed only a church (religious), a surgeon (medicinal) and one or two shopkeepers (De Vries and Van der Woude, 1997). The agricultural sector was relatively small, but highly productive during the 19th century, where it engaged 45% of the male population. The fraction of the rural population involved in agriculture increased from 66% in 1800 to 77% in 1849 (Allen, 2000). However, during the period 1820 to 1850, the average relative food prices increased dramatically, with immense increases during the 1840's (Haines, 2004). A decrease in adult stature, slow increase in income per capita and

drastic increases in relative food prices, especially throughout the 1830's to 1860's, all indicate a critical and difficult socio-economical period, particularly for the wage-workers (Haines, 2004).

Figure 2.4. A map of the Netherlands and its provinces. The position of Alkmaar and Bloemendaal (Meerenberg) in relation to the city of Amsterdam are indicated (Provinces of the Netherlands, 2015).

The economic growth between 1820 and 1860 was quite slow; an enhanced growth in the income per capita and the standard of living only came about between1860 and 1913 (De Vries, 1968; Allen, 2001a; Haines, 2004; Deneweth *et al.*, 2014). Although slow and laborious in its recovery, the Dutch managed to recover their economy by the second half of the 19th century. After the recovery, a certain albeit precarious economic growth and industrialisation occurred, whilst further groundwork for a steady economy continued (De Vries, 1968; Haines, 2004). Colonial investment in the larger cities (such as Amsterdam) during 1870 further facilitated the revival of the economy (Goldberg and Graham, 2013).

Economic development escalated within the Netherlands, ranking the country as one of the most urbanised countries in Europe at that time, with a rather wealthy upper and middle class.

Rapid population growth occurred during and after the 1870's, with a total population increase of around 1.9 million individuals; from 2.6 million in the early 19th century to 4.5 million during only the 1870s (Deneweth *et al.*, 2014). Figure 2.5 (Deneweth *et al.*, 2014: 82) provides a summary of the standard of living of Dutch labourers from 1700 to 1910 by means of a welfare ratio (Allen, 2001a,b). The welfare ratio represents a price index of the average annual wage of a labourer divided by the estimated cost of basic needs per family of four (one male, one female and two children). The welfare ratio is described in terms of a 'poverty line', represented by the 1.00 on the y-axis. A welfare ratio of less than 1.00 indicates that families could not afford all the basic commodities to sustain an adequate standard of living while families could likely afford some luxuries or more basic commodities in times where the welfare ratio was greater than 1.00.

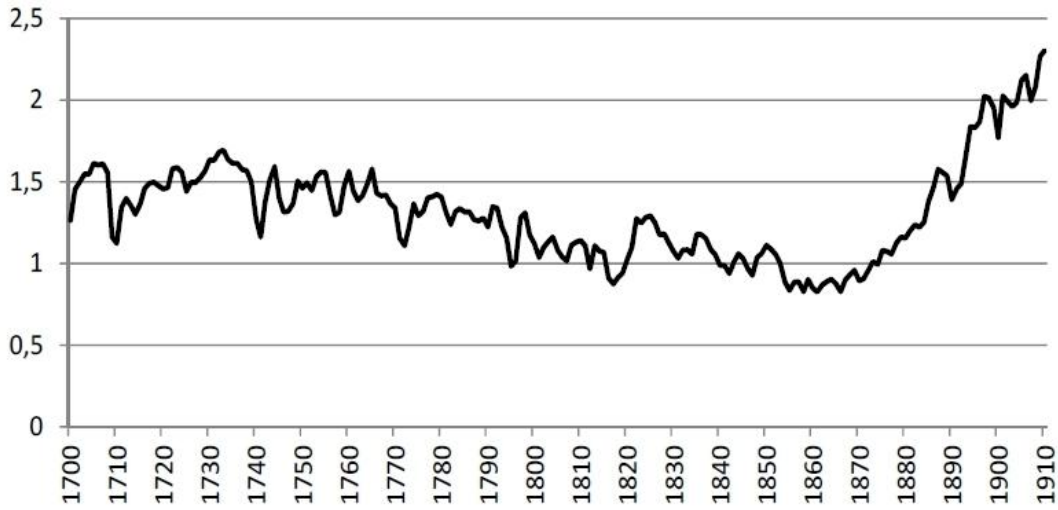

Figure 2.5. The welfare ratio of Dutch labourers, 1700-1910 (Deneweth et al., 2014: 82).

Despite the economic growth that occurred throughout the 19th century, high unemployment rates were still apparent during the majority of the 19th century, which kept a major part of the nation suffering under a general worsening of the living standards. Additional factors that contributed to the decline in the standard of living until the late 1870's (see Figure 2.5) include the rapid rate of urbanisation, integration of disease environments, and commercialisation that accompanied the transport revolution (Haines, 2004; Deneweth *et al.*, 2014). Haines (2004) argues that the confluence of the aforementioned factors is

sufficient to explain the concurrent decline in adult stature in the middle of the 19th century – not just in the Netherlands, but also in the United States and England, which experienced similar economic challenges during the 19th century.

In the late 18th century, the Dutch were the second tallest people in Europe, surpassed only by the British (Allen, 2001a). Average adult height within the Netherlands declined substantially from the mid-thirties to the mid-sixties of the 19th century, after which it gradually increased. Between the mid-forties and the 1850's the average national height slightly increased, after which it again declined rapidly until the 1860's. However, the average height in the urban areas declined all through 1827 to 1850. Overall, the height decline was much greater in the urban areas compared to the rural areas, which also concurred with higher urban mortality rates during this time (Allen, 2001b; Haines, 2004). The average height decline was not limited to this short period but has been shown to have decreased in general from the Roman Period up to the first half of the 19th century. The greatest decrease in adult stature occurred during the Late Medieval Period and reached an ultimate low during the 17th and 18th centuries (Maat, 2005). Stature increased yet again in the late 19th century and continued throughout the 20th century (Allen, 2001a; Haines, 2004; Maat, 2005). In contrast to stature, there was no decline in the national life expectancy at birth over the above mentioned periods, but rather a slight increase between 1840 and 1870 (Haines, 2004). Figure 2.6 (Haines, 2004: 252) illustrates adult height and life expectancy at birth for Dutch males from 1824 to 1915. Birth rates only started to decline at the end of the 19th century (Haines, 2004).

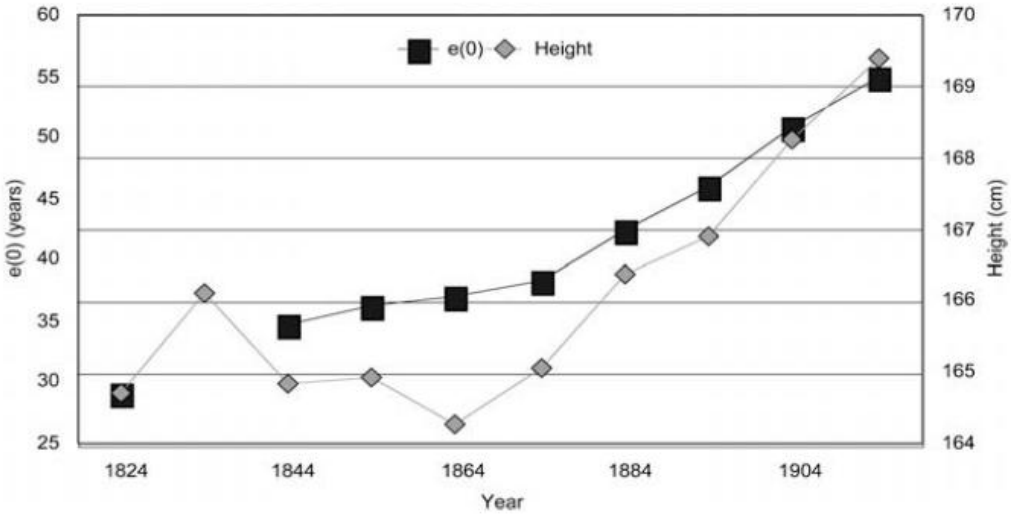

Figure 2.6. Heights and life expectancy at birth for Dutch adult males, 1824-1915; e(o) = life expectancy (Haines, 2004: 252).

Summary

The 18th to early 19th century Dutch economy started and ended amidst the remnants of economic recessions; with a period of slow economic growth in between (1740-1780). While the economic growth was rather turbulent in its course, the average standard of living decreased over the entire time period, reaching an ultimate low at the turn of the century. This latter poor state of living standards resulted from the stagnation of wage increases and an increase in the cost of living, together with the economic recession of 1795-1813. This first period (1700-1830) depicts the socio-economic circumstances in which the individuals buried in the Grote Kerk (Alkmaar) lived, while the early 19th to early 20th century economy influenced the living conditions of the Meerenberg individuals. This latter period saw a rise in agriculture and the overall economy in the early 19th century, followed by rapid rates of industrialisation and wage increases during the late 19th century. Although the national earnings per capita showed an overall, albeit turbulent, increase throughout the 19th and early 20th century, a decline in the average stature and an impoverished standard of living was evident from the 1830's to 1860's. From about 1870 onward, the country experienced rapid population growth together with an increase life expectancy and standard of living. Overall, the socio-economic environment of the Meerenberg individuals seems to have been more stable compared to the Grote Kerk individuals.

2.7. History of study collections

2.7.1. Groote Kerk of Alkmaar

The Grote or St Laurens church, located in the city of Alkmaar, the Netherlands, was built as its current structure between 1470 and 1520. The church was likely founded in the late tenth century, although historians dispute this date. Reasons for the dispute include the sparseness of information on the church before 1470 and the belief that some historical information has been falsified in subsequent centuries (Bitter, 2002). As was customary for the time-period, the church floor served as a graveyard for the people of Alkmaar until 1830. While it is not clear when the first burials occurred within the church of Alkmaar, church burials already took place from as early as the Middle Ages. However, only one excavated grave from the Grote Kerk is assumed to date from before 1470, as suggested by the decomposed state of the skeleton and the different colour of the sand in the burial pit compared to the rest of the graves, which are assumed to date from after 1470 (Bitter, 2002). The church held 1755 registered gravesites, marked by gravestones, which also served as the

church floor. Most graves were 2.00 to 2.30 meters deep (some even deeper) and contained up to eight coffins on top of each other (Baetsen, 2001; Bitter, 2002). Figure 2.7 (Baetsen, 2001: 7) illustrates the arrangement of grave sites within the church, as according to the historical grave administration. At the time of excavation, only a few graves differed in location to the floor arrangement of 1624/34. Individuals not buried within the church floor were laid to rest within one of the two graveyards on the north and south end of the church.

Figure 2.7. Layout of the gravesites in the Grote Kerk of Alkmaar according to the historical grave administration of 1624 / 1634 (Baetsen, 2001: 7).

Burial within the church was substantially more expensive than in the graveyard and served as a major source of income for the church. The family was also charged extra for the ringing of church bells, arriving late, or conducting the funeral by evening or night as opposed to the afternoon (Bitter, 2002). Therefore, the majority of individuals buried within the church can be assumed to be of a middle to higher socioeconomic status (SES), although church burials only became excessively expensive for the citizens of Alkmaar at the end of the 18th century (Baetsen *et al.*, 1997; Baetsen, 2001; Bitter, 2002). The foul smell of decomposing bodies and the rubble caused by the digging of the graves spurred an escalation of complaints against church burials. In 1827, church burials were banned by law and all new burials were to take place within a new cemetery outside the urban area. The last burial within the Grote Kerk of Alkmaar took place on 13 September 1830, and three days later, the first funeral took place in the new general cemetery (‘Algemene Begraafplaats’) of Alkmaar (Bitter, 2002).

Extensive restorations to the church between 1989 and 1995 included the installation of an underfloor heating system, which ultimately led to the excavation of numerous graves (Baetsen, 2001). Due to time and financial constraints, only 35% of the floor of the Grote Kerk was excavated. The excavations took place from July 1994 to May 1995, unearthing approximately 1175 individuals, contained within 901 coffins and 62 bone-boxes (Baetsen, 2001; Bitter, 2002). A small proportional subset (250) of the excavated individuals were chosen for further study by Baetsen *et al.* (2001). The proportional subset of individuals was chosen from the top layers of the graves, as historical sources contained the greatest amount and the most reliable information for the correct identification of these individuals. Therefore, individuals from the most recent burials were chosen to be included in the above-mentioned subset. In addition, the sample was chosen to represent the entire (excavated) floor of the church, as the individuals of highest socio-economic status were deemed to have been buried in certain areas of the church, such as in the choir or the stalls. A random sample would have distorted the sample in terms of socio-economic status (Baetsen, 2001). The majority of the individuals included in the subset could be positively identified through the linkage of information from the burial registers to the preliminary anthropological analyses. The burial registry contains information on the date of death, as well as the name and age at death of the deceased individual. In some instances, children's names were omitted and written under that of a parent, usually the father's name, such as 'the son/daughter/child/baby of…' the parent (Baetsen, 2001; Bitter, 2002).

However, it is likely that information contained within the burial register was not always correct. The main reason for the possible error relates to the payment and grave rights. Besides moderate to large sums of money that were paid to the church for the actual burial, the owners of the grave were also held responsible for the maintenance of the church floor. If payment for the grave has ceased, if the owners gave up ownership of the graves, or when the graves in the church were full, the graves were *'geschut'*, meaning that the remains of these individuals were excavated and placed in smaller wooden boxes. These small boxes were then either placed within the grave pit or reburied along the sides of the church. A new burial could then take place in the top grave, causing a shift in the levels of the grave. If the burial register was not changed accordingly, the wrong information would be associated with a certain set of remains (Bitter, 2002).

Adult individuals constitute the largest proportion of the sample, with about 101 females and 87 males. The average age at death is 60 and 50 years for males and females respectively. Approximately 56 individuals are subadults (< 20 years of age), among which

the majority (71%) were less than five years of age at the time of death (Baetsen *et al.*, 1997; Baetsen, 2001). The burials date to the 18th and early 19th century, with the majority of the burials dating from the late 18th to the early 19th century (Baetsen *et al.*, 1997; Baetsen, 2001). Combined, the identified individuals lived from 1709 (earliest individual born) to 1830 (last individuals died).

2.7.2. Meerenberg

During the 17th and 18th centuries, Dutch individuals with psychiatric aberrations were either treated at home or placed in so-called 'dolhuisen' (lit. madhouses) when posing a physical threat to society or to themselves. Even though an official verdict in 1818 mandated the treatment of psychiatric patients within an institution, the initiative for the opening of such an institution was only taken seriously years later. The inauguration of an insanity law ('krankzinnigenwet') in 1841 sparked an earnest motion to open a medicinal facility for the mentally ill within the Netherlands, such as the Meerenberg psychiatric hospital (Vijselaar, 1982). Built in the late 1840's, the Meerenberg psychiatric hospital was the only mental hospital in the whole province of North Holland, including Amsterdam, until the late 1880's (Vijselaar, 1982; Van Twuyver, 2000; Goldberg and Graham, 2013). What started out as 31.1 hectare grounds, tripled to about 90 hectares by 1929 (Van Twuyver, 2000). Meerenberg was the largest and most prestigious mental asylum in the Netherlands during the 19th century and offered residence to patients of low and high SES (Boschma, 2003; Voermans, 2009). Patient clothing, rooms, dining halls and meals were divided according to five classes based on SES, with the first four classes designated for the financially well-off patients (Vijselaar, 1982; Van Twuyver, 2000). Treatment within a mental asylum was expensive; therefore, municipal departments, churches or foundations carried the expenses for most of the low SES patients (fifth class). Between 1880 and 1910, about 90% of all patients in the Netherlands were dependent on the aforementioned organisations' financial care, suggesting that most of the patients would have been of a lower SES. Even though municipal departments and foundations tried to limit the number of patients under their care, overcrowding within mental asylums was common (Vijselaar, 1982).

In 1867, a train station was built in Santpoort, a city close to Meerenberg, after which the railroad was extended to Meerenberg in 1888 for the transport of goods to and from Meerenberg. By 1897, this train station, then known as 'Santpoort-Meerenberg', had a separate waiting area for the patients of Meerenberg (Vijselaar, 1982; Van Twuyver, 2000). Within the same year, Meerenberg enjoyed international attention, mostly due to its nursing

training program in psychiatry, established in 1892 (Van Twuyver, 2000). After 1910, some of the newer clinics became University Clinics, which mainly accepted the 'healthier' patients into their care (Goldberg and Graham, 2013). Over time, Meerenberg became "*the mental hospital for the chronic and difficult patients of Amsterdam*" (Goldberg and Graham, 2013: 38), housing patients with higher levels of mental illness compared to the other mental asylums of that time. In 1918, the name was changed to the Provinciaal Ziekenhuis nabij Santpoort (lit. Provincial Hospital near Santpoort), which ultimately closed its doors in 1994 (Van Twuyver, 2000; Goldberg and Graham, 2013). Meerenberg became the first psychiatric institution within the Netherlands to adopt a non-restraint treatment plan as part of a moral treatment initiative. This treatment plan was based on practices in the UK, studied and chosen by Dr. Everts, the first physician director of Meerenberg (1847 to 1874). Dr Everts died in 1883 and was buried in the general cemetery of Meerenberg, although it is believed that his grave was later lost due to negligence (Van Twuyver, 2000).

Unfortunately, information regarding the patients is sparse, as the Meerenberg hospital refused to keep a patient register, even after the king mandated it in 1877. Reasons for not adhering to this law included, amongst others, concealment of the identity of high status patients (Voermans, 2009). Fortunately, doctors and nursing staff of Meerenberg collected general information on patients and their illnesses over the years, giving an overall picture of the psychiatric patients and their care in the Netherlands. Most patients exhibited initial signs of mental illness between the ages of 20 and 40 years, single individuals seemed to be more prone to mental illness than married individuals, and relatively more patients were admitted from urban, than from rural environments (Vijselaar, 1982).

In 1905, twelve categories of mental illness were in use for the diagnosis of patients: mania (rage), melancholy (depression), confusion, insanity epileptica, insanity hysterica, insanity neurasthenica, insanity toxica (delirium tremens), paranoia, dementia paralytica, dementia senilis, imbeciles and idiots (Vijselaar, 1982; Van Twuyver, 2000). About a third of all admitted patients were considered healed and discharged from mental institutions, mostly within the first two years after admittance. Other patients, especially those who suffered from dementia senilis and dementia paralytica, died within the first two years of admittance. The chance of discharge into society became smaller for patients the longer their stay in a mental institution. Chronic patients usually resided for more than ten years before being discharged, although a great number of these patients ultimately died within the institution. While their deaths were mostly related to their mental illness, such as chronic exhaustion, about 50% of patients died from infectious diseases. Overcrowding, poor patient health, and inadequate

hygiene in the asylums all contributed to an increased susceptibility to infectious diseases, such as tuberculosis and pneumonia (Vijselaar, 1982). Many patients admitted to Meerenberg suffered from what was presumed to be tuberculosis, and occasionally also infected staff members with the illness (Van Twuyver, 2000)

Once a patient had died, permission was obtained from the family (unless the patients had no living or known relatives) to conduct an autopsy on the deceased. An important part of the autopsy was the macro- and microscopic study of the brain. Fixated and sectioned brains, as well as skulls with peculiar shapes, were gathered from the various institutions to form pathology museums (Vijselaar, 1982). Most of the information on the psychiatric hospitals of the late 18th century is now housed within one museum, 'Het Dolhuys' (lit.The Madhouse) in Haarlem, the Netherlands. Unfortunately, none of the abovementioned skulls are part of the current exhibition. After completion of the pathological examination, the patient was laid to rest in the cemetery of the institution. Some institutions had more than one cemetery, divided based on the various religious beliefs of the patients. Meerenberg had both a Catholic and a Jewish cemetery on the grounds. The Catholic cemetery was closed in 1937, and it was thought that all the individuals were reburied in the general cemetery on the Meerenberg grounds (Vijselaar, 1982; Van Twuyver, 2000). Both patients and staff members were buried in the cemeteries.

The accidental disturbance of the original Catholic cemetery by property development in 2009 led to the exhumation of 66 graves. The graves dated from 1891 to 1914 and contained mostly single interments, as well as a number of charnel pits (Van der Merwe *et al.*, 2013). Figures 2.8 and 2.9 illustrate the position of the excavated graves on the Meerenberg grounds. The individuals buried in the aforementioned graves formed part of the current study.

Figure 2.8. Bird's eye view of the excavation site on the Meerenberg grounds. The cemetery is indicated in yellow.

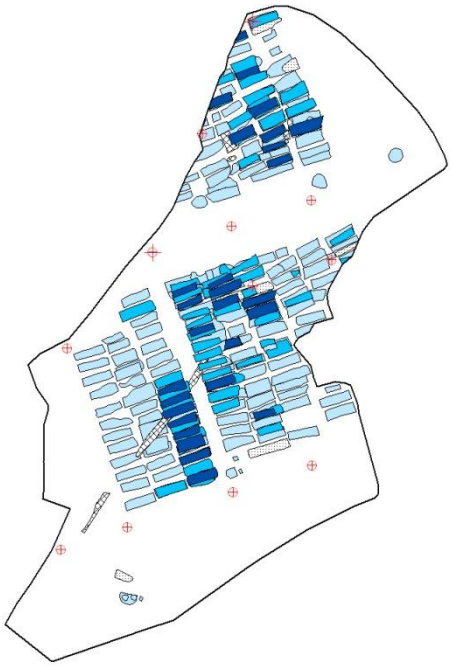

Figure 2.9. A site map of the excavated graves, indicated in blue. The shades of blue represent the levels of a burial pit, from one layer in light blue to three layers in dark blue.

Chapter 3: Materials and Methods

3.1. Materials

The sample used in this study comprised of two urban archaeological collections; the Grote Kerk (St Laurens church) skeletal collection from Alkmaar (n=171) and the Meerenberg skeletal collection (n=106) from Bloemendaal, both housed at the Academic Medical Centre in Amsterdam, the Netherlands. The historical setting and disinterment of these remains have been discussed in the literature review (refer to Section 2.7).

3.1.1. Grote Kerk collection

The Grote Kerk (GRK) sample comprises of 250 nearly complete individuals with the majority of the elements well preserved. The sample of 250 is a subsample of the approximately 1175 individuals who were unearthed from a church floor in Alkmaar during restorations to the church (Baetsen *et al.*, 1997; Baetsen, 2001). As a result of time constraints, and the fact that the GRK sample is markedly larger in size compared to the Meerenberg (MeB) sample, individuals from the GRK sample were randomly chosen from carts to be included in the current study. The GRK sample was stored in such a manner that the remains (contained in boxes) were stored in on eight carts within a storeroom. Carts were chosen at random and all remains per chosen cart were analysed and included in the study. An extra cart, containing only subadult remains, was also included in the study, in an effort to increase the number of subadult remains. As a result, 171 individuals were included in the study, of which the majority (86.6%) were adults (56.8% female, 41.2% male, 2.0% indeterminate; see Table 3.1).

Some graves contained additional bony elements, mostly smaller bones such as those of the hand, foot or vertebral column. This is not unusual since often only the larger bones of individuals were excavated, collected and placed in smaller wooden boxes once the payment for the grave has ceased or when the graves within the church were full. These small boxes were then either placed within the grave pit or reburied along the sides of the church. Some of these boxes contained skeletal elements of up to six individuals (Baetsen *et al.*, 1997; Baetsen, 2001). For the purpose of this study, in cases where more than one individual was either buried or stored together (and not individually marked), the left and right bones per element or the skull and mandible were matched per individual with great caution. Every matched pair of skeletal elements (either the skull and mandible or the left and right elements

of the long bones) was recorded as a separate individual. When a positive match between bilateral elements (left and right long bones) could not be made with a high degree of certainty, the element(s) were excluded from the study.

3.1.2. Meerenberg collection

The MeB collection comprises of skeletal remains excavated from 66 graves previously buried in a Catholic cemetery on the grounds of the Meerenberg psychiatric hospital. The circumstances surrounding the disinterment of the remains together with the archaeological conditions contributed to a moderate to poor state of preservation of the skeletal remains. While the graves contained mostly single internments, a number of charnel pits were also excavated (Van der Merwe *et al.*, 2013). All individuals from the MeB collection were included in this study. After death, the patients of Meerenberg were often autopsied (Vijselaar, 1982). This included the cutting of the skull for removal of the brain, and sometimes the removal of the spinal cord by cutting the vertebral spines posteriorly.

Similar to what was the case in the GRK sample, bones that were buried or stored together were matched per bilateral element (left and right long bones or skull to mandible) with great caution, and all left and right long bone elements, and skull and mandibles were treated as separate individuals. Because of this method of pairing, the number of individuals recorded in the current study would have been higher than the minimum number of individuals included in the Meerenberg population (estimated at approximately 80 individuals). When a positive match between bilateral elements could not be made with a high degree of accuracy, the element(s) were excluded from the study. Taking the aforementioned 'pairing' into consideration, this study included 106 individuals (97.2% adult, of which 54.4% female, 28.16% male, 17.5% indeterminate; see Table 3.1).

Table 3.1. Sample sizes included in the study for adults and subadults per population

	Grote Kerk	Meerenberg
Adult	148	103
Subadult	23	3
Total	171	106

3.2. Methods

Although studies on the general demographic profile and skeletal pathologies have to an extent been conducted on both the GRK and MeB collections (Baetsen, 2001; Van der Merwe *et al.*, 2013), all individuals were reassessed for the purpose of this study. Estimations of sex and age by the author of the current study were correlated with the information available within the burial registers. Where the information did not correlate, the estimation of the author was used within this study. Information on the sex and age of subadults were available for only a few individuals within the burial registers, of which the majority was for adolescent individuals. Some graves also contained more than one child, although the burial register noted only a single burial. Therefore, subadult sex and age estimations of the author were used for this study. This prevents possible errors within the analyses or results due to misplacement of, or damage to, the archaeological remains, which may have occurred throughout the years. An estimation of ancestry was not included in this study, as all individuals were deemed to be of Dutch origin (see Section 2.7).

3.2.1. Demographic profile estimation

The estimation of sex based on the examination of human skeletal remains can be accomplished by means of metric and morphological techniques. Metric methods are mostly based on size or metric differences between males and females. Nonmetric or morphological methods evaluate skeletal traits that are considered characteristically different between the sexes and include size differences. Even though morphological techniques are more subjective in comparison to metric techniques, morphologic methods are regarded as less time-consuming and easier to use (Walker, 2008; Garvin, 2012). Additionally, the poor preservation and relatively small sample sizes often encountered in archaeological samples complicate the use of metric techniques (Walker, 2008). Sexual dimorphism also varies by population, necessitating the use of population-specific methods, especially with the use of metrics (Acsádi and Nemeskéri, 1970; Walker, 2008; Garvin, 2012). While the visual scoring of sexually dimorphic traits is believed to be influenced by both the experience of the observer as well as the observer's familiarity with the population, current discriminant techniques for scoring traits allows for a less biased and more practical method for sex estimation, comparable to metric discriminant functions (Phenice, 1969; Walker, 2008; Klales *et al.*, 2012).

Skeletal differences between the sexes are essentially an expression of size and shape dimorphism due to differential expression of secondary sexual characteristics, as well as functional and biomechanical differences. On average, males tend to be larger, taller and heavier, with more prominent muscle attachment sites than females. Sexually dimorphic traits do not simply classify as masculine and feminine but form a continuum from hyper-masculine to hyper-feminine, such that an individual can, for example, be classified as a gracile male or a robust female. Additionally, the expression of sexual dimorphism changes with age; young adult males tend to exhibit more female characteristics, while mature adult females (after menopause) tend to be more masculine. Hence, sex estimations are the most accurate after skeletal maturity has been reached (Acsádi and Nemeskéri, 1970; Walker, 2008; Garvin, 2012). Although the estimation of sex from subadult remains is possible, only a few population specific techniques exist, and most results proved unreliable and inaccurate (Acsádi and Nemeskéri, 1970; Stull and Godde, 2013).

In addition to sex, age at death estimations were also conducted on the remains. Various factors complicate and influence the estimation of age at death, especially from adulthood onwards. These factors include biological, cultural and social aspects, such as activity levels, health, and nutrition. This is because the physiological age of an individual, known as biological age, is used to predict chronological age. Chronological age refers to the actual age of an individual, or the numbers of years lived since birth (Acsádi and Nemeskéri, 1970; Garvin *et al.*, 2012). Similar to sex estimations, the estimation of age from skeletal remains will be the most accurate with the use of population specific methods. The use of multiple indicators or methods is preferred for both sex and age estimations, as it increases the accuracy of the estimations (Garvin, 2012; Garvin *et al.*, 2012).

3.2.1.1. Sex

As no population-specific techniques exist for the metric estimation of sex for the two Dutch populations included in this study, adult sex was primarily estimated by means of morphological techniques. Where sex could not be estimated with reasonable accuracy using the morphological techniques, metric analyses were conducted against the measurements of individuals within the population who could be sexed with acceptable accuracy. The latter analysis is described below.

Pelvic (Phenice, 1969; Klales *et al.*, 2012) and cranial (Buikstra and Ubelaker, 1994; Walker, 2008) morphological traits were used for the estimation of sex in older adolescents and adults. The pelvis is considered as the most sexually dimorphic skeletal element,

followed by the cranium. General sexual dimorphic traits of the pelvis are closely related to function, typified by a lower and wider female pelvis, versus a higher and narrower male pelvis. Additional sexually dimorphic traits of the pelvis include a laterally divergent ilium, an elliptical or oval pelvic inlet, a broader and less curved sacrum, a wider greater sciatic notch, a triangular obturator foramen and a wide subpubic angle in females, while the male pelvis exhibits a more vertical ilium, heart-shaped pelvic inlet, a narrower and more arched sacrum, an oval obturator foramen and a narrow subpubic angle (Acsádi and Nemeskéri, 1970; Garvin, 2012).

In some cases, sex could not be estimated with reasonable accuracy, either due to incomplete remains or the lack of expression of distinctive sexual characteristics. Therefore, for each population, several long bone (left-side) measurements of individuals with unknown sex were plotted against the corresponding values of individuals for which sex could be estimated. This was conducted by means of linear discriminant analysis. Linear discriminant analysis is a statistical technique that applies multivariate tests to the differences between groups of known measurements (predictor variables) in order to classify unknown data/measurements into groups (Morrison, 1969). In this case the classification was into one of two groups: male or female. This enabled the individuals of unknown sex to be categorised as either male or female. Long bone measurements included in this analysis were HXMS, HIMS, HDT, FML, FXMS, FIMS, FSIH, TXNF and TINF (refer to Table 3.2 for abbreviations). Individuals for whom none of the above measurements were available remained classified as ‘indeterminate’ sex. The rest of the long bone measurements were excluded from this metric analysis due to small sample sizes, which would have decreased the overall sample size for comparison.

No attempt was made to estimate the sex of subadult remains, as no population specific data are currently available.

3.2.1.2. Age

Age at death for adults were assessed through cranial suture closure (Acsádi and Nemeskéri, 1970; Meindl and Lovejoy, 1985), as well as age related changes in the pubic symphyseal surfaces (Brooks and Suchey, 1990; Hartnett, 2010), and sternal rib ends (İşcan *et al.*, 1984a,b, 1985), when possible. Changes in the pubic symphyseal surfaces and sternal rib ends were given more weight in the estimation of adult age than cranial suture closure, due to the large standard deviations and resultant wide are ranges associated with using closure of the cranial sutures (Meindl and Lovejoy, 1985; Garvin *et al.*, 2012). Subadult age

at death analyses included the evaluation of dental development and eruption (Moorrees *et al.*, 1963a,b; AlQahtani *et al.*, 2010), the degree of union of primary ossification centres and the fusion of epiphyseal growth plates (Buikstra and Ubelaker, 1994; Schaefer *et al.*, 2009). Dental eruption and development were deemed more reliable for age estimation, as dental development is less sensitive to environmental stressors than bone growth (Garvin *et al.*, 2012).

Due to a lack of population-specific data and the fragmentary state of some skeletal remains, the estimated age ranges were relatively wide. As the estimation of age-at-death in this study was only for the purpose of placement into broad age categories, the resultant age ranges were categorised by means of average age as calculated from the estimated age ranges. Following suggestions by Storm (2009) and Falys and Lewis (2011), both subadults and adults were divided into sub-categories in order to facilitate comparisons by age, and to allow for future comparisons with other FA studies. The four subadult age categories included foetal age to infant (F-I; prenatal to 12 months of age), early childhood (EC; 1-6 years of age), late childhood (LC; 7-12 years of age) and adolescence (AD; 13-19 years of age). Adult age subcategories included young adult (YA; 20-34 years of age), middle adult (MDA; 35-45 years of age) and mature adult (MA; > 46 years of age). Where it was not possible to assign a specific age range to an adult individual (due to incomplete remains), the individual was categorised simply as an adult (A; > 20 year of age).

3.2.2. Analysis of pathology

In order to assist in the interpretation of FA magnitudes within and among the populations, all individuals were assessed for four general macroscopic pathological lesions associated with metabolic and nutritional diseases: cribra orbitalia, porotic hyperostosis, subperiosteal bone reactions (periostitis) and enamel hypoplasia (see Section 2.5). It must be noted that the evaluation of skeletal markers of pathology was not the main objective of this study; therefore, the four pathological lesions were only assessed on a present-absent basis. Due to time constraints and no available experienced observer to confirm the observations, no inter- or intra-observer error was obtained for the pathological lesions.

Standard palaeopathological textbooks served as diagnostic aids in the analyses of the observed pathological lesions (Mann and Murphy, 1990; Ortner, 2003; Brickley and Ives, 2008; Waldron, 2009).

3.2.3. Measurements

A range of bilateral cranial, mandibular, long bone, and dental measurements were recorded for each individual. These measurements were chosen based on their high informative value for population comparisons of asymmetry, as well as to allow for comparisons with previous asymmetry studies on human skeletal remains (Storm, 2009). All measurements were based on previously defined measurements and procedures(Howells, 1973; Kieser, 1990; Buikstra and Ubelaker, 1994; Guatelli-Steinberg *et al.*, 2006; Storm, 2009), except for three cranial measurements specifically defined and modified for DA and FA analyses by Storm (2009). These include mastoid length (MPL), mastoid breadth (MPB) and mandibular length (MAL). A detailed description of all the measurements is shown in Appendix 1. Various long bone measurements were recorded on the humerus, radius, femur and tibia. Tooth measurements were taken on all deciduous and permanent teeth, excluding the third molars, as third molars are generally irregular and variable in shape (Hillson, 1996). Because sub-adult and especially foetal bones are still growing, mineralising and fusing, their bones are void of certain structures or landmarks that are present on adult or mature bones (Buikstra and Ubelaker, 1994; Scheuer *et al.*, 2000). Therefore, certain measurements can only be taken from early childhood onwards or only from foetal age to adolescence, while other measurements can only be recorded on adult bones. Table 3.2 lists the measurement abbreviations and age categories for each measurement that was taken, as adapted from Storm (2009).

Sliding callipers (to the nearest 0.01 mm), and spreading callipers (to the nearest 0.1 mm), as well as an osteometric board (to the nearest 1 mm) were utilised to obtain the measurements. In order to ensure consistency and to minimise session bias (David *et al.*, 1999), both the right and left sides of each measurement were taken by the primary investigator during the same sessions. In order to ensure inter- and intra-observer repeatability, a subset of measurements was repeated by the primary investigator and by a second observer, respectively. Repeated measurements were recorded on different days than the first measurements, and both the left and right sides of a trait (per individual) were measured in the same session, in order to reduce session bias.

Some of the skulls, as well as femoral and humeral heads (usually only on one side), were previously cut for study purposes. The femoral and humeral head cuts were made for the estimation of age by means of the complex method (WEA, 1980). The majority of skulls from Meerenberg were cut during autopsy (Vijselaar, 1982), resulting in varying degrees of distortion of the skull cap. All cut bone cases were noted on the scoring sheet, and the

measurements omitted if they were noticeably affected the measurements. Due to the fragmentary and incomplete condition of some of the archaeological remains, it was not always possible to record all the measurements on each individual. Measurements were only taken on elements exhibiting marked taphonomic, traumatic or pathologic changes if these conditions did not affect the required measurements.

Measurements of teeth with excessive attrition, carious lesions, restorations, fractures and/or marked calculus deposits were excluded if the maximum buccolingual (BL) or mesiodistal (MD) diameters of the tooth were affected (Kieser, 1990; Guatelli-Steinberg *et al.*, 2006). For the dentition, the following nomenclature was used: d = deciduous, i = incisor, c = canine, pm = premolar, m = molar, l = lower, u = upper, bl = buccolingual, md = mesiodistal. For example, di2u_bl refers to the buccolingual diameter of the second deciduous upper (maxillary) incisor. Individuals for whom no bilateral traits could be measured were excluded.

Table 3.2. Measurements recorded, including age categories for which each measurement was recorded (adapted from Storm, 2009)

Measurement	Abbreviation	Age Group*
Cranium	**C**	
Orbital breadth	COBB	A
Orbital height	COBH	A
Diagonal orbital breadth	CNOR	A
Chord: fmt-n (frontomalare-nasion length)	CFMTN	F-A
Chord: fmt-ns (frontomalare-nasospinale)	CFMTNS	A
Malar height	CMAH	F-A
Chord: ectomolare-intermaxillary suture	CECMIS	C-A
Chord: fmt-b (frontomalare-bregma)	CFMTB	C-A
Chord: b-zo (bregma-zygoorbitale)	CBZO	A
Length of mastoid process	CMPL	C-A
Breadth of mastoid process	CMPB	C-A
Chord: ms-ast (mastoidale-asterion)	CMSAST	C-A
Length of occipital condyle	COCL	F-A
Chord: o-p (opisthion-porion)	COPO	A
Chord: ba-po (basion-porion)	CBAPO	A
Chord: n-ms (nasion-mastoidale)	CNMS	A
Chord: b-po (bregma-porion)	CBPO	A
Chord: b-ast (bregma-asterion)	CBAST	A
Chord: l-fmt (lambda-frontomalare)	CLFMT	A
Chord: l-ast (lambda-asterion)	CLAST	A
Mandible	**M**	
Mandibular length	MAL	F-A
Maximum ramus height	MRH	F-A
Maximum ramus breadth	MXRB	F-A
Minimum ramus breadth	MIRB	F-A
Humerus	**H**	
Maximum length	MHL	F-A
Maximum diameter at midshaft	HXMS	F-A
Minimum diameter at midshaft	HIMS	F-A
Maximum diameter at deltoid tuberosity	HDT	C-A
Superoinferior diameter of the head	HSIH	C-A

Table 3.2 continued

Measurement	Abbreviation	Age Group*
Humerus	**H**	
Epicondylar breadth	HEB	A
Maximum distal mediolateral width	HSMLD	F-Ad
Maximum proximal mediolateral width	HSMLP	F-Ad
Radius	**R**	
Maximum length	RML	F-A
Maximum diameter at midshaft	RXMS	F-A
Minimum diameter at midshaft	RIMS	F-A
Maximum diameter of the head	RGH	F-A
Distal end mediolateral width	RSMLD	F-Ad
Distal end/epiphysis mediolateral width	RMLD	C-A
Femur	**F**	
Maximum length	FML	F-A
Physiological length	FPL	F-A
Maximum diameter at midshaft	FXMS	F-A
Minimum diameter at midshaft	FIMS	F-A
Epicondylar breadth	FEB	C-A
Distal end mediolateral width	FSMLD	F-Ad
Maximum supero-inferior diameter of the head	FSIH	C-A
Maximum proximal end width	FMLP	F-A
Tibia	**T**	
Maximum length	TML	F-A
Maximum diameter at nutrient foramen	TXNF	F-A
Minimum diameter at nutrient foramen	TINF	F-A
Maximum distal end mediolateral breadth	TSMLD	F-Ad
Maximum distal end/epiphysis mediolateral width	TMLD	C-A
Maximum proximal end mediolateral breadth	TSMLP	F-Ad
Maximum proximal end/epiphysis mediolateral width	TMLP	C-A
Dentition	**D**	
Maximum buccolingual diameter	BL	C-A
Maximum mesiodistal diameter	MD	C-A

*Age Groups: A=Adult, F-A=Foetal age to Adult; F-Ad=Foetal age to Adolescence; C-A=Early childhood to Adult

3.3. Statistical analyses

Before the statistical tests and procedures are described, an explanation of the use of the respective indices, namely FA8, DA1, FA4a, ME3, ME5, and FA17, as well as raw FA score, is warranted (Table 3.3). Numerous indices have been developed to test the levels of FA while controlling for other factors that may influence its level of expression. Some of these factors include size dependency, a combination of multiple traits in an individual, directional asymmetry and measurement error. The indices also differ concerning what they utilise for comparisons, such as the mean, variance, the difference between left and right measurements (right - left) or log transformations (Palmer and Strobeck, 2003). Table 3.3 gives a brief explanation of the aim of each of these indices. The formulae for each of these indices are indicated, and the aim described in more detail in the subsequent sections.

Table 3.3. Description of the aim of each index utilised for FA evaluation

Index	Description
Raw FA score	The difference between the left and right measurements of a trait (right - left)
FA8	The difference between the natural logs of the left and right measurements of a trait, in absolute values. These values were utilised for the majority of statistical analyses and are referred to as FA values
FA17	Average FA values computed from the FA8 values for multiple traits (see Table 3.3 for the various combinations/indices of FA17)
DA1	Calculates the level of DA by means of a log transformation index from the left and right measurements. Together with FA4a, it tests whether the levels of FA are confounded by DA or if the asymmetry distribution is one-sided (expressing DA)
FA4a	Calculates the average deviation of individual FA scores (raw) around the mean. Together with DA1, it tests whether the levels of FA are confounded by high levels of DA
ME3	The percentage measurement error of FA values for repeated intra- and inter-observer measures
ME5	An indication of the repeatability of the FA measures for both intra- and inter-observer measures

All statistical analyses were conducted in R (R Core Team, 2015), except for the calculation of FA8, DA1, FA17, FA4a, Technical error of measurement (TEM), percentage technical error of measurement (%TEM), ME3 and ME5, which were conducted in Microsoft Office Excel (2007). All indices related to FA or DA were taken from Palmer (1994) and Palmer and Strobeck (2003). The respective abbreviations and numbering of each index were kept for ease of reference against the multiple formulae (per type of index) listed in those publications.

3.3.1. Measurement error

Measurement Error (ME) has similar properties, and is similar in magnitude, to FA, particularly in the sense that an increase in ME will result in an increased variance. Because FA is, in essence, an estimation of variance, it is essential to test for ME before conducting tests for FA (Palmer, 1994; Møller and Swaddle, 1997; Palmer and Strobeck, 2003). Two types of analyses were utilised for the evaluation of intra- and interobserver error: a technical error of measurement (TEM) for the repeatability of measurements for a trait (left or right), and a measurement error of FA by means of an ANOVA for the repeatability of the

asymmetry scores (right – left). The latter analysis is necessary because the repeatability of FA does not depend on the repeatability of trait size measurements (right or left), but rather on the repeatability of the difference between the left and right sides (Fields *et al.*, 1995). Asymmetry scores (R-L) have small values, therefore, the between-sides difference due to FA needs to be significantly greater than the between-sides differences due to ME in order for the resultant asymmetry to be due to more than just ME (Palmer and Strobeck, 1986, 2003; Palmer, 1994). It follows that because FA values constitute only a small percentage of trait size (right or left), a high repeatability of trait size will not necessarily implicate a high repeatability of FA (right - left).

For the intraobserver error, 45 individuals were randomly selected from the entire Dutch sample for a minimum of 10 repeated bilateral measures of each measurement or trait. . Due to small sample sizes and fragmentary remains, repeated measures obtained for sub-adult measurements are few and was therefore only included in the TEM analysis.

Due to time constraints and no available experienced observer to repeat the measurements, the interobserver error could not be conducted on the Dutch population, but was conducted on the Pretoria Bone Collection (PBC), housed at the University of Pretoria, South Africa (L'Abbé *et al.*, 2005). Fifteen individuals were measured by the main investigator and a second observer for a minimum of 10 repeated bilateral measures of each measurement or trait. Unfortunately, due to a lack of subadult individuals within the PBC, no subadult measurements were obtained.

3.3.1.1. Error and repeatability of measurements

Intra- and inter-observer repeatability of the measurements were evaluated for each trait by means of a technical error of measurement (TEM):

$$\text{TEM} = \sqrt{\frac{(\sum d^2)}{2n}}$$

Where d is the difference between the repeated measurements and n is the number of individuals measured (Dahlberg, 1940; Ulijaszek and Kerr, 1999; Perini *et al.*, 2005). A TEM test does not assess the error in between-side differences, but rather verifies the degree of accuracy of repeated measures on one side of a trait only (right or left). A lower TEM indicates a higher accuracy or repeatability of the measurements (Geeta *et al.*, 2009). Subsequently, relative TEM (%TEM) was calculated from the TEM:

$$\%TEM = \left(\frac{TEM}{\bar{x}}\right) \times 100$$

where $\bar{x}$ is the trait average value per trait (the average of the sum of the mean of the repeated measurements). Guidelines for the acceptability of %TEM range from 1.5 - 7.5% (intraobserver) and 2 - 10% (interobserver) for beginner observers, and from 1 - 5% (intraobserver) to 1.5 - 7.5% (interobserver) for skilled observers (Perini *et al.*, 2005). For this study the observer error was aimed to fall within the range for skilled observers. Left and right side measurements were combined for the TEM analysis.

3.3.1.2. Measurement error of asymmetry

Two-way analyses of variance (ANOVAs), with 'sides' fixed and 'individuals' random, were conducted to assess the repeatability and error of the between-side differences. For ANOVA, 'sides' are taken as the right and left measurements for each trait and 'individuals' as the repeated measurements for each trait (Palmer, 1994; Palmer and Strobeck, 2003). The ANOVA procedure assessed whether the between-side difference due to ME is smaller than the between-side differences (R-L) due to the FA measured. Measurements for which the raw asymmetry score was not significantly higher ($p < 0.05$) relative to ME were removed from further analyses.

A two-way side by individual ANOVA presents output values such as the sides by individual mean squares (MS) for each factor, the interaction of the two factors ($MS_{interaction}$), and the measurement error or residual (MS_m; Dawson and Trapp, 2004). The aforementioned descriptors of ME relative to FA were calculated from the abovementioned ANOVA results, namely the percentage ME (ME3) and the repeatability of each measurement (ME5; Palmer and Strobeck, 2003):

$$ME3 = \frac{MS_m}{MS_{interaction}} \times 100$$

$$ME5 = \frac{MS_{interaction} - MS_m}{MS_{interaction} + (n-1)MS_m}$$

where $MS_{interaction}$ is the sides by individual MS (expected means squares), MS_m is the measurement error (as measured by the variance of repeat measurements) from a two-way ANOVA, and n is the number of measurement repeats. ME5 results range from -1 to +1 and provide an estimate of the true FA variation as a proportion of the total between-sides

variation – including ME. Therefore, the larger the repeatability, the smaller the ME relative to FA. Measurement error descriptors ME3 and ME5 are independent of units of measurement (Palmer, 1994; Palmer and Strobeck, 2003).

3.3.2. Descriptive statistics and initial inspection of the data

Raw right - left differences as well as FA8 values (see Section 3.3.4) were calculated for each trait and individual. In order to ensure that outlier values or individuals did not confound FA estimates (Palmer and Strobeck, 2003), population outliers were removed (per trait) prior to any further statistical analyses. Population outliers were removed for raw (right-left) values as well as for FA8 values (see Section 3.3.4) visually by means of histograms, boxplots (Laurikkala *et al.*, 2000) and statistically by Grubbs' test (Grubbs, 1969) statistic. Adults and subadults were analysed separately. Adults were analysed per population while for subadults the populations were pooled due to small sample sizes per population (see Table 3.1). Additionally, in order to ensure that the outliers were not removing valuable information about, for example, differences between the populations (Storm, 2009), the mean and median FA values for all the outliers were compared between the populations and against the rest of the sample (with outliers removed).

Descriptive statistics were generated for each population per sex and age category for adults, and per age category for subadults (with populations pooled) from all FA8 values and FA17 indices for each trait measured: mean, median, standard deviation, coefficient of variation, and range (minimum and maximum).

3.3.3. Normality and antisymmetry

Because FA indices are sensitive to the presence of antisymmetry in a trait, and as the presence of antisymmetry will artificially inflate the FA index used in this study (FA8; see Section 3.3.4 below) (Palmer, 1994; Palmer and Strobeck, 2003), all raw (right - left) scores for each measurement were tested for normality and antisymmetry prior to FA analyses. Kolmogorov-Smirnov (K-S) tests and student's *t*-tests (skewness) were utilised to test for normality of raw (right - left) distributions (Massey, 1951; Bai and Ng, 2005). In addition, the degree of kurtosis within the population was examined for the presence of platykurtosis, as an indication of antisymmetry (Palmer, 1994; Møller and Swaddle, 1997).

3.3.4. Fluctuating Asymmetry

Fluctuating asymmetry increases with trait size. Therefore, the measured asymmetry needs to be standardized for scale; otherwise substantial trait variation within a sample can confound tests for FA relative to ME and for departures from normality. For example, the length of the long bones of an elephant will be more variable (in absolute terms) than the long bone length of a mouse, which will result in larger asymmetry values for the larger (elephant) trait. In order to eliminate size dependence of FA estimates and to allow for comparisons between traits of different sizes, the log transformation of standard asymmetry formulae were utilised to calculate each trait's FA value (Palmer and Strobeck, 2003):

$$FA8 = |\ln(Rj/Lj)|$$

where R_j and L_j are the measurements taken on the right and left sides of each trait respectively (Palmer, 1994; Palmer and Strobeck, 2003).

In addition to the elimination of size dependence, the log transformation of measurements also allows FA values to be averaged for multiple traits in an individual, such as with its corresponding index FA17 (Section 3.3.4.2). However, the FA8 index is especially sensitive to DA, antisymmetry and measurement error, therefore other indices such as DA1, FA4a, ME3 and ME5 are needed to ensure that these factors do not confound the apparent levels of FA (Palmer and Strobeck, 2003).

3.3.4.1. Effect of DA on interpreting FA data

As both DA and FA can occur in unison, it is essential to test whether DA is a significant factor in departures from symmetry (Palmer, 1994; Palmer and Strobeck, 2003). Directional asymmetry values were calculated using the log transformation formula:

$$DA1 = \ln(R_j/L_j)$$

where R_j and L_j are the measurements taken on the right and left sides of each trait respectively. As with FA8, DA1 corrects for trait size and are reported to the nearest mm. Positive DA1 values are considered to favour the right side while negative values are considered to favour the left side (Palmer, 1994; Palmer and Strobeck, 2003).

One sample student's *t*-tests were employed (per pooled age and per adult age respectively) to test whether the mean DA differed significantly from zero (Palmer, 1994; Palmer and Strobeck, 2003). Due to small sample sizes, median subadult DA1 values per trait were assessed by non-parametric sign tests (Dixon and Mood, 1946). To further assess the

effect of DA on FA, each trait's mean (right - left) score was compared to the average deviation about the mean. The average deviation around the mean (right - left) was calculated by the equation:

$$FA4a = 0.798\sqrt{Var(R\text{-}L)}$$

A trait for which the average deviation around mean (right - left) is larger than the mean (right - left), is argued to exhibit mainly developmental instability (FA), and the effect of DA is assumed to be minimal (Palmer and Strobeck, 2003).

3.3.4.2. FA for multiple traits

Fluctuating asymmetry indices for multiple traits per individual were calculated with the formula (Palmer and Strobeck, 2003):

$$FA17 = \sum|\ln(R_j/L_j)| / T$$

where R_j and L_j are the measurements taken on the right and left sides of each trait respectively, and T is the total number of traits per index. The FA indices are listed in Table 3.4 (adapted from Storm 2009). In essence, FA17 calculates the average FA (FA8) per individual for various combinations of traits. For the purpose of this study, all FA17 indices were calculated for each individual regardless of whether one or more measurements for a trait were not available. For example, for the index 'cranium', FA17 was calculated for individuals with all 20 available measurements, as well as for individuals with less than 20 available measurements. In each individual case, the 'T' value was adjusted accordingly.

Table 3.4. Fluctuating asymmetry indices (FA17) for multiple traits

Indices	Included measurements
Individual	All skeletal and dental measurements
Skeleton	All skeletal measurements
Dentition	All dental measurements
Dentition: Permanent	All measurements of permanent teeth
Dentition: Deciduous	All measurements of deciduous teeth
Dentition: Mandible	All measurements on mandibular teeth
Dentition: Maxilla	All measurements on maxillary teeth
Cranium	All cranial measurements
Cranium: Orbit	COBB, COBH, CNOR
Cranium: Facial	CFMTN, CFMTNS, CMAH, CECMIS, CFMTB, CBZO
Cranium: Temporal	CMPL, CMPB, CMSAST
Cranium: Base	COCL, COPO, CBAPO, CNMS
Cranium: Vault	CBPO, CBAST, CLFMT, CLAST
Mandible	All mandibular measurements
Humerus	All humeral measurements
Radius	All radial measurements
Femur	All femoral measurements
Tibia	All tibial measurements
Upper limb	All humeral and radial measurements
Lower limb	All femoral and tibial measurements
Midshafts	HXMS, HIMS, RXMS, RIMS, FXMS, FIMS, TXNF, TINF
Upper limb midshafts	HXMS, HIMS, RXMS, RIMS
Lower limb midshafts	FXMS, FIMS, TXNF, TINF
Lengths	HML, RML, FML, TML
Upper limb lengths	HML, RML
Lower limb lengths	FML, TML

3.3.4.3. Trait and index comparisons

Due to the possibility of skewed and non-normal asymmetry distributions for the majority of traits (Section 3.3.3), and because the FA8 values are truncated at zero (absolute values), skewing the distributions to the right, non-parametric tests were utilised for all comparisons (Palmer and Strobeck, 1986; Dawson and Trapp, 2004). Before tests for comparison of FA levels between the populations were conducted, non-parametric Mann-Whitney U (Wilcoxon rank sum) tests were performed to test for sex differences per populations pooled, and within each population. Where there were no significant differences or where sample sizes per sex category were too small, samples for sex were combined for further analyses. For each population and for the populations pooled, a non-parametric Kruskal-Wallis analysis of variance (ANOVA) was employed to test for significant differences between the three adult (YA, MDA, and MA) age categories. A Mann-Whitney U test was used to evaluate the difference between the subadult and adult FA values. In

addition, FA values were also compared between the deciduous and permanent dentition. Where no significant difference existed, the age categories were combined for further analyses. Where significant differences were identified by the Kruskal-Wallis ANOVA, Mann-Whitney U tests were employed for a multiple comparison of the means in order to compare each sub-group to one another (Dawson and Trapp, 2004). Indeterminate sex and 'A' adult category were not included in the analyses between the sexes and between the adult age categories, respectively. Where no significant differences existed between the age or sex categories in both populations (in unison), and where no population differences existed in FA magnitude, the populations were combined for further analyses regarding age and sex.

A Mann-Whitney U test was utilised to assess whether significant differences in FA exist between the two populations for pooled ages and per adult age. Furthermore, a Mann-Whitney U test assessed the difference in FA levels between the skeleton and dentition for adult age and permanent dentition, subadult age and deciduous dentition, as well as for the age categories combined. All comparisons between the populations were tested for each individual trait (Table 3.2) and FA17 indices (Table 3.4).

The level of significance for all statistical tests was chosen as $p < 0.05$ (α at 0.95). A Holm's adjustment (Holm, 1979) for multiple comparisons of the mean was conducted for all statistical analyses between groups as well as for the Grubb's outlier test. A Holm's adjustment entails adjusting the p-values for multiple comparisons of the means by means of a Bonferroni correction. The procedure reduces the size of α for each comparison and is employed from the smallest to the greatest probability up until the first non-significant test. In essence, a Holm's adjustment increases the difference needed to be significant, decreasing the chances of a type I error (Dawson and Trapp, 2004).

3.3.5. Frequency and FA of pathological lesions

The following pathological lesions, which are regarded as general indicators of stress, were included in the analysis of pathological lesions: cribra orbitalia, porotic hyperostosis, subperiosteal bone reactions, and enamel hypoplasia. Due to similar aetiologies cribra orbitalia and porotic hyperostosis were combined for the analyses. The frequency of the observed macroscopic pathological lesions within each population was calculated and compared between the populations by means of Chi-squared (χ^2) tests. Additionally, χ^2–tests were also utilised to evaluate differences in the frequency of each pathological lesion between the two populations (against the frequency of no skeletal lesions). Chi-squared tests

determine whether significant differences in the prevalence of the pathological lesions exist between the different subgroups (Dawson and Trapp, 2004).

Significant differences in the FA values of all individuals who showed signs of at least one of the three lesions between the populations were assessed by means of a Mann-Whitney U test. In addition, a Mann-Whitney U test was utilised for the assessment of the significant difference between the FA values of individuals with at least one of the three skeletal lesions and FA values of all individuals without any skeletal lesions.

Chapter 4: Results

Detailed information on the sample sizes per population, sex and age category are given in Table 4.1, and the descriptive results per trait and index are summarised in Tables 4.2, 4.3 and A3.1 – A3.5). Differences in sample size per trait or index are due to fragmented remains or missing elements, such as when only the left or right side of an element was present.

Table 4.1. Sample sizes included in the study per population, sex and age category

Grote Kerk							Meerenberg						
Adult					Subadult		Adult					Subadult	
	M	**F**	**I**	**Total**				**M**	**F**	**I**	**Total**		
YA	0	5	1	6	**FI**	9	**YA**	1	3	0	4	**FI**	0
MDA	51	43	1	95	**EC**	7	**MDA**	13	10	2	25	**EC**	0
MA	9	29	1	39	**LC**	5	**MA**	7	20	0	27	**LC**	1
A	1	7	0	8	**AD**	2	**A**	8	23	16	47	**AD**	2
Total	61	84	3	148	**Total**	23	**Total**	29	56	18	103	**Total**	3

M=male, F=female, I=indeterminate; YA=young adult, MDA=middle adult, MA=mature adult, A=adult; FI=foetal age to infant, EC=early childhood, LC=late childhood, AD=adolescence

In the comparison of FA levels between the sexes, age categories, populations and trends within the skeleton, all traits exhibiting marked directional asymmetry (DA) or measurement error (ME; Sections 4.4 and 4.5) were excluded from the analyses, as suggested by Palmer and Strobeck (2003). This is in accordance with the practices followed in similar studies (e.g. Hoover *et al.*, 2005; DeLeon, 2007; Storm, 2009), However, the trait descriptive results included in the respective tables (Section 4.2; Tables 4.2, 4.3 and A3.1-3.5), even though all skeletal traits exhibiting the aforementioned factors have been removed from the respective indices, including the section on descriptive results. Despite the presence of higher levels of ME for the majority of dental traits, all dental traits were retained within the respective indices in order to allow for some comparison between the dentition of various groups, as well as between the dentition and the skeleton. Additionally, FA of the dental traits was analysed for general patterns and trends within the classes and types of dentition.

4.1. Outliers

Grubb's outlier test and visual examination of the data revealed 37 values as outliers, which were removed from the dataset (see Appendix 2). Of these outliers, 36 values were

from adult individuals: 20 from Grote Kerk (GRK) and 16 from Meerenberg (MeB). The one subadult outlier was from GRK. Twenty of the outlier values were not statistically significantly different after a Holm's adjustment of the Grubb's test. However, not all the variable distributions complied with the assumptions of Grubb's outlier test, namely to follow a normal distribution (refer to Section 4.4.), or to have a large sample size (small subadult sample sizes). Therefore, visual examination of the data by means of frequency histograms, boxplots and scatterplots (Laurikkala *et al.*, 2000), in conjunction with the tests for normality, skew and kurtosis (Livesey, 2007) were conducted. The visual examination revealed 20 additional outliers that may confound the mean values of the variables unjustly. The removal of the 20 additional values improved both the normality and skewness of the respective trait distributions.

Further examinations of the 37 outlier values revealed that 23 values were from female individuals (0.65% of all female values included in the current study); 11 values were from males (0.44% of all male values included in the study), and two values from indeterminate sex (0.90% of all indeterminate sex values). Outliers within the skeleton of the GRK population included only cranial and lower limb traits while outliers in the MeB population were mostly from the cranium and upper limbs. Cranial outliers within GRK were located in the cranial base (COCL, COPO) and vault (CLAST), and the long bone outliers in the distal and proximal femur (FEB, FSIH) and midshaft of the tibia (TXNF, TINF). For MeB, the cranial outliers were located in the upper facial region (COBH) as well as in the cranial base (COCL). Long bone outliers of MeB included the proximal and distal humerus (HIMS, HEB), and the midshafts of the humerus, radius and tibia (HXMS, RIMS, TINF). Outliers within the dentition of both populations showed no tendency towards a specific tooth class or jaw.

The average median fluctuating asymmetry (FA) for the outlier values is 15% ($\bar{x}$ = 20%, σ = 20%), which is substantially greater than the median value per individual (2.4%) in the rest of the adult sample (with outliers removed; see Section 4.2). Median outlier values are identical between the two populations at 15%, although GRK's mean FA (29%) is more than two times greater in magnitude than MeB's mean (12%).

4.2. Descriptive statistics

The average median FA per adult individual was 2.4% ($\bar{x}$ = 2.5%, σ = 0.9%), with the lowest and highest median FA value per individual within the populations at 0% and 7.3%

respectively. Traits with the highest median FA were CMPL (5.0%), CMPB (5.0%), CMAH (4.0%), COCL (4.0%) and m2u_md (4.0%; Table 4.2). The aforementioned skeletal traits also exhibited the greatest range or highest standard deviation in FA8 values: CMPL ($\bar{x}$ = 6.6%, σ = 5.5%), CMPB ($\bar{x}$ = 5.8%, σ = 4.9%), COCL ($\bar{x}$ = 4.9%, σ = 4.2%), CMAH ($\bar{x}$ = 4.3%, σ = 3.9%), followed by the dental trait i2u_md ($\bar{x}$ = 3.7%, σ = 3.7%). Twenty-three traits exhibited the lowest median FA of 1.0%, namely COBB, CNOR, CFMTN, CFMTNS, CBZO, CFMTB, CBAST, CLFMT, MAL, HML, HEB, RML, FPL, FEB, FSIH, FMLP, TML, TMLP, m2l_bl, i1u_md, c1u_md, pm1u_bl and m1u_bl. The smallest range was observed for the traits TML (σ = 0.6%), FPL (σ = 0.7%), FML (σ = 0.8%), CLFMT (σ = 0.8%) and RML (0.8%).

The highest median FA for the indices included the temporal bone of the cranium (4.8%), the midshafts of the upper limb (3.3%), the midshafts (3.0%), the mandible (2.8%) and the lower limb midshafts (2.8%). The lowest median FA was observed in the lengths of the lower (0.5%) and upper (1.0%) limb bones, long bone lengths (1.0%) and the cranial vault (1.5%). Indices with the widest range included the temporal bone of the cranium ($\bar{x}$ = 5.6%, σ = 3.4%), the upper limb midshafts ($\bar{x}$ = 3.6%,σ = 2.1%) and the radius ($\bar{x}$ = 2.8%, σ = 2.0%), while the smallest range was observed for the lower limb lengths ($\bar{x}$ = 0.7%, σ = 0.6%), the cranium ($\bar{x}$ = 2.3%, σ = 0.8%), and all long bone lengths ($\bar{x}$ = 0.9%, σ = 0.8%). . All indices have been adjusted according to methods described in sections 4.4 and 4.5.

Table 4.2. Descriptive results for adult fluctuating asymmetry values (permanent dentition also includes subadult individuals). Explanations of abbreviations can be found in Appendix 1

Trait	N	Median	Mean	SD	Min	Max
COBB	119	0.0100	0.0176	0.0153	0.0000	0.0700
COBH	121	0.0200	0.0211	0.0149	0.0000	0.0700
CNOR	119	0.0100	0.0162	0.0131	0.0000	0.0500
CFMTN	127	0.0100	0.0173	0.0131	0.0000	0.0600
CFMTNS	111	0.0100	0.0161	0.0147	0.0000	0.0700
CMAH	123	0.0400	0.0432	0.0385	0.0000	0.2300
CMPL	116	0.0500	0.0662	0.0551	0.0000	0.2500
CMPB	126	0.0500	0.0584	0.0490	0.0000	0.2000
CMSAST	88	0.0300	0.0395	0.0322	0.0000	0.1600
COCL	134	0.0400	0.0485	0.0422	0.0000	0.2400
COPO	143	0.0200	0.0266	0.0236	0.0000	0.1100
CBAPO	152	0.0200	0.0241	0.0212	0.0000	0.1100
CECMIS	48	0.0250	0.0298	0.0251	0.0000	0.1000
CNMS	96	0.0200	0.0175	0.0151	0.0000	0.0800
CBZO	95	0.0100	0.0115	0.0097	0.0000	0.0400
CFMTB	108	0.0100	0.0174	0.0138	0.0000	0.0600
CBPO	128	0.0200	0.0181	0.0153	0.0000	0.0600
CBAST	107	0.0100	0.0165	0.0135	0.0000	0.0700
CLFMT	101	0.0100	0.0095	0.0079	0.0000	0.0300
CLAST	100	0.0200	0.0244	0.0225	0.0000	0.1100
MAL	94	0.0100	0.0138	0.0127	0.0000	0.0500
MRH	79	0.0200	0.0335	0.0310	0.0000	0.1200
MXRB	95	0.0300	0.0339	0.0253	0.0000	0.1400
MIRB	108	0.0300	0.0384	0.0275	0.0000	0.1200
HML	90	0.0100	0.0131	0.0098	0.0000	0.0400
HXMS	131	0.0300	0.0371	0.0291	0.0000	0.1700
HIMS	132	0.0300	0.0320	0.0261	0.0000	0.1300
HDT	129	0.0300	0.0332	0.0259	0.0000	0.1200
HSIH	111	0.0200	0.0177	0.0147	0.0000	0.0700
HEB	61	0.0100	0.0177	0.0163	0.0000	0.0700
RML	82	0.0100	0.0095	0.0082	0.0000	0.0300
RXMS	113	0.0300	0.0439	0.0360	0.0000	0.1500
RIMS	114	0.0200	0.0289	0.0269	0.0000	0.1200
RGH	53	0.0200	0.0251	0.0203	0.0000	0.0900
RMLD	94	0.0200	0.0200	0.0177	0.0000	0.0800
FML	90	0.0100	0.0078	0.0075	0.0000	0.0300
FPL	93	0.0100	0.0073	0.0072	0.0000	0.0300
FXMS	152	0.0200	0.0278	0.0226	0.0000	0.1000
FIMS	151	0.0200	0.0246	0.0211	0.0000	0.1200
FEB	67	0.0100	0.0106	0.0100	0.0000	0.0400
FSIH	108	0.0100	0.0144	0.0121	0.0000	0.0500
FMLP	75	0.0100	0.0168	0.0128	0.0000	0.0500
TML	102	0.0100	0.0062	0.0063	0.0000	0.0200
TXNF	155	0.0200	0.0316	0.0281	0.0000	0.1500
TINF	157	0.0300	0.0357	0.0301	0.0000	0.1400
TMLD	80	0.0200	0.0173	0.0150	0.0000	0.0700
TMLP	54	0.0100	0.0093	0.0104	0.0000	0.0400
i1l_bl	42	0.0200	0.0243	0.0229	0.0000	0.1100
i1l_md	40	0.0150	0.0176	0.0144	0.0000	0.0700
i2l_bl	46	0.0150	0.0200	0.0156	0.0000	0.0600

Table 4.2 Continued

Trait	N	Median	Mean	SD	Min	Max
i2l_md	43	0.0200	0.0234	0.0149	0.0000	0.0600
c1l_bl	60	0.0200	0.0250	0.0230	0.0000	0.1000
c1l_md	61	0.0200	0.0228	0.0183	0.0000	0.0900
pm1l_bl	73	0.0300	0.0294	0.0198	0.0000	0.0900
pm1l_md	75	0.0200	0.0354	0.0334	0.0000	0.1500
pm2l_bl	54	0.0300	0.0319	0.0249	0.0000	0.1100
pm2l_md	57	0.0300	0.0373	0.0319	0.0000	0.1400
m1l_bl	27	0.0150	0.0195	0.0157	0.0000	0.0500
m1l_md	28	0.0200	0.0248	0.0186	0.0000	0.0800
m2l_bl	33	0.0150	0.0228	0.0202	0.0000	0.0600
m2l_md	40	0.0300	0.0285	0.0231	0.0000	0.0800
i1u_bl	50	0.0200	0.0225	0.0175	0.0000	0.0900
i1u_md	30	0.0100	0.0192	0.0198	0.0000	0.0700
i2u_bl	40	0.0250	0.0322	0.0243	0.0000	0.0800
i2u_md	26	0.0300	0.0423	0.0380	0.0000	0.1600
c1u_bl	56	0.0200	0.0233	0.0200	0.0000	0.0700
c1u_md	55	0.0100	0.0189	0.0179	0.0000	0.0800
pm1u_bl	46	0.0100	0.0146	0.0153	0.0000	0.0700
pm1u_md	47	0.0300	0.0364	0.0277	0.0000	0.1200
pm2u_bl	50	0.0200	0.0223	0.0214	0.0000	0.0800
pm2u_md	47	0.0350	0.0416	0.0336	0.0000	0.1600
m1u_bl	34	0.0100	0.0104	0.0106	0.0000	0.0500
m1u_md	36	0.0300	0.0407	0.0313	0.0000	0.1400
m2u_bl	35	0.0200	0.0282	0.0219	0.0000	0.0800
m2u_md	40	0.0400	0.0462	0.0359	0.0000	0.1400
Individual	251	0.0239	0.0251	0.0083	0.0000	0.0733
Skeleton	249	0.0233	0.0247	0.0091	0.0000	0.0733
Dentition	115	0.0263	0.0282	0.0114	0.0050	0.0700
Dentition: permanent	123	0.0263	0.0282	0.0114	0.0050	0.0700
Dentition: mandible	99	0.0250	0.0278	0.0127	0.0100	0.0733
Dentition: maxilla	93	0.0250	0.0281	0.0127	0.0029	0.0700
Cranium	172	0.0224	0.0232	0.0076	0.0100	0.0600
Cranium: orbit	119	0.0200	0.0188	0.0101	0.0000	0.0550
Cranium: facial	138	0.0200	0.0219	0.0125	0.0000	0.1150
Cranium: temporal	126	0.0483	0.0562	0.0337	0.0000	0.1900
Cranium: base	162	0.0267	0.0288	0.0172	0.0000	0.1033
Cranium: vault	136	0.0150	0.0171	0.0112	0.0000	0.0900
Mandible	123	0.0275	0.0304	0.0158	0.0000	0.0850
Humerus	148	0.0267	0.0280	0.0172	0.0000	0.1500
Radius	130	0.0225	0.0281	0.0196	0.0000	0.1150
Femur	161	0.0157	0.0188	0.0126	0.0000	0.0800
Tibia	168	0.0233	0.0269	0.0189	0.0000	0.1050
Upper limb	174	0.0250	0.0281	0.0160	0.0000	0.1500
Lower Limb	186	0.0200	0.0224	0.0121	0.0000	0.0725
Midshafts	199	0.0300	0.0324	0.0161	0.0050	0.1400
Upper limb: midshafts	156	0.0325	0.0356	0.0205	0.0000	0.1500
Lower limb: midshafts	185	0.0275	0.0298	0.0152	0.0050	0.0800
Lengths	161	0.0100	0.0094	0.0076	0.0000	0.0400
Upper limb: lengths	118	0.0100	0.0117	0.0090	0.0000	0.0400
Lower limb: lengths	121	0.0050	0.0069	0.0057	0.0000	0.0200

Subadult sample sizes were small (n=26), therefore all subadult age groups and populations were combined for all analyses. Despite this combination, ≤ five measurements were recorded for 60% of the traits. The average median FA per subadult individual (2.3%, $\bar{x}$ = 2.4%, σ = 0.8%) was slightly lower than the adult median, with the FA levels for subadults ranging from 1.0% to 4.4% (Table 4.3). One dental and one cranial trait exhibited the highest median FA, namely dm2l_md (6.5%), COCL (5.0%), followed by four dental (di2l_bl, dm1l_bl, di2u_bl, dm1u_bl) and three skeletal (CMPB, CECMIS, TSMLP) traits at 4.0%. Four traits (FML, FPL, dm2u_bl, dm2u_md) produced the lowest median of 0%. Indices with the highest median FA include the deciduous dentition (3.2%), temporal bone of the cranium, mandible, radius and midshafts of the lower limb, all at 3.0%. The indices for long bone lengths (upper, lower and combined) exhibited the lowest median FA (0.5%). The former three indices also indicated the least spread in asymmetry values: upper limb length and combined long bone length ($\bar{x}$ = 0.6%, σ = 0.4%), and lower limb length ($\bar{x}$ = 0.6%, σ = 0.6%). The widest spread was observed for the temporal bone of the cranium ($\bar{x}$ = 6.3%, σ = 5.4%) and the tibia ($\bar{x}$ = 2.5%, σ = 1.7%) indices.

Descriptive results of adults and subadults combined per population, adults per population, per age category and per sex, as well as subadults per age category, are available in Appendix 3 (Tables A3.1-A3.5). All indices have been adjusted according to methods described in sections 4.4 and 4.5.

Table 4.3. Descriptive results for subadult fluctuating asymmetry values. Explanations of abbreviations can be found in Appendix 1

Trait	N	Median	Mean	SD	Min	Max
CFMTN	5	0.0100	0.0120	0.0130	0.0000	0.0300
CMAH	4	0.0200	0.0225	0.0222	0.0000	0.0500
CMPL	5	0.0300	0.0480	0.0517	0.0200	0.1400
CMPB	5	0.0400	0.0900	0.1125	0.0300	0.2900
CMSAST	1	0.0100	0.0100	NA	0.0100	0.0100
COCL	2	0.0500	0.0500	0.0000	0.0500	0.0500
CECMIS	5	0.0400	0.0460	0.0270	0.0200	0.0900
CFMTB	0	NA	NA	NA	NA	NA
MAL	5	0.0100	0.0060	0.0055	0.0000	0.0100
MRH	5	0.0200	0.0260	0.0134	0.0100	0.0400
MXRB	5	0.0300	0.0320	0.0084	0.0200	0.0400
MIRB	11	0.0300	0.0327	0.0210	0.0000	0.0700
HML	8	0.0100	0.0063	0.0052	0.0000	0.0100
HXMS	13	0.0200	0.0231	0.0160	0.0000	0.0600
HIMS	13	0.0200	0.0238	0.0222	0.0000	0.0800
HDT	7	0.0200	0.0343	0.0310	0.0000	0.0700
HSIH	2	0.0100	0.0100	0.0000	0.0100	0.0100
HSMLD	8	0.0100	0.0188	0.0300	0.0000	0.0900
HSMLP	9	0.0300	0.0311	0.0232	0.0000	0.0700
RML	7	0.0100	0.0057	0.0053	0.0000	0.0100
RXMS	13	0.0300	0.0369	0.0287	0.0000	0.0900
RIMS	13	0.0300	0.0362	0.0257	0.0000	0.1000
RGH	0	NA	NA	NA	NA	NA
RSMLD	10	0.0200	0.0300	0.0294	0.0000	0.1000
RMLD	1	0.0200	0.0200	NA	0.0200	0.0200
FML	9	0.0000	0.0011	0.0033	0.0000	0.0100
FPL	5	0.0000	0.0040	0.0055	0.0000	0.0100
FXMS	13	0.0200	0.0254	0.0203	0.0000	0.0600
FIMS	13	0.0200	0.0269	0.0175	0.0100	0.0700
FEB	2	0.0150	0.0150	0.0071	0.0100	0.0200
FSMLD	9	0.0200	0.0267	0.0235	0.0000	0.0700
FSIH	3	0.0300	0.0233	0.0115	0.0100	0.0300
FMLP	7	0.0100	0.0129	0.0170	0.0000	0.0500
TML	10	0.0100	0.0090	0.0057	0.0000	0.0200
TXNF	14	0.0350	0.0350	0.0228	0.0000	0.0800
TINF	13	0.0100	0.0246	0.0247	0.0000	0.0700
TSMLD	10	0.0200	0.0250	0.0246	0.0000	0.0800
TMLD	1	0.0200	0.0200	NA	0.0200	0.0200
TSMLP	4	0.0400	0.0400	0.0082	0.0300	0.0500
TMLP	2	0.0150	0.0150	0.0071	0.0100	0.0200
di1l_bl	4	0.0150	0.0200	0.0141	0.0100	0.0400
di1l_md	3	0.0200	0.0267	0.0208	0.0100	0.0500
di2l_bl	5	0.0400	0.0420	0.0239	0.0100	0.0700
di2l_md	3	0.0300	0.0433	0.0321	0.0200	0.0800
dc1l_bl	4	0.0300	0.0425	0.0250	0.0300	0.0800
dc1l_md	5	0.0100	0.0100	0.0071	0.0000	0.0200
dm1l_bl	4	0.0400	0.0375	0.0330	0.0000	0.0700
dm1l_md	6	0.0300	0.0367	0.0308	0.0100	0.0900
dm2l_bl	2	0.0350	0.0350	0.0354	0.0100	0.0600
dm2l_md	2	0.0650	0.0650	0.0212	0.0500	0.0800

Table 4.3 Continued

Trait	N	Median	Mean	SD	Min	Max
di1u_bl	5	0.0200	0.0200	0.0122	0.0100	0.0400
di1u_md	4	0.0200	0.0200	0.0082	0.0100	0.0300
di2u_bl	3	0.0400	0.0433	0.0058	0.0400	0.0500
di2u_md	3	0.0100	0.0267	0.0289	0.0100	0.0600
dc1u_bl	6	0.0200	0.0217	0.0204	0.0000	0.0600
dc1u_md	6	0.0100	0.0217	0.0279	0.0000	0.0700
dm1u_bl	7	0.0400	0.0343	0.0294	0.0000	0.0800
dm1u_md	4	0.0350	0.0525	0.0532	0.0100	0.1300
dm2u_bl	5	0.0000	0.0100	0.0173	0.0000	0.0400
dm2u_md	4	0.0000	0.0150	0.0300	0.0000	0.0600
Individual	26	0.0232	0.0243	0.0076	0.0100	0.0440
Skeleton	24	0.0225	0.0242	0.0087	0.0100	0.0440
Dentition	15	0.0275	0.0247	0.0091	0.0092	0.0392
Dentition: deciduous	10	0.0317	0.0282	0.0105	0.0100	0.0400
Dentition: mandible	13	0.0300	0.0292	0.0092	0.0140	0.0417
Dentition: maxilla	15	0.0200	0.0209	0.0106	0.0063	0.0413
Cranium	7	0.0200	0.0229	0.0147	0.0050	0.0500
Cranium: facial	6	0.0150	0.0150	0.0118	0.0000	0.0300
Cranium: temporal	5	0.0300	0.0630	0.0543	0.0300	0.1550
Mandible	11	0.0300	0.0268	0.0120	0.0000	0.0400
Humerus	13	0.0225	0.0233	0.0106	0.0025	0.0450
Radius	14	0.0300	0.0308	0.0107	0.0125	0.0550
Femur	16	0.0163	0.0196	0.0110	0.0080	0.0500
Tibia	15	0.0260	0.0251	0.0168	0.0000	0.0600
Upper limb	17	0.0243	0.0264	0.0089	0.0125	0.0400
Lower Limb	19	0.0200	0.0233	0.0136	0.0000	0.0500
Midshafts	23	0.0275	0.0288	0.0122	0.0138	0.0600
Upper limb: midshafts	16	0.0225	0.0286	0.0146	0.0100	0.0625
Lower limb: midshafts	18	0.0300	0.0297	0.0147	0.0100	0.0600
Lengths	17	0.0050	0.0060	0.0044	0.0000	0.0150
Upper limb: lengths	11	0.0050	0.0059	0.0044	0.0000	0.0100
Lower limb: lengths	14	0.0050	0.0061	0.0059	0.0000	0.0200

4.3. Normality and antisymmetry

The Kolmogorov-Smirnov test indicated the distributions of 49 adult traits to deviate significantly from a normal distribution, of which 30 were skeletal (12 cranial, three mandibular and 15 long bone) and 19 permanent dentition (10 mandibular and 9 maxillary) traits (Table 4.4). Seven non-normally distributed traits exhibited a significantly skewed distribution; four skewed to the right (RIMS, c1u_md, pm1u_bl, and pm2u_bl), and three skewed to the left (ill_bl, ill_md and c1l_md). Additionally, the skewness test indicated two additional traits to be skewed to the right (CMAH, HEB), and one skewed to the left (FIMS). Test results for kurtosis indicated only eight trait distributions to be significant. Seven of these traits were leptokurtic (high peak with long tails): COCL, CNMS, CLAST, HXMS, FIMS, TXNF, and pm1l_md, while only one trait exhibited statistically significant

platykurtosis (low peak with short or 'fat' tails, an indication of antisymmetry), namely m1l_bl. While m1l_bl can be considered to exhibit antisymmetry, no statistically significant platykurtosis was indicated when the trait was analysed per population and per adult age category (Tables A4.3-4). Therefore, the trait was not excluded from the rest of the statistical analyses. Four of the aforementioned traits significant for leptokurtosis, namely CNMS, CLAST, HXMS, and pm1l_md, did also not follow a normal distribution.

Overall, when analysed per population and per adult age category, fewer trait distributions were statistically significantly non-normal, kurtotic and skew.

Table 4.4. Normality, kurtosis and skew results for adult raw (left - right) asymmetry values per trait, populations pooled (permanent dentition also contains subadult individuals). Explanations of abbreviations can be found in Appendix 1

	Kolmogorov-Smirnov			Kurtosis		Skew	
Trait	**N**	**D**	**P**	**Kurtosis**	**P**	**Skewness**	**P**
COBB	119	0.0903	0.2858	0.1162	0.7074	0.4641	0.0030
COBH	121	0.0664	0.6596	-0.4842	0.1186	0.1031	0.5057
CNOR	119	0.1693	0.0022	-0.7191	0.0208	0.1224	0.4294
CFMTN	127	0.1578	0.0036	-0.1845	0.5512	-0.1041	0.5013
CFMTNS	111	0.1089	0.1434	0.9214	0.0032	-0.0857	0.5801
CMAH	123	0.1023	0.1526	0.9299	0.0029	0.5369	<0.001**
CMPL	116	0.2712	<0.001**	0.1592	0.6072	-0.0082	0.9577
CMPB	126	0.1863	<0.001**	0.2065	0.5049	0.1020	0.5102
CMSAST	88	0.3280	<0.001**	0.5302	0.0876	0.0758	0.6244
COCL	134	0.1382	0.0120	1.3365	<0.001**	-0.0162	0.9164
COPO	143	0.1970	<0.001**	0.3684	0.2346	-0.2297	0.1386
CBAPO	152	0.1973	<0.001**	0.5070	0.1023	0.2067	0.1824
CECMIS	48	0.0952	0.7766	-0.5240	0.0914	0.3508	0.0241
CNMS	96	0.3106	<0.001**	1.8231	<0.001**	0.0569	0.7131
CBZO	95	0.3150	<0.001**	0.0209	0.9461	-0.1601	0.3014
CFMTB	108	0.3506	<0.001**	-0.3058	0.3236	-0.0597	0.6996
CBPO	128	0.2507	<0.001**	0.3290	0.2883	-0.1543	0.3192
CBAST	107	0.2763	<0.001**	0.4865	0.1169	0.3717	0.0169
CLFMT	101	0.2446	<0.001**	-0.5515	0.0757	0.3314	0.0331
CLAST	100	0.2464	<0.001**	1.1714	<0.001**	0.2880	0.0637
MAL	94	0.2065	<0.001**	0.3889	0.2097	0.2802	0.0711
MRH	79	0.2468	<0.001**	0.0695	0.8224	0.0754	0.6261
MXRB	95	0.2506	<0.001**	0.2209	0.4756	0.1407	0.3638
MIRB	108	0.1329	0.0441	-0.4314	0.1643	0.1036	0.5033
HML	90	0.6776	<0.001**	-0.1443	0.6413	0.2219	0.1525
HXMS	131	0.2839	<0.001**	1.6378	<0.001**	0.1352	0.3828
HIMS	132	0.1631	0.0018**	-0.0347	0.9108	-0.1338	0.3877
HDT	129	0.2512	<0.001**	0.0491	0.8739	0.3191	0.0400

Table 4.4 Continued

	Kolmogorov-Smirnov			Kurtosis		Skew	
Trait	**N**	**D**	**P**	**Kurtosis**	**P**	**Skewness**	**P**
HSIH	111	0.1182	0.0902	0.0686	0.8245	-0.0515	0.7391
HEB	61	0.2324	0.0027	-0.1126	0.7161	0.5457	<0.001**
RML	82	0.4942	<0.001**	-0.0299	0.9230	0.1498	0.3336
RXMS	113	0.1782	0.0015**	-0.0288	0.9260	0.0717	0.6434
RIMS	114	0.2755	<0.001**	0.6107	0.0494	0.6583	<0.001**
RGH	53	0.1730	0.0837	0.5379	0.0832	-0.1583	0.3068
RMLD	94	0.2170	<0.001**	0.4688	0.1307	-0.0934	0.5465
FML	90	0.3550	<0.001**	-0.3847	0.2146	0.0973	0.5296
FPL	93	0.3751	<0.001**	-0.2185	0.4804	0.2764	0.0750
FXMS	152	0.0540	0.7666	-0.1180	0.7030	-0.1149	0.4579
FIMS	151	0.1192	0.0274	1.2473	<0.001**	-0.5585	<0.001**
FEB	67	0.3806	<0.001**	-0.1665	0.5908	-0.0115	0.9410
FSIH	108	0.1528	0.0129	0.0011	0.9971	0.1354	0.3821
FMLP	75	0.1999	0.0050	-0.6304	0.0425	-0.1935	0.2120
TML	102	0.2825	<0.001**	0.7085	0.0228	-0.0712	0.6456
TXNF	155	0.0773	0.3129	1.0743	<0.001**	0.3484	0.0251
TINF	157	0.1576	<0.001**	0.7823	0.0120	-0.0211	0.8913
TMLD	80	0.2375	<0.001**	-0.4739	0.1267	-0.1025	0.5081
TMLP	54	0.3333	<0.001**	-0.0298	0.9234	-0.2475	0.1107
i1l_bl	42	0.3936	<0.001**	0.3543	0.2297	-0.5780	<0.001**
i1l_md	40	0.4168	<0.001**	0.3162	0.2837	-0.6603	<0.001**
i2l_bl	46	0.3834	<0.001**	0.1199	0.6840	-0.2105	0.1537
i2l_md	43	0.3897	<0.001**	-0.7800	0.0085	-0.1717	0.2443
c1l_bl	60	0.3374	<0.001**	0.8194	0.0057	-0.1727	0.2416
c1l_md	61	0.3733	<0.001**	0.6091	0.0394	-0.7901	<0.001**
pm1l_bl	73	0.3334	<0.001**	-0.5121	0.0830	-0.0885	0.5483
pm1l_md	75	0.3040	<0.001**	1.2873	<0.001**	-0.2570	0.0818
pm2l_bl	54	0.3187	<0.001**	-0.3179	0.2811	0.1475	0.3170
pm2l_md	57	0.2985	<0.001**	-0.0423	0.8859	0.3646	0.0138
m1l_bl	27	0.3483	0.0029	-1.0882	<0.001**	-0.0304	0.8365
m1l_md	28	0.2981	0.0138	-0.0605	0.8373	-0.4190	0.0047
m2l_bl	33	0.3106	0.0034	-0.1412	0.6319	-0.0433	0.7690
m2l_md	40	0.2906	0.0023	-0.6768	0.0222	0.0758	0.6072
i1u_bl	50	0.3520	<0.001**	0.1165	0.6925	-0.2790	0.0590
i1u_md	30	0.3286	0.0031	0.4059	0.1690	-0.2314	0.1170
i2u_bl	40	0.3270	<0.001**	-0.7484	0.0115	-0.1091	0.4590
i2u_md	26	0.3474	0.0038	-0.2800	0.3424	-0.4700	0.0016
c1u_bl	56	0.3156	<0.001**	-0.3992	0.1762	0.0990	0.5015
c1u_md	55	0.3831	<0.001**	0.9350	0.0017	0.8064	<0.001**
pm1u_bl	46	0.4147	<0.001**	0.9953	<0.001	1.0959	<0.001**
pm1u_md	47	0.2946	<0.001**	0.1213	0.6806	-0.3322	0.0248
pm2u_bl	50	0.3097	<0.001**	0.2947	0.3176	0.5945	<0.001**
pm2u_md	47	0.2983	<0.001**	0.8260	0.0054	0.3245	0.0283

Table 4.4 Continued

	Kolmogorov-Smirnov			Kurtosis		Skew	
Trait	**N**	**D**	**P**	**Kurtosis**	**P**	**Skewness**	**P**
m1u_bl	34	0.3502	<0.001**	0.1971	0.5036	0.2844	0.0544
m1u_md	36	0.2798	0.0071	0.6648	0.0247	0.1460	0.3222
m2u_bl	35	0.3104	0.0024	-0.4834	0.1017	-0.0005	0.9972
m2u_md	40	0.2733	0.0051	-0.3010	0.3074	-0.0128	0.9309

**significant after a Holm's adjustment, p-value < 0.05; D = test statistic for the Kolmogorov-Smirnov test

No subadult trait distributions were statistically significant ($p < 0.05$) for the Kolmogorov-Smirnov, skewness or kurtosis test after a Holm's adjustment (Table 4.5). However, before the Holm's adjustment, five subadult traits indicated a significant non-normal distribution (COCL, HIMS, RIMS, FIMS and TSMLP), 18 traits indicated a platykurtic distribution (3 cranial, 1 mandibular, 5 long bone, and 9 dental), while 6 trait distributions were skewed (3 to the left and 3 to the right). However, it must be noted that the sample sizes for most traits were small and, therefore, conclusions from the test results should be made with caution. Small sample sizes increase the chances of making a type II error, rejecting the null hypothesis when it is, in fact, true (Nunnally, 1960; Guadagnoli and Velicer, 1988).

Normality and antisymmetry analyses results for the subadults, as well as for pooled ages per population, adults per population, and adults per age category are included in Appendix 4 (Tables A4.1-4).

Table 4.5. Normality, kurtosis and skew results for subadult raw (left - right) asymmetry values per trait, populations pooled. Explanations of abbreviations can be found in Appendix 1

	Kolmogorov-Smirnov			Kurtosis		Skew	
Trait	**N**	**D**	**P**	**Kurtosis**	**P**	**Skewness**	**P**
CFMTN	5	0.2207	0.9227	-1.6395	0.1003	0.3978	0.4155
CMAH	4	0.4483	0.2973	-2.1107	0.0375	0.2163	0.6563
CMPL	5	0.3910	0.3337	-1.1676	0.2356	-0.8167	0.1015
CMPB	5	0.4808	0.1397	-1.1987	0.2237	0.7270	0.1427
CMSAST	1	NA	NA	NA	NA	NA	NA
COCL	2	0.8790	0.0293	-2.7500	0.0084	0.0000	1.0000
CECMIS	5	0.4340	0.2272	-2.0259	0.0452	-0.0498	0.9183
CFMTB	0	NA	NA	NA	NA	NA	NA
MAL	5	0.2761	0.7557	-1.9717	0.0508	0.0610	0.9000
MRH	5	0.2700	0.7776	-2.1569	0.0339	-0.0913	0.8508
MXRB	5	0.4879	0.1289	-1.1992	0.2235	0.8173	0.1013
MIRB	11	0.2512	0.4913	-0.5893	0.5451	-0.5593	0.2553
HML	8	0.3085	0.4315	-1.3264	0.1796	-0.6979	0.1587
HXMS	13	0.3669	0.0604	0.8289	0.3965	-1.2236	0.0174
HIMS	13	0.3936	0.0356	0.6033	0.5358	-1.0557	0.0375

Table 4.5 Continued

	Kolmogorov-Smirnov			Kurtosis		Skew	
Trait	**N**	**D**	**P**	**Kurtosis**	**P**	**Skewness**	**P**
HDT	7	0.3859	0.1896	-1.7906	0.0742	-0.1860	0.7019
HSIH	2	0.3669	0.8906	-2.7500	0.0084	0.0000	1.0000
HSMLD	8	0.3707	0.1709	-0.4599	0.6364	0.9349	0.0629
HSMLP	9	0.1314	0.9916	-1.5512	0.1190	0.1639	0.7357
RML	7	0.3571	0.3338	-1.4762	0.1370	0.1669	0.7311
RXMS	13	0.3399	0.0992	-0.8775	0.3698	0.1913	0.6939
RIMS	13	0.3707	0.0413	-1.0495	0.2851	-0.5186	0.2907
RGH	0	NA	NA	NA	NA	NA	NA
RSMLD	10	0.2974	0.2795	-0.7908	0.4182	0.1191	0.8063
RMLD	1	NA	NA	NA	NA	NA	NA
FML	9	0.3085	0.3584	1.1808	0.2305	1.4970	0.0046
FPL	5	0.3000	0.7591	-1.3650	0.1678	0.3488	0.4746
FXMS	13	0.3300	0.1179	0.4113	0.6722	0.9037	0.0716
FIMS	13	0.3821	0.0449	-0.6304	0.5177	0.6766	0.1713
FEB	2	0.3708	0.8833	-2.7500	0.0084	0.0000	1.0000
FSMLD	9	0.3255	0.2959	1.4426	0.1457	1.6348	0.0022
FSIH	3	0.2576	0.9639	-2.3333	0.0227	-0.2517	0.6050
FMLP	7	0.2936	0.4926	0.3018	0.7560	-1.3749	0.0084
TML	10	0.3413	0.1526	0.0588	0.9517	-0.2973	0.5416
TXNF	14	0.2327	0.3758	-1.3311	0.1781	-0.0713	0.8831
TINF	13	0.2611	0.2854	-0.8865	0.3650	0.1971	0.6851
TSMLD	10	0.2372	0.5500	1.5648	0.1159	1.5542	0.0034
TMLD	1	NA	NA	NA	NA	NA	NA
TSMLP	4	0.7157	0.0133	-2.0276	0.0450	0.3452	0.4790
TMLP	2	0.7611	0.1141	-2.7500	0.0084	0.0000	1.0000
di1l_bl	4	0.4801	0.2239	-1.8913	0.0602	0.1334	0.7835
di1l_md	3	0.5160	0.2971	-2.3333	0.0227	-0.3381	0.4880
di2l_bl	5	0.4052	0.2954	-1.4340	0.1481	-0.5120	0.2967
di2l_md	3	0.4404	0.4841	-2.3333	0.0227	0.0840	0.8626
dc1l_bl	4	0.4364	0.3288	-2.1195	0.0368	-0.2835	0.5603
dc1l_md	5	0.4801	0.1409	-1.7863	0.0748	0.4509	0.3569
dm1l_bl	4	0.5080	0.1748	-2.2164	0.0296	0.0162	0.9733
dm1l_md	6	0.4602	0.1104	-1.7865	0.0748	-0.1624	0.7382
dm2l_bl	2	0.5557	0.3949	-2.7500	0.0084	0.0000	1.0000
dm2l_md	2	0.6950	0.1861	-2.7500	0.0084	0.0000	1.0000
di1u_bl	5	0.4602	0.1747	-1.9305	0.0554	-0.1515	0.7550
di1u_md	4	0.4641	0.2585	-2.4274	0.0182	-0.0053	0.9914
di2u_bl	3	0.5753	0.1819	-2.3333	0.0227	0.2078	0.6690
di2u_md	3	0.5239	0.3825	-2.3333	0.0227	0.3849	0.4305
dc1u_bl	6	0.4602	0.1104	-1.1393	0.2468	0.6829	0.1675
dc1u_md	6	0.4090	0.2679	-0.8377	0.3916	-0.7680	0.1224
dm1u_bl	7	0.4681	0.0632	-1.9523	0.0529	-0.0277	0.9544
dm1u_md	4	0.5319	0.1402	-1.7331	0.0833	-0.6762	0.1716
dm2u_bl	5	0.4522	0.2581	-1.2012	0.2228	0.7836	0.1154
dm2u_md	4	0.4880	0.2084	-1.6933	0.0902	0.7409	0.1356

D = test statistic for the Kolmogorov-Smirnov test

4.4. Measurement error

4.4.1. Intra-observer error

The relative technical error of measurement (%TEM) ranged from 0.06 to 7.94% for intraobserver repeated measures (Table 4.6). Most traits fell within the acceptable range for skilled intraobserver error (1-5%), indicating adequate repeatability of the measurements (Perini *et al.*, 2005). One skeletal and five deciduous dental traits fell outside the acceptable %TEM for skilled intraobserver repeatability, namely the breadth of the mastoid process (CMPB; 5.85%), dm1l_bl (6.91%), dm1l_md (5.86%), dm2l_bl (7.94%), dm2l_md (6.94%), and dm2u_bl (5.09%).

Table 4.6. Intraobserver technical error of measurement (TEM) values. Explanations of abbreviations can be found in Appendix 1

Trait	N	TEM	Mean	%TEM	Trait	N	TEM	Mean	%TEM
COBB	34	0.39	39.51	1.00	TSMLP	4	0.08	25.48	0.33
COBH	38	0.36	33.95	1.07	TMLP	20	0.45	71.73	0.62
CNOR	38	0.48	54.18	0.88	di1l_bl	8	0.03	3.72	0.82
CFMTN	40	0.32	54.87	0.59	di1l_md	6	0.02	3.94	0.55
CFMTNS	36	0.41	75.99	0.54	di2l_bl	10	0.10	4.19	2.43
CMAH	40	0.23	22.16	1.05	di2l_md	6	0.10	4.60	2.26
CMPL	30	0.88	29.12	3.01	dc1l_bl	8	0.21	5.26	3.92
CMPB	34	1.59	27.18	5.85	dc1l_md	10	0.21	5.91	3.57
CMSAST	28	0.43	48.44	0.88	dm1l_bl	8	0.50	7.23	6.91
COCL	38	0.40	25.17	1.59	dm1l_md	10	0.44	7.50	5.86
COPO	36	0.51	69.10	0.73	dm2l_bl	4	0.73	9.16	7.94
CBAPO	38	0.53	58.51	0.91	dm2l_md	4	0.64	9.28	6.94
CECMIS	28	0.40	29.04	1.37	di1u_bl	10	0.08	4.76	1.63
CNMS	28	0.69	123.95	0.56	di1u_md	8	0.08	5.89	1.42
CBZO	28	0.64	130.83	0.49	di2u_bl	6	0.11	4.74	2.22
CFMTB	36	0.52	114.26	0.46	di2u_md	6	0.10	5.12	1.91
CBPO	35	0.77	123.83	0.63	dc1u_bl	12	0.13	5.69	2.34
CBAST	30	0.47	133.72	0.35	dc1u_md	10	0.16	6.21	2.53
CLFMT	36	0.54	169.53	0.32	dm1u_bl	14	0.33	7.97	4.08
CLAST	32	0.93	89.41	1.04	dm1u_md	8	0.37	7.46	4.96
MAL	34	0.34	115.34	0.29	dm2u_bl	8	0.47	9.30	5.09
MRH	30	0.99	56.40	1.76	dm2u_md	6	0.40	9.18	4.36
MXRB	36	0.44	40.64	1.08	i1l_bl	30	0.11	5.61	1.90
MIRB	42	0.12	27.99	0.43	i1l_md	26	0.15	5.31	2.83
HML	30	0.38	257.79	0.15	i2l_bl	24	0.07	6.24	1.13
HXMS	40	0.28	19.11	1.45	i2l_md	18	0.08	5.83	1.33
HIMS	40	0.25	15.49	1.58	c1l_bl	30	0.12	7.70	1.51
HDT	32	0.47	22.16	2.12	c1l_md	25	0.10	6.46	1.47
HSIH	30	0.27	44.26	0.62	pm1l_bl	30	0.12	7.68	1.50
HEB	22	0.08	60.88	0.14	pm1l_md	34	0.11	6.61	1.73
HSMLD	8	0.10	23.19	0.44	pm2l_bl	30	0.16	8.09	1.96
HSMLP	12	0.32	21.10	1.53	pm2l_md	32	0.17	6.97	2.37
RML	28	0.26	206.56	0.13	m1l_bl	20	0.33	10.32	3.23
RXMS	38	0.14	13.49	1.03	m1l_md	22	0.30	10.75	2.79
RIMS	38	0.10	9.39	1.08	m2l_bl	20	0.20	10.09	1.97

Table 4.6 Continued

Trait	N	TEM	Mean	%TEM	Trait	N	TEM	Mean	%TEM
RGH	20	0.10	23.09	0.44	m2l_md	26	0.21	10.55	2.00
RSMLD	14	0.35	14.37	2.46	i1u_bl	32	0.10	6.93	1.38
RMLD	30	0.20	33.21	0.60	i1u_md	26	0.07	8.19	0.88
FML	30	0.23	382.38	0.06	i2u_bl	26	0.11	6.21	1.81
FPL	26	0.26	416.56	0.06	i2u_md	18	0.07	6.59	1.11
FXMS	40	0.32	25.88	1.22	c1u_bl	26	0.18	8.20	2.16
FIMS	40	0.22	21.20	1.02	c1u_md	26	0.19	7.58	2.46
FSMLD	12	0.11	32.23	0.33	pm1u_md	30	0.16	6.67	2.39
FSIH	28	0.17	43.34	0.38	pm2u_bl	29	0.12	9.00	1.31
FMLP	28	0.61	85.03	0.72	pm2u_md	30	0.18	6.50	2.78
TML	33	0.42	309.08	0.31	m1u_bl	20	0.35	10.64	3.32
TXNF	40	0.26	27.56	0.93	m1u_md	22	0.44	10.54	4.16
TINF	38	0.16	19.74	0.80	m2u_bl	22	0.20	10.77	1.90
TSMLD	12	0.91	21.25	4.27	m2u_md	26	0.32	9.94	3.24
TMLD	30	0.68	46.60	1.45					

Although the overall intraobserver percentage ME (ME3) and repeatability (ME5) of the between side differences were broad, ranging from 0.29 to 282.67%, and -0.47 to 0.99 respectively, only five skeletal traits, CMPB, CECMIS, HDT, TMLD, and TMLP, exhibited significantly higher ME relative to the between side differences due to FA (Table 4.7). Of these five traits, only CMPB exhibited a relative TEM value outside the acceptable range for skilled observers. Eighteen out of the 28 permanent dental measurements displayed significantly higher ME relative to the between side difference due to FA. Additionally, the percentage of ME (ME3) was high (≥ 22%) and the repeatability (ME5) moderate to low (-0.48 to 0.64) for these 18 traits. Relative TEM values ranged from 1.3 – 4.16%. Due to the smaller overall size of teeth, smaller magnitudes of ME are needed for the ME to significantly affect the asymmetry values. Therefore, a high percentage of ME in the dentition is not unanticipated (Palmer, 1994; Palmer and Strobeck, 2003).

Table 4.7. Intraobserver measurement error results for asymmetry values from a two-way side by individual ANOVA and subsequent indices. Explanations of abbreviations can be found in Appendix 1

	Sides x Individuals				Error			
Trait	**df**	**MS**	**F**	**P**	**df**	**MS**	**ME3 (%)**	**ME5**
COBB	15	0.6698	4.1292	<0.001**	32	0.1622	24.2179	0.6101
COBH	17	0.7853	5.8517	<0.001**	36	0.1342	17.0891	0.7081
CNOR	17	0.9111	3.8415	<0.001**	36	0.2372	26.0312	0.5869
CFMTN	17	0.3559	3.5794	<0.001**	36	0.0994	27.9376	0.5633
CFMTNS	16	2.3692	14.7390	<0.001**	34	0.1607	6.7847	0.8729
CMAH	17	1.3564	27.2334	<0.001**	36	0.0498	3.6720	0.9292
CMPL	12	5.1935	5.9406	<0.001**	26	0.8742	16.8333	0.7118
CMPB	14	4.5728	2.0281	0.0511	30	2.2547	49.3069	0.3395
CMSAST	11	4.3867	23.3692	<0.001**	24	0.1877	4.2791	0.9179
COCL	16	5.2353	33.6303	<0.001**	34	0.1557	2.9735	0.9422
COPO	16	6.0729	22.9016	<0.001**	34	0.2652	4.3665	0.9163
CBAPO	17	3.3661	11.2605	<0.001**	36	0.2989	8.8806	0.8369
CECMIS	11	0.5585	3.3439	0.0064*	24	0.1670	29.9050	0.5396
CNMS	12	4.2813	10.3547	<0.001**	26	0.4135	9.6575	0.8239
CBZO	12	2.4599	5.5616	<0.001**	26	0.4423	17.9805	0.6952
CFMTB	16	4.1572	14.8783	<0.001**	34	0.2794	6.7212	0.8740
CBPO	15	4.5156	7.4508	<0.001**	33	0.6061	13.4214	0.7633
CBAST	13	2.9866	17.1538	<0.001**	28	0.1741	5.8296	0.8898
CLFMT	16	2.2541	7.9627	<0.001**	34	0.2831	12.5586	0.7769
CLAST	14	8.4060	9.5557	<0.001**	30	0.8797	10.4650	0.8105
MAL	12	6.9787	64.1899	<0.001**	26	0.1087	1.5579	0.9693
MRH	10	12.0032	10.1401	<0.001**	22	1.1837	9.8618	0.8205
MXRB	14	2.6163	19.2048	<0.001**	30	0.1362	5.2070	0.9010
MIRB	14	1.7414	94.1742	<0.001**	30	0.0185	1.0619	0.9790
HML	9	20.3951	130.5289	<0.001**	20	0.1563	0.7661	0.9848
HXMS	14	0.3960	4.1286	<0.001**	30	0.0959	24.2215	0.6100
HIMS	14	0.2832	3.6150	0.0015**	30	0.0784	27.6622	0.5666
HDT	13	0.2565	1.0308	0.4516	28	0.2489	97.0092	0.0152
HSIH	13	0.6718	11.0228	<0.001**	28	0.0609	9.0721	0.8336
HEB	9	0.2098	31.4005	<0.001**	20	0.0067	3.1847	0.9383
RML	10	9.0352	122.3231	<0.001**	22	0.0739	0.8175	0.9838
RXMS	13	0.5906	23.2300	<0.001**	28	0.0254	4.3048	0.9175
RIMS	13	0.1103	8.8411	<0.001**	28	0.0125	11.3108	0.7968
RGH	9	0.3063	29.8504	<0.001**	20	0.0103	3.3500	0.9352
RMLD	13	0.4687	11.4481	<0.001**	28	0.0409	8.7351	0.8393
FML	10	14.6852	234.9636	<0.001**	22	0.0625	0.4256	0.9915
FPL	10	19.2659	339.0800	<0.001**	22	0.0568	0.2949	0.9941
FXMS	14	0.5719	4.4039	<0.001**	30	0.1299	22.7073	0.6299
FIMS	14	1.0206	17.1644	<0.001**	30	0.0595	5.8260	0.8899
FEB	9	0.6868	4.7778	0.0017**	20	0.1438	20.9302	0.6538
FSIH	11	2.2615	89.2465	<0.001**	24	0.0253	1.1205	0.9778
FMLP	10	2.2957	4.9359	<0.001**	22	0.4651	20.2595	0.6631
TML	11	5.2026	5.4391	<0.001**	23	0.9565	18.3855	0.6894
TXNF	13	2.7026	31.6910	<0.001**	28	0.0853	3.1555	0.9388
TINF	13	1.0949	40.2358	<0.001**	28	0.0272	2.4853	0.9515
TMLD	13	1.2181	2.6727	0.0143*	28	0.4558	37.4154	0.4554
TMLP	9	0.5484	2.9247	0.0252*	18	0.1875	34.1921	0.4904
i1l_bl	10	0.0203	1.7642	0.1283	22	0.0115	56.6815	0.2765
i1l_md	8	0.0303	1.4568	0.2405	18	0.0208	68.6451	0.1859

Table 4.7 Continued

	Sides x Individuals				Error			
Trait	**df**	**MS_{int}**	**F**	**P**	**df**	**MS_m**	**ME3 (%)**	**ME5**
i2l_bl	11	0.0216	4.3549	0.0013**	24	0.0050	22.9627	0.6265
i2l_md	8	0.0139	2.3068	0.0672	18	0.0060	43.3506	0.3952
c1l_bl	14	0.0161	1.1981	0.3263	30	0.0135	83.4621	0.0901
c1l_md	11	0.0140	1.5506	0.1754	25	0.0090	64.4904	0.2159
pm1l_bl	13	0.0646	5.2815	<0.001**	28	0.0122	18.9339	0.6816
pm1l_md	15	0.0485	3.7137	<0.001**	32	0.0131	26.9270	0.5757
pm2l_bl	14	0.0434	1.6634	0.1224	28	0.0261	60.1178	0.2491
pm2l_md	14	0.1068	3.6630	0.0014**	30	0.0292	27.3000	0.5711
m1l_bl	5	0.0158	0.6602	0.6604	12	0.0239	151.4679	-0.2047
m1l_md	6	0.0885	4.5447	0.0092*	14	0.0195	22.0038	0.6393
m2l_bl	10	0.0422	1.0666	0.4295	20	0.0396	93.7553	0.0322
m2l_md	12	0.1209	2.7192	0.0159*	26	0.0445	36.7756	0.4622
i1u_bl	12	0.0324	3.8490	0.0019**	26	0.0084	25.9810	0.5875
i1u_md	9	0.0571	10.4311	<0.001**	20	0.0055	9.5868	0.8250
i2u_bl	11	0.0910	6.7677	<0.001**	24	0.0134	14.7760	0.7425
i2u_md	7	0.0685	15.3005	<0.001**	16	0.0045	6.5357	0.8773
c1u_bl	12	0.0331	1.0542	0.4337	26	0.0314	94.8607	0.0264
c1u_md	12	0.0498	1.4343	0.2130	26	0.0347	69.7215	0.1784
pm1u_bl	13	0.0162	0.7478	0.7029	26	0.0217	133.7190	-0.1443
pm1u_md	13	0.0368	1.9611	0.0661	28	0.0188	50.9926	0.3246
pm2u_bl	13	0.0646	4.5415	<0.001**	27	0.0142	22.0191	0.6391
pm2u_md	13	0.0531	1.5165	0.1726	28	0.0350	65.9409	0.2052
m1u_bl	5	0.0096	0.7387	0.6089	12	0.0130	135.3797	-0.1503
m1u_md	6	0.0681	0.3538	0.8960	14	0.1924	282.6711	-0.4774
m2u_bl	9	0.2781	8.0298	<0.001**	20	0.0346	12.4536	0.7785
m2u_md	11	0.2765	2.4876	0.0300*	24	0.1112	40.2001	0.4265

*p < 0.05; **significant after a Holm's adjustment, p < 0.05; df = degrees of freedom; MS_{int} = $MS_{interaction,}$ sides by individual expected mean squares; F = test statistic of two-way ANOVA; MS_m = measurement error or residual;

4.4.2. Inter-observer error

Although on average higher than intraobserver error, most interobserver %TEM fell within the acceptable range for skilled observers (1.5 – 7.5%) (Perini *et al.*, 2005), ranging from 0.15 to 10.06% (Table A5.1). Only CMPL (9.15%) and CMPB (10.06%) fell outside the acceptable range.

Similar to the TEM results, interobserver ME values were markedly higher compared to intraobserver ME (Table A5.2). Most interobserver percentage ME (ME3) of the FA values were high, ranging from 2.59 to 1739.12%, and the overall repeatability (ME5) ranged from very low to very high (-0.02 to -0.89 and 0.01 to 0.95). The extremely high percentage of measurement error (in excess of a thousand percent), occurs when the MS_m (ME or residual) value is more than 10 times greater than the $MS_{interaction}$ (interaction of the 'sides' and 'individual' factors) value within the two-way ANOVA . Low percentages of ME3 are obtained when the MS_m is smaller than the $MS_{interaction}$, indicating less ME.

The traits with the higher ME included CFMTN, CMAH, CLFMT, TMLD, m2l_md, and i1u_bl. Only 10 traits indicated significantly less variation due to ME as compared to the between side difference due to FA: CMSAST, MIRB, RML, RXMS, RIMS, RGH, FML, FPL, FSIH, and i2u_md. Although this does not indicate a good interobserver repeatability of FA values, the repeatability of the majority of individual measurements (right or left) fell within the accepted range for skilled observers. It must also be noted that the majority of measurements utilised in the current study were not the standard osteometric measurements utilised for anthropometric analyses or studies (Buikstra and Ubelaker, 1994), therefore, the second observer was not familiar with all the measurements.

Based on the presence of high intra- and interobserver measurement error for both FA values and left/right sides, the following skeletal traits were removed from further analyses: CMPL, CMPB, CECMIS, HDT, TMLP, and TMLD. Additionally, all individual dental traits were removed from further analyses but were included in the dental indices to enable their comparison to the average skeletal FA of the samples.

4.5. Effect of DA on FA

Only ten mean asymmetry values (DA1) differed significantly from zero. These included two cranial and eight long bone traits: CNOR, CFMTN, HML, HXMS, HDT, HEB, RML, RXMS, RMLD and FEB (Table 4.8). The majority of the long bone traits were from the upper limb and included the maximum lengths, maximum diameters and distal diaphyseal breadth. The one lower limb trait was the epicondylar breadth of the femur. Both cranial traits were from the upper facial area, although subsequent analyses within adult individuals only indicated the mean asymmetry value of CFMTN not to differ significantly from zero (see Table A6.1). While the remaining nine traits could be argued to exhibit DA, only one trait, (maximum humeral length; HML), had a mean asymmetry value greater than the variation about the mean, and could be considered to exhibit significant directional asymmetry (Palmer and Strobeck, 2003). Therefore, HML was removed from further analyses per trait. Because only one trait exhibited significant DA, HML was retained within the indices for length (lengths and upper limb lengths), in order for a more realistic indication of the level of asymmetry within the indices.

Seven juvenile traits (one skeletal, six dental) also exhibited mean asymmetry values greater than the variation around the mean: TSMLP, dm1l_bl, dm2l_bl, dm2l_md, di2u_bl, di2u_md and dm1u_bl. These traits did not differ significantly from zero, and the sample

sizes were small ($n \leq 7$). They were therefore not excluded from the analysis of fluctuating asymmetry.

Table 4.8. Results for the evaluation of the effect of directional asymmetry on the interpretation of fluctuating asymmetry by means of one sample student t-tests and a comparison of mean (right - left) and FA4a (results for 'subadult only' traits are from non-parametric sign tests). Explanations of abbreviations can be found in Appendix 1

Trait	N	t-value	p-value	Mean (R-L)	FA4a
COBB	113	1.4202	0.1582	0.1463	0.7173
COBH	121	0.8803	0.3804	0.0740	0.6944
CNOR	119	4.6157	<0.001**	0.4183	0.8143
CFMTN	132	3.3632	0.0010**	0.3039	0.8795
CFMTNS	112	0.7815	0.4362	0.1001	1.3490
CMAH	127	2.0141	0.0461	0.2229	0.9550
CMPL	121	-2.1193	0.0361	-0.4027	1.8685
CMPB	131	2.0672	0.0407	0.3024	1.5213
CMSAST	89	2.1577	0.0337	0.5583	1.9063
COCL	136	-0.0534	0.9575	-0.0207	1.2528
COPO	143	-0.0235	0.9813	0.0233	1.9357
CBAPO	152	1.9404	0.0542	0.3052	1.4447
CECMIS	53	0.5426	0.5897	0.0775	0.8982
CNMS	96	1.3338	0.1855	0.3750	2.1615
CBZO	95	2.7640	0.0069	0.5368	1.4495
CFMTB	108	2.2988	0.0235	0.5093	1.9309
CBPO	128	-0.7461	0.4570	-0.1523	2.2629
CBAST	107	-0.2256	0.8220	-0.0701	2.2266
CLFMT	101	1.9610	0.0527	0.4505	1.4795
CLAST	100	-0.6016	0.5488	-0.1374	2.3880
MAL	99	-0.4913	0.6243	-0.0887	1.7094
MRH	84	-0.9269	0.3567	-0.3362	2.0701
MXRB	101	-2.1420	0.0346	-0.3473	1.3314
MIRB	119	-0.0984	0.9218	-0.0183	1.0066
HML	98	9.0752	<0.001**	3.2512•	2.8998
HXMS	144	7.1638	<0.001**	0.5017	0.6842
HIMS	145	2.2674	0.0249	0.1444	0.5198
HDT	136	5.5701	<0.001**	0.4479	0.6867
HSIH	113	1.7890	0.0763	0.1901	0.7941
HEB	62	4.0329	<0.001**	0.7242	1.1080
HSMLD	8	3.0000	1.0000	0.2425	0.4825
HSMLP	9	4.0000	1.0000	0.0056	0.6735
RML	90	5.2351	<0.001**	1.4462	2.0219
RXMS	127	4.0736	<0.001**	0.2783	0.6670
RIMS	128	1.7909	0.0757	0.0715	0.3400
RGH	53	1.2441	0.2191	0.1213	0.5811

Table 4.8 Continued

Trait	N	t-value	p-value	Mean (R-L)	FA4a
RSMLD	10	5.0000	1.0000	0.1070	0.3623
RMLD	95	3.8927	<0.001**	0.3026	0.6415
FML	99	-1.0743	0.2853	-0.1674	3.3851
FPL	98	-1.4070	0.1626	-0.4692	3.2696
FXMS	165	-0.5471	0.5850	-0.0644	0.8153
FIMS	165	0.5982	0.5506	0.0218	0.6223
FEB	69	4.9949	<0.001**	0.5804	0.7839
FSMLD	9	2.0000	0.2891	0.1167	1.3021
FSIH	110	1.8233	0.0710	0.1521	0.6654
FMLP	82	0.3665	0.7150	0.0256	1.5170
TML	113	1.1066	0.2708	0.3005	2.3246
TXNF	169	0.8564	0.3930	0.0890	1.0627
TINF	170	2.6601	0.0086	0.2078	0.7833
TSMLD	10	4.0000	1.0000	0.1740	0.7390
TMLD	81	2.1971	0.0309	0.2573	0.8345
TSMLP	4	4.0000	0.1250	0.8225•	0.2271
TMLP	57	2.5187	0.1466	0.4046	0.8363
i1l_bl	37	-2.5996	0.0129	-0.0727	0.1416
i1l_md	34	-1.1591	0.2533	-0.0038	0.0985
i2l_bl	44	0.5830	0.5628	0.0191	0.1235
i2l_md	41	-0.7285	0.4704	-0.0149	0.1268
c1l_bl	58	-0.1526	0.8792	-0.0100	0.2078
c1l_md	58	1.0198	0.3119	0.0274	0.1450
pm1l_bl	69	-0.5404	0.5906	-0.0175	0.2091
pm1l_md	71	-0.1920	0.8483	-0.0193	0.2463
pm2l_bl	53	0.8037	0.4252	0.0458	0.2477
pm2l_md	56	-0.1336	0.8942	0.0000	0.2625
m1l_bl	20	-1.0000	0.3265	-0.0115	0.2079
m1l_md	21	0.1301	0.8974	-0.0362	0.2725
m2l_bl	32	-0.9929	0.3282	-0.0466	0.2481
m2l_md	39	1.6326	0.1106	0.1082	0.2964
i1u_bl	44	-0.8805	0.3829	-0.0350	0.1603
i1u_md	24	-0.1326	0.8954	-0.0217	0.1771
i2u_bl	36	0.0000	1.0000	-0.0056	0.2030
i2u_md	22	-1.4227	0.1672	-0.1018	0.2639
c1u_bl	55	0.7025	0.4853	0.0151	0.1948
c1u_md	54	1.5410	0.1292	0.0317	0.1473
pm1u_bl	41	1.2497	0.2179	0.0383	0.1397
pm1u_md	42	0.0000	1.0000	0.0090	0.2373
pm2u_bl	47	0.2272	0.8212	0.0211	0.2163
pm2u_md	44	-0.1120	0.9113	-0.0007	0.2624
m1u_bl	27	0.1703	0.8658	-0.0426	0.1245
m1u_md	29	2.6114	0.0132	0.1890	0.4127
m2u_bl	34	-2.2960	0.0280	-0.1326	0.2884

Table 4.8 Continued

Trait	N	t-value	p-value	Mean (R-L)	FA4a
m2u_md	39	2.5269	0.0157	0.2123	0.4353
di1l_bl	4	1.0000	0.6250	-0.0550	0.0656
di1l_md	3	0.0000	0.2500	-0.1067	0.0724
di2l_bl	5	4.0000	0.3750	0.0900	0.1661
di2l_md	3	2.0000	1.0000	0.1133	0.2200
dc1l_bl	4	2.0000	1.0000	-0.0525	0.2037
dc1l_md	5	2.0000	1.0000	0.0140	0.0566
dm1l_bl	4	3.0000	0.2500	0.2575•	0.1734
dm1l_md	6	2.0000	0.6875	-0.2150	0.2263
dm2l_bl	2	2.0000	0.5000	0.3400•	0.2257
dm2l_md	2	2.0000	0.5000	0.5700•	0.0677
di1u_bl	5	2.0000	1.0000	-0.0400	0.1005
di1u_md	4	2.0000	1.0000	-0.0325	0.1085
di2u_bl	3	3.0000	0.2500	0.2033•	0.0122
di2u_md	3	3.0000	0.2500	0.1367•	0.1060
dc1u_bl	6	3.0000	1.0000	0.0800	0.1442
dc1u_md	6	2.0000	1.0000	-0.0217	0.1778
dm1u_bl	7	5.0000	0.2187	0.2543•	0.2138
dm1u_md	4	0.0000	0.1250	-0.4100	0.3624
dm2u_bl	5	0.0000	0.1250	0.0680	0.1613
dm2u_md	4	1.0000	1.0000	0.1275	0.2146

**significant after a Holm's adjustment, $p < 0.05$; •mean (R-L) is larger than the deviation around the mean (FA4a)

4.6. Comparisons among and between groups

For all comparisons between the sexes, age categories and populations, no significant differences remained after a Holm's adjustment. However, attention was given to significant differences before the Holm's adjustment, as well as to general differences and trends in the magnitude of FA.

4.6.1. Comparisons between the sexes

Median FA values between the sexes were similar within both the Grote Kerk (GRK) and the Meerenberg (MeB) populations. Males and females from GRK exhibited average median asymmetry values per individual of 2.3% ($\bar{x}$ = 2.4%%, σ = 0.7%), and 2.4% ($\bar{x}$ = 2.5%, σ = 0.8%), respectively, while MeB male and female individual median values were 2.6% ($\bar{x}$ = 2.6%, σ = 0.6%), and 2.3% ($\bar{x}$ = 2.5%, σ = 1.0%) respectively (see Table A3.6). Only a few traits and indices differed significantly between the sexes; one index (mandible) within GRK and two traits (COBB, RMLD) and one index (mandible) within MeB. The

aforementioned results are indicated in Table 4.9. Interestingly, both GRK and MeB showed a significant sex difference in FA of the mandible. However, females exhibited higher mandibular asymmetry in GRK, while males exhibited higher mandibular asymmetry in MeB (Table A7.2). Both COBB and RMLD asymmetry levels were significantly greater in males.

When the two populations were combined, only the cranial trait COPO differed significantly between males and females, with a higher FA value in males (Table A7.1). Due to the small differences between the sexes and a lack of statistically significant differences (after a Holm's adjustment), the sexes were pooled for all subsequent analyses. The lack of significant differences between the sexes was also reflected in an evaluation of the magnitude of mean FA values (Table A3.5) between the sexes.

Table 4.9. Significant Mann-Whitney U test results for differences in fluctuating asymmetry levels between the sexes for both populations. Explanations of abbreviations can be found in Appendix 1

	Grote Kerk				Meerenberg			
Trait	Male (n)	Female (n)	W	p-value	Male (n)	Female (n)	W	p-value
COBB	39	40	812.00	0.751	12	23	78.50	0.033*
RMLD	31	28	435.00	0.994	8	25	52.00	0.039*
mandible	32	42	905.00	0.011*	11	25	74.50	0.031*

*p-value < 0.05; W = test statistic for the Mann-Whitney U test

Although the differences between the sexes were small and insignificant, an attempt was made to analyse and portray the trends in the differences in FA magnitude between males and females in the current study. The differences in magnitude are described below.

Females exhibited higher mean asymmetry values in 38 traits, of which six were cranial traits, three mandibular, two humeral, three radial, and three femoral traits. The cranial traits were located in the orbital, facial, and basal areas of the cranium, although no cranial indices indicated higher mean asymmetry levels in females. However, the following indices indicated a higher mean FA for females in the skeleton: the mandible, radius, tibia, upper limb and lower limb. While the mean FA indices for both mandibular and maxillary dentition were higher in females, the dentition as a whole did not differ between the sexes. Overall, females exhibited a higher mean and median FA per individual than males.

Thirty-three traits were higher in mean asymmetry for males, namely ten cranial, one mandibular, two humeral, two radial, three femoral, and two tibial traits. Similar to females, the cranial traits were located in the orbital, facial, basal, and vault regions of the cranium. However, only the indices for the cranium as a whole, the cranial base and the vault of the cranium were higher in mean male asymmetry compared to female asymmetry values.

Additional indices with higher mean asymmetry values were the midshafts of the long bones, lower limb midshafts, the lengths of all limbs and the lower limb lengths.

Three traits showed no mean difference between the sexes in mean FA while eight indices indicated no sex differences: the skeleton, dentition, orbital and facial areas of the cranium, humerus, femur, and lengths and midshafts of the upper limb.

Although females exhibited higher mean asymmetry in the majority of traits (n=38) and in overall mean and median asymmetry values, it was only slightly higher than the amount of traits that exhibited higher FA levels in males (n=33). This corroborates the insignificance of the results mentioned above. A clear trend in the level of asymmetry between the sexes is not apparent.

4.6.2. Comparisons between the age groups

The average median FA per individual was almost identical between the age categories ranging from 2.35% ($\bar{x}$ = 2.7%, σ = 1.3%) for young adults, to 2.37% ($\bar{x}$ = 2.4%, σ = 0.7%) for middle adults and 2.43% ($\bar{x}$ = 2.5%, σ = 0.6%) for mature adults (Table A3.3). Kruskal-Wallis analysis of variance (ANOVA) comparisons between the adult age categories indicated only RGH and FIMS to differ significantly between the ages (although insignificant after a Holm's adjustment). The results for only the aforementioned significant differences are shown in Table 4.10. Results for the remaining traits and indices are available in Appendix 7 (Table A7.3). When analysed per population, RGH remained significantly different between the GRK adult ages. No significant differences were apparent between the adult age categories within the MeB population (Table A7.4). Because of the lack of significant differences between the adult age categories, the categories were pooled into one adult group for subsequent analyses between the populations.

Table 4.10. Significant Kruskal-Wallis ANOVA test results for differences in fluctuating asymmetry levels between the adult age categories: young adult (YA), middle adult (MDA) and mature adult (MA), GRK and MeB populations pooled. Explanations of abbreviations can be found in Appendix 1

Trait	YA (n)	MDA (n)	MA (n)	df	Chi^2	p-value
RGH	1	27	20	2	6.532	0.038*
FIMS	4	80	47	2	8.558	0.014*

*p-value < 0.05; df = degrees of freedom; Chi^2 = test statistic for the Kruskall-Wallis ANOVA

Post hoc Mann-Whitney U tests indicated the differences in RGH to be between middle and mature adults and FIMS to be between both young adults and middle adults, and

between middle adults and mature adults (Tables 4.11 and 4.12). Asymmetry values were higher in middle adults compared to mature adults for RGH, while mature adults exhibited a greater magnitude of FA than middle adults in FIMS. Young adults exhibited less asymmetry than middle adults for FIMS.

Table 4.11. Post hoc results for significant differences between adult age categories, GRK and MeB populations pooled

RGH					
	W			**p-value**	
	MDA	MA		MDA	MA
YA	12.00	23.50	YA	0.799	0.228
MDA		379.00	MDA		0.018*
FIMS					
	W			**p-value**	
	MDA	MA		MDA	MA
YA	152.00	228.00	YA	0.041*	0.141
MDA		1414.00	MDA		0.018*

*p < 0.05; YA=young adult, MDA=middle adult, MA=mature adult; W = test statistic for the Mann-Whitney U test

Table 4.12. Post hoc results for significant differences between adult age categories, GRK

RGH					
	W			**p-value**	
	MDA	MA		MDA	MA
YA	-	-	YA	-	-
MDA		188.50	MDA		0.007*

*p < 0.05; YA=young adult, MDA=middle adult, MA=mature adult; W = test statistic for the Mann-Whitney U test

Although the differences between the adult age categories were statistically insignificant, an attempt was made to analyse and portray the trends within the differences in FA magnitude between the three adult age categories. The differences in magnitude are described below.

When compared across the adult age categories (Table A3.3), the mean FA levels of the dentition as a whole, the mandibular dentition, the cranium, the base of the cranium, the mandible and the femur increased with increasing age. Traits following the same pattern included only cranial and femoral traits: CNOR, CFMTNS, CLFMT, FIMS, FSIH, and FMLP. On the other hand, the tibia and the long bone lengths (combined, upper and lower) decreased with increasing age. However, only four traits, of which only one was a long bone length, followed this trend: CFMTN, HXMS, RMLD, and TINF. The mean asymmetry value

per individual, as well as for the indices skeleton, orbital, facial and temporal regions of the cranium, humerus, radius, upper limbs, lower limbs, midshafts of the lower and upper limbs (and combined) decreased in middle adults from young adults, but increased again from middle adults to mature adults. Traits following this trend included six cranial (COBH, CMSAST, COCL, CBAPO, CFMTB, CLAST), one mandibular (MXRB), one humeral (HIMS), two radial (RXMS, RIMS), two femoral (FXMS, FEB) and one tibial (TXNF) traits.

Because the subadult measurements were too few per trait to separate into age categories, all analyses were pooled for both age and populations and compared to adult FA (pooled for age and populations groups). Adult median asymmetry per individual (2.5%; Table 4.2) was similar to the subadult median asymmetry (2.4%; Table 4.3). Significant differences in FA between adults and subadults were only apparent for one trait and two indices, namely FML, the maxillary dentition and upper limb maximum lengths, of which the results are shown in Table 4.13. The trait and indices were greater in FA magnitude for adults. Results of the comparison of all traits and indices are available in Table A7.5. Despite the significant difference in FA levels between adult and subadult maxillary dentition, a comparison between the entire permanent and deciduous dentition revealed no significant difference in the level of FA (Table A7.6).

Table 4.13. Significant Mann-Whitney U test results for differences in fluctuating asymmetry levels between adults and subadults, GRK and MeB populations pooled. Explanations of abbreviations can be found in Appendix 1

Trait	Adult (n)	Subadult (n)	W	p-value
FML	90	9	610.50	0.007*
Dentition: maxilla	93	15	940.00	0.031*
Upper limb: lengths	118	11	906.00	0.026*

*p-value < 0.05; W = test statistic for the Mann-Whitney U test

In a comparison between the adult and subadult mean asymmetry values, the average FA per individual, as well as the skeletal and dental indices, were higher in adults than in subadults (Tables 4.2 and 4.3). However, when comparing the permanent dentition of adults and subadults combined to the deciduous dentition, no difference in the level of mean FA was observed (Table A7.6). Additionally, the maxillary dentition, the mandible, humerus, tibia, upper limb, midshafts, midshafts of the upper limb, and the long bone lengths (combined, upper and lower) indicated a higher mean FA in adults. The cranium and midshafts of the lower limb produced no difference between adults and subadults, while the mandibular dentition, facial area of the cranium, radius, femur and lower limb exhibited lower mean FA

in subadults. A consideration of the traits revealed three cranial, four mandibular, three humeral, two radial, four femoral and one tibial trait with greater mean FA in adults; and only one cranial, one radial, three femoral and two tibial traits with greater mean FA values in subadults.

4.6.3. Comparisons between the populations

The GRK and MeB median asymmetry per individual was comparable in magnitude at 2.39% ($\bar{x}$ = 2.5%, σ = 0.8%) for GRK and 2.37% ($\bar{x}$ = 2.6%, σ = 1.0%) for MeB (Table A3.1). Correspondingly, only five traits (4.95%) differed significantly between the populations. Table 4.14 indicates the results for the significant traits only. Results for all traits and indices can be seen in Table A7.7. The traits included two traits located in the cranial vault (CBPO and CLFMT), one mandibular (MRH), one upper limb (RXMS) and one lower limb (FEB) trait. The traits CBPO and MRH exhibited higher FA in the GRK population, while the traits CLFMT, RXMS and FEB expressed higher FA levels in the MeB population. A comparison of only adult measurements between the populations indicated similar results, with the only difference in radial traits (Table A7.8): RML was significantly different between the populations. This trait exhibited higher FA values in the GRK population (Table A3.2).

Table 4.14. Mann-Whitney U test results for differences in fluctuating asymmetry levels between the populations, ages pooled

Trait	N GRK	N MeB	W	p-value
CBPO	104	24	1577.00	0.040*
CLFMT	79	22	579.50	0.011*
MRH	57	27	1025.50	0.013*
RXMS	77	49	1449.50	0.028*
FEB	46	23	308.50	0.003*

*p-value < 0.0; W = test statistic for the Mann-Whitney U test 5

Despite the lack of significant differences between the GRK and MeB populations, an evaluation of mean FA levels (Table A3.2) revealed the majority of skeletal traits (n=22) to exhibit greater magnitudes of asymmetry in the GRK population, of which eight were cranial, three mandibular, four humeral, three radial, two femoral and two tibial traits. Meerenberg exhibited greater mean FA in 19 skeletal traits, of which seven were cranial, one mandibular, two humeral, three radial, four femoral and two tibial traits, while three traits (two cranial and one femoral) did not differ in mean asymmetry between the populations. Nevertheless, the

average mean FA per individual was slightly greater in the MeB population. The following indices also exhibited a higher asymmetry value for MeB: the cranium as a whole, the face and vault regions of the cranium, the radius, tibia, upper limb, midshafts of all limbs and upper limb midshafts. Indices that indicated a higher mean FA for the GRK populations pertained mostly to the dentition (dentition, permanent dentition, mandibular and maxillary dentition), mandible and cranial base, as well as the humerus and the upper and lower long bone lengths.

4.6.4. Comparisons between the skeleton and dentition

Contrary to the comparisons between the sexes, age, and populations, the comparison between the FA levels of the skeletal and dental traits exhibited statistically significant results between both the entire skeleton (median = 2.4%; $\bar{x}$ = 2.6%, σ = 1.0%) and dentition (ages pooled; median = 2.6%; $\bar{x}$ = 2.8%, σ = 1.1%), and between the adult skeleton (median = 2.4%; $\bar{x}$ = 2.6%, σ = 1.0%) and permanent dentition (median = 2.6%; $\bar{x}$ = 2.8%, σ = 1.1%; Tables 4.2, 4.15-16). These results remained statistically significant after a Holm's adjustment of the p-values. Since no significant differences in the level of FA between the two populations were observed with regard to the skeletal and dental indices, the populations were combined for the analysis between the dental and skeletal FA. For both the age groups combined and per adult comparison, the asymmetry values of the dentition were greater in FA magnitude than those of the skeleton.

Table 4.15. Mann-Whitney U test results for differences in fluctuating asymmetry levels between the skeleton and dentition, GRK and MeB populations pooled

Skeleton (n)	Dentition (n)	W	p-value
273	130	20891.00	0.004**

**significant after a Holm's adjustment, $p < 0.05$; W = test statistic for the Mann-Whitney U test

Table 4.16. Mann-Whitney U test results for differences in fluctuating asymmetry levels between the adult skeleton and permanent dentition, GRK and MeB populations pooled

Skeleton (n)	Permanent dentition (n)	W	p-value
249	123	17877.00	0.009**

**significant after a Holm's adjustment, $p < 0.05$; W = test statistic for the Mann-Whitney U test

A Mann-Whitney U test revealed no significant difference in the median FA values between the subadult skeleton (2.3%; $\bar{x}$ = 2.4%, σ = 0.9%) and deciduous dentition (3.2%; $\bar{x}$ = 2.8%, σ = 1.1%), although the deciduous dentition exhibited a higher median and mean asymmetry than the skeleton (Tables 4.3 and 4.17).

Table 4.17. Mann-Whitney U test results for differences in fluctuating asymmetry levels between the subadult skeleton and deciduous dentition, GRK and MeB populations pooled

Skeleton (n)	Deciduous dentition (n)	W	p-value
24	10	146.00	0.335

W = test statistic for the Mann-Whitney U test

4.6.4.1. Trends in the skeleton

When considering the mean asymmetry of the traits and indices in the adult skeleton (Table 4.2) within the cranium, mandible, and limbs, a general pattern can be distinguished for some of the traits. Within the regions of the cranium, the facial traits, specifically CBZO, CFMTNS, CFMTN and CFMTB exhibited the least amount of (mean) FA, while the traits located in the cranial base, specifically COCL, COPO and CBAPO, exhibited higher mean levels of FA. However, one facial trait, CMAH, exhibited the second highest mean FA value. The mean FA of traits located in the orbital and cranial vault ranged from low to high. The one temporal trait that was not excluded due to measurement error, CMSAST, exhibited the third highest mean FA.

Within the mandible, the maximum and minimum ramus breadths exhibited the highest mean FA, followed by the height of the ramus and mandibular length. The mean FA levels in the long bones followed a similar pattern to that of the mandible. The maximum and minimum midshaft diameters exhibited the most asymmetry, followed by the diameters of the head (humerus) or the breadth of the distal end (radius, femur) while the long bone lengths exhibited the least asymmetry. Concordantly, the index for long bone midshafts exhibited higher asymmetry values than the index for long bone lengths. In a comparison between the mean FA of the four long bones, the femur exhibited the least asymmetry, followed by the tibia, humerus and radius. This is also reflected in the indices for the upper and lower limbs, in which the upper limbs exhibited the most asymmetry. However, an evaluation of FA of the individual long bone traits revealed two tibial traits (TXNF and TINF) to exhibit higher asymmetry values, while one radial (RML) and two humeral (HEB, HSIH) traits exhibited lower asymmetry values.

4.6.4.2. Trends in the dentition

A comparison between the maxillary and mandibular permanent dentition indicated no significant difference in the level of median FA (Table 4.18). The mean values are almost identical; that of the mandible being $\bar{x}$ = 0.0278 and that of the maxilla $\bar{x}$ = 0.0281.

Table 4.18. Mann-Whitney U test results for differences in fluctuating asymmetry levels between the mandibular and maxillary permanent dentition, GRK and MeB populations pooled

Mandibular (n) dentition	Maxillary (n) dentition	W	p-value
112	108	6263.50	0.648

W = test statistic for the Mann-Whitney U test

An evaluation of the mean FA in mandibular and maxillary teeth (Table 4.2) within each tooth class revealed a pattern in terms of the crown diameter and the sequence of a tooth in each class (from mesial to distal). Within each tooth class, the mesiodistal crown diameters are more asymmetric than the buccolingual crown diameters. In the canines, however, this pattern is reversed, and in the incisors, the mesiodistal diameter of the central incisors exhibited less asymmetry than the corresponding buccolingual diameter. This trend was identical for the maxillary and mandibular dentition. For the premolars, molars, maxillary incisors and mesiodistal diameter of the mandibular incisors, the level of asymmetry increased from mesial to distal within each tooth class. The only exception was the buccolingual diameter of the mandibular incisors, in which the second incisor exhibited less asymmetry than the first incisor.

When the mean level of asymmetry was compared among all tooth classes per upper and lower jaw, no clear pattern could be distinguished, except that all the mandibular premolars exhibited the highest mean FA within the mandible. Compared to all the dental traits, the buccolingual diameters of the maxillary first premolar and first molar exhibited the least asymmetry, while the mesiodistal diameters of the maxillary second incisor and second molar exhibited the most asymmetry.

4.7. Pathology between populations

4.7.1. Frequency of skeletal lesions between populations

The frequency of skeletal lesions differed between the populations, with more GRK individuals exhibiting cribra orbitalia/porotic hyperostosis, subperiosteal bone reactions and

enamel hypoplasia (EH; Table 4.19). Within both populations, subperiosteal bone reactions were observed most frequently, while the presence of cribra orbitalia/porotic hyperostosis was uncommon (GRK=5.3%, MeB=2.8%). In a comparison between the frequencies of all three pathological lesions (cribra orbitalia/porotic hyperostosis, subperiosteal bone reactions and EH) between the two populations, Fisher's exact test revealed no significant differences (Table 4.19).

Table 4.19. Contingency table with proportions (%) and Fisher's exact test results for three types of pathological lesions present in the individuals per population. C/P = cribra orbitalia/porotic hyperostosis; P = subperiosteal bone reactions; and EH = enamel hypoplasia

	C/P			P			EH		
	n	**N**	**%**	**n**	**N**	**%**	**n**	**N**	**%**
GRK	171	9	5.3	171	42	25	171	33	19
MeB	106	3	2.8	106	25	24	106	13	12
Total	277	12	8.1	277	67	49	277	46	31
p-value: 0.687									

n=number of individuals investigated; N=number of individuals affected

When the frequency of each type of skeletal lesion was compared against the frequency of no skeletal lesions between the two populations, none of the pathological lesions showed a significant difference in frequency between the populations (Table 4.20).

Table 4.20. Contingency tables for each type of pathological lesion observed on the individuals per population.

Cribra orbitalia/Porotic hyperostosis				
	Lesion (n)	**No lesion (n)**	**Total**	**p-value**
GRK	9	162	171	-
MeB	3	103	106	-
Total	12	265	277	0.3831
Subperiosteal bone reactions				
	Lesion (n)	**No lesion (n)**	**Total**	**p-value**
GRK	42	129	171	-
MeB	25	81	106	-
Total	67	210	277	0.886
Enamel hypoplasia				
	Lesion (n)	**No lesion (n)**	**Total**	**p-value**
GRK	33	138	171	-
MeB	13	93	106	-
Total	46	231	277	0.138

4.7.2. The presence of skeletal lesions and the level of FA

The median and mean FA per individuals who also exhibited one of the three skeletal lesions (see Section 4.7.1) was slightly greater in the Meerenberg population (2.57%; $\bar{x}$ = 2.56%, σ = 0.66%), than the Grote Kerk population (2.46%; $\bar{x}$ = 2.54%, σ = 0.54%). However, Mann-Whitney U analyses revealed no statistically significant difference in the median FA between the populations (Table 4.21).

Table 4.21. Mann-Whitney U test results for differences in fluctuating asymmetry levels per individual between GRK and MeB, for individuals with skeletal lesions

GRK (n)	MeB (n)	W	p-value
67	34	1132.5	0.9656

W = test statistic for the Mann-Whitney U test

The comparison between the median FA of the individuals with a skeletal lesion(s) (2.47%; $\bar{x}$ = 2.55%, σ = 0.58%) to individuals without any of the three skeletal lesions (2.30%; $\bar{x}$ = 2.48%, σ = 0.93%) revealed a significant difference, albeit insignificant after a Holm's adjustment (Table 4.21). Median asymmetry values were higher in individuals with skeletal lesions. However, the mean FA per individual differed only slightly between the groups with and without skeletal lesions.

Table 4.22. Mann-Whitney U test results for differences in fluctuating asymmetry levels per individual between individuals with and without skeletal lesions

No lesion (n)	Lesion (n)	W	p-value
176	101	7509	0.0317*

* $p < 0.05$; W = test statistic for the Mann-Whitney U test

Chapter 5: Discussion

5.1. Introduction

Patterns and trends in the magnitude of FA within and between the two Dutch archaeological populations are discussed in the subsequent sections in terms of the trends observed within the skeleton and dentition, differences between the sexes and age categories, and the association with skeletal and dental indicators of stress. Possible correlations or contradictions with previous studies are examined and reasons for differences or lack thereof are discussed. Additionally, the outlier values, the osteological paradox in terms of the sample selection and frequency of pathological lesions, limitations of the current study, and opportunities for future research are considered.

5.2. Asymmetry trends throughout the skeleton and dentition

The results of the current study concur with previous research suggesting that the magnitude of FA is variable across traits and indices (Møller and Swaddle, 1997; Storm, 2009; Blackburn, 2011). The differential expression of FA across traits has been linked to the differential canalisation strength and ability of each trait (Waddington, 1957; Wagner *et al.*, 1997). Canalisation can be described as the internal ability of an organism to buffer the effect of environmental stressors on developmental pathways. The buffering or canalisation ability does not only differ between organisms but also between different traits within an organism. In addition, traits also differ in their ability to buffer different stressors. That is to say, the effect of one type of stressor will be buffered differently than another type of stressor by the same trait (Waddington, 1957; Møller and Swaddle, 1997; Wagner *et al.*, 1997).

The average FA per individual ranged from a minimum of zero to a maximum of 7.3% (not considering the traits associated with a high measurement error such as mastoid length), although the maximum midshaft dimension of the humerus exhibited asymmetry values of up to 17%. The lowest maximum asymmetry value for a trait was 3% (maximum length of the tibia). In comparison to the current study, Storm (2009) reported a wider range of maximum asymmetry values that ranged from 1.7% to 31.76% within an English archaeological skeletal sample.

Storm (2009) stated that measurements with the lowest measurement error, smallest range (standard deviation) and the smallest magnitude of average FA are potentially the best indicators for the detection of developmental instability. The least informative measurements

are those with the highest measurement error and the greatest standard deviations. Accordingly, all long bone lengths (especially those of the lower limb), and five cranial measurements (CLFMT, CFMTNS, CBZO, CFMTB and CBAST), three from the upper facial region, and two vault measurements could be considered the most informative traits for developmental instability within the two Dutch populations. Traits that could be considered weak indicators of developmental instability included CMPL, CMPB, CMAH, and COCL (two temporal, one facial and one base region of the cranium respectively) and the majority of the dental traits, especially those of the mandibular dentition. This is in agreement with findings by Storm (2009) for an English archaeological sample, where long bone maximum lengths, CLFMT (vault), CBZO (facial), CNMS (base) and CFMTN (facial) provided the most reliable information on developmental instability. The least informative measurement in Storm's (2009) study, similar to CMPL and CMPB in the current study, was located in the temporal region of the cranium, namely the height of the mastoid process.

The patterns and trends of FA within the cranium, long bones and dentition are discussed in the following sections.

5.2.1. Cranium and mandible

Similar to findings of other studies (e.g., DeLeon, 2007; Gawlikowska *et al.*, 2007a; Bigoni *et al.*, 2013), FA was greatest in magnitude in the cranial base and lowest in the facial area. Results from this study, however, differed from the previous studies in terms of the FA levels of the cranial vault and the orbital regions. In the current study, the magnitudes of FA for traits belonging to the vault and orbital regions were highly variable with no clear pattern.

The trend observed in the cranial vault differs from the findings of previous studies (DeLeon, 2007; Gawlikowska *et al.*, 2007a; Bigoni *et al.*, 2013), although the trends in the magnitude of FA in the vault region of these studies also differ from each other. According to Gawlikowska *et al.*'s (2007a) study, the cranial vault exhibited the least FA within a Medieval male sample, while it exhibited the most FA when assessed in a modern male sample. De Leon (2007) on the other hand, observed the greatest magnitude of FA within the vault or neurocranium of Mediaeval Nubian crania, while results from a previous study on fluctuating asymmetry of the cranium revealed cranial vault FA to be intermediate to asymmetry levels of the cranial base and upper face.

The varying results of various studies in terms of FA magnitude of the cranial vault in relation to FA levels of the cranial base and face provide additional support for the differential buffering capacity or sensitivity of traits to various stressors (DeLeon, 2007).

While it might be argued that the populations in each study differ in their buffering capacity to certain stressors, the populations could be argued to have been subjected to different levels of stress. One population might have experienced more acute or longer periods of stress than other populations, and would therefore exhibit more asymmetry in, for example, the cranial vault (Van Valen, 1962; Clarke, 1995). Along the same line of thought these differences might also be an indication that, as suggested by Storm (2009) and implied in the current study, the cranial vault is a sensitive indicator of developmental instability and would, therefore, show more variation between studies and populations in response to the differential levels and types of developmental stress that the populations were subjected to.

The presence of directional asymmetry (DA) within the cranium did not confound the detection of FA, although two traits within the upper facial area (diagonal orbital breadth (CNOR) and frontomalare-nasion length (CFMTN) exhibited discernible levels of DA in addition to FA. The presence of DA within the cranium is not unexpected. Mild degrees of asymmetries within the cranium, especially of the facial region, are considered typical and are linked to functional asymmetries of the brain (Ulijaszek and Mascie-Taylor, 1994). Functional asymmetries of the brain typically manifest as structural asymmetries of the brain, which may, in turn, manifest as asymmetry of the overlying cranium (Woo, 1931; Ulijaszek and Mascie-Taylor, 1994; Thoma *et al.*, 2002). However, this does not mean that any observed FA of the cranium should be disregarded as only the expression of natural functional asymmetries of the brain. Fluctuating asymmetries within the cranium have been shown to increase with nutritional and systemic stress and are associated with increased frequencies of stress indicators such as EH, cribra orbitalia and delayed skeletal growth (DeLeon, 2007; Hoover and Matsumura, 2008). These studies provide evidence that the cranium also expresses some degree of FA that can be utilised as an indicator of developmental instability.

Fluctuating asymmetry levels within the mandible were greatest for the minimum and maximum breadths (of the ramus and upper limb respectively) and the least for mandibular length. The FA magnitude of ramus height was intermediate between the FA magnitude of the ramus breaths (minimum and maximum) and mandibular length. The observed pattern in the mandible is identical to findings by Storm (2009) on a large sample of English archaeological populations, but contradictory to Storm and Knüsel (2005), where the breadth of the ramus exhibited the least asymmetry, and ramus height the most. The latter study, however, was conducted on a small subsample of English archaeological populations of only 20 individuals, and might not be representative of the entire population.

The muscular function of the mandible has been shown to mainly affect components of the mandibular ramus, such as the condylar and coronoid processes, and the angle of the mandible (Scott, 1953; Kiliaridis, 2006). Kiliaridis (2006) concluded that the craniofacial skeleton, including the mandible, adapts to loading in a similar manner as the long bones. Directional loading of the mandible due to habitual masticatory function (Shah and Joshi, 1987; Pirttiniemi, 1998), therefore, can be argued to unevenly affect the growth and adaptation to bony responses of the mandible, and the mandibular ramus in particular, contributing to an increased FA of the breadths and height.

5.2.2. Long bones

The results of this study concur with previous research that the upper limbs exhibit more fluctuating asymmetry than the lower limbs (Trivers *et al.*, 1999; Storm, 2009). This pattern is not confined to FA. Research on DA of the long bones has also indicated the upper limb bones, specifically the humerus, are more asymmetric than the lower limb bones (e.g. Čuk *et al.*, 2001; Auerbach and Ruff, 2006; Blackburn, 2011). One possible explanation for the lower levels of asymmetry in the lower limbs is their important function in locomotion or gait. This suggests that the lower limb bones possess a higher canalisation or buffering capacity, and are therefore developmentally more stable than the upper limbs. An increased directional loading from handedness in the upper limbs, or an increased susceptibility to mechanical loading might also explain the greater asymmetry of the upper limb although more in the sense of directional asymmetry (Auerbach and Ruff, 2006). Tests for the confounding effect of DA on FA revealed eight long bone traits exhibited marked DA, of which seven belonged to the upper limb: HML, HXMS, HDT, HEB, RML, RXMS, RMLD, FEB (refer to Appendix 1 for abbreviations). Only the DA of humeral length seemed to markedly influence the observed magnitude of fluctuating asymmetry.

The greater expression of DA than FA in the humerus was also observed in the English archaeological populations, from which Storm (2009) concluded that the humerus is therefore more susceptible to biomechanical stimuli than developmental instability. The rest of the humeral and other long bone traits in the current study did not reveal a marked expression of DA, and therefore provided ample information for an observation of FA within the long bones, such as the difference in FA magnitude between the upper and lower limbs.

In addition to the difference in FA magnitude between the upper and lower limbs, the distal element of each limb (radius, tibia) was more asymmetric than the proximal element (humerus, femur). It could be argued that the proximal elements are more stable in their

development, or more buffered against developmental stressors, than the distal elements. However, an analogous pattern was observed in the limbs of rhesus macaques and was attributed to differential mechanical influences during skeletal growth on the limb elements (Hallgrímsson, 1999).

Within both the upper and lower long bones in this study, the greatest FA magnitude was observed in the minimum and maximum midshaft diameters, and the least in the long bone lengths. This trend was reflected in the indices for the long bone midshafts versus the long bone lengths and was previously reported for directional asymmetry of the limbs (Čuk *et al.*, 2001; Auerbach and Ruff, 2006; Auerbach and Raxter, 2008; Kujanová *et al.*, 2008). A previous study on FA of the limbs noted a similar pattern in the lower limb and radius, while, in the humerus, asymmetry of the maximum length was greater than its midshaft diameters (Storm, 2009). Fluctuating asymmetry magnitudes for the proximal (head diameters) and distal breadths within the current study were intermediate to those of the midshaft diameters and lengths.

Midshaft diameters of the long bones have previously been shown to be more sensitive in their response to mechanical stimuli or muscle tension on the bones than the lengths or proximal and distal breadths (Auerbach and Ruff, 2006). Therefore, the increased FA in the midshaft diameters could also indicate an increase in functionality of one of the extremities due to handedness. It could also be argued that the greater asymmetry in the diaphyseal or midshaft diameters within the current study indicates a low canalisation or buffering ability to external (or internal) effects and, therefore, they exhibit more fluctuating asymmetry than the lengths or articular dimensions. The long bone lengths and articular dimensions might therefore have been more resistant to external factors such as mechanical loading or increased functionality. Auerbach and Ruff (2006) argued that, similar to the difference in asymmetry between the upper and lower limbs, this trend might be related to locomotor function or gait, as increased asymmetry in lengths or articular dimensions, especially in the lower limb, would negatively impact the function of the long bones.

It could be argued that, although the lower limbs, proximal limb elements and the long bone lengths are more stable and less susceptible to external and internal stressors than the upper limbs, distal limb elements and midshaft diameters respectively, they are also less affected by directional loading. This increased stability or decreased susceptibility to directional loading or mechanical stimuli might, in turn, be related to an increased need for homeostasis during development in order for normal functioning of the limbs (Møller and Swaddle, 1997).

5.2.3. Dentition

The results of this study concur with previous research indicating that there is an increase in FA magnitude from mesial to distal within each permanent tooth class (Garn *et al.*, 1966; Perzigian, 1977; Harris and Nweeia, 1980; Townsend and Brown, 1980; Khalaf *et al.*, 2005). One exception is the buccolingual crown diameter of the mandibular incisors. Also similar to previous studies, the mesiodistal crown diameters were found to be more asymmetric than the buccolingual crown diameters (Townsend and Brown, 1980; Khalaf *et al.*, 2005), but only within each tooth class. In the canines, however, the pattern was reversed. It would seem that crown formation within the dentition is more stable for the more mesial or first tooth in each morphogenic class, as well as for the buccolingual diameter of a tooth within a morphogenic class. This correlates with the general order of tooth and crown formation (most mesial tooth first), and with previous findings that the later forming teeth are more variable that the earlier forming teeth (Liversidge, 2003 and references within).

Outside each tooth class, no pattern in the magnitude of FA was discernible, although the two highest and two lowest asymmetry values were mesiodistal and buccolingual diameters respectively. The mesiodistal diameters of the maxillary second incisor and maxillary second molars were the most asymmetric while the buccolingual diameters of the maxillary first premolar and maxillary first molar were the least asymmetric.

In contrast to previous FA studies on dentition (e.g., Townsend and Brown, 1980; Hoover *et al.*, 2005; Khalaf *et al.*, 2005), no difference was observed in the magnitude of FA between the permanent mandibular and maxillary dentitions. While the previous studies have found the maxillary dentition to be more asymmetrical than the mandibular dentition, the differences in this study were not significant, suggesting a similar dental developmental pattern between the two jaws.

5.3. Asymmetry between the sexes

The results of this study are in agreement with previous studies (e.g., Perzigian, 1977; Costa, 1986; Hallgrímsson, 1999; Khalaf *et al.*, 2005) concerning a lack of significant differences in FA magnitude between the sexes. However, females did demonstrate slightly higher FA levels per individual than males. This is in contrast to the trend observed by Weisensee (2013) in the craniofacial skeletons of adult individuals from Portugal, in which males demonstrated slightly higher FA levels than females despite no significant differences between the sexes. Additionally, within the removed outliers (see Section 4.1), a greater

percentage of female measurements were regarded as outlier values than male measurements. However, this may be attributable to the skewed sex distribution of the two samples. Both samples have more females, especially the MeB sample (refer to Table 4.1). A higher percentage of outlier values in female measurements due to the inclusion of more females within the study might be plausible, but not necessarily the only cause.

Further disparity regarding the slightly higher FA values per female individual in the current study is perceived when the greatest differences in FA between the sexes were analysed by population. One cranial (orbital breadth) and one radial (distal end mediolateral width) trait, as well as the mandibular index, exhibited higher FA values for males within the MeB population. However, the mandibular index showed greater asymmetry for GRK females. The lack of statistically significant differences and the ambiguous results of the study leads one to conclude that no real difference in FA magnitude exists between the sexes. From this study, it seems that males and females do not differ in their buffering capacity or developmental stability.

5.4. Asymmetry and age

The current study found no significant difference between adult and subadult FA levels, although adult FA levels per individual were slightly higher than the subadult levels. This is in contrast with the results of previous studies, which found subadults exhibited greater magnitudes of FA than adults (Rossi *et al.*, 2003; Storm, 2009). In the current study, the greatest difference in asymmetry magnitude between adults and subadults was observed for the maximum length of the femur, the lengths of the upper limbs, and the maxillary dentition. The greatest accumulation of asymmetry occurs during ontogeny (Møller and Swaddle, 1997; Hallgrímsson, 1999; Storm, 2009), from fertilisation to adulthood. Therefore, the magnitude of FA can be expected to increase with increasing age until adulthood is reached. A higher magnitude of FA within adult individuals can also be an indication that the adults were under greater amounts of stress during ontogeny (worse environmental conditions, for example) than the subadults, or that they were more susceptible to the stressors.

Similar to a study by Hallgrímsson (1999), no asymmetry differences were observed between the permanent and deciduous dentition. The lack of significant differences might be an indication that the level or type of stress during the development of the deciduous and permanent dentition was similar. This is because different levels or types of stress during the

development of the deciduous dentition and the development of the permanent dentition may affect the expressed magnitude of FA within the dentition. It is also possible that, because the dentition is more developmentally stable than the skeleton (Cardoso, 2007), the occurred stress would not have influenced the symmetry of the dentition as much as the bony elements during differing periods and magnitudes of stress. Even though the stress could have differed in intensity and duration between the development of the deciduous and permanent dentition, the dentition would not have differed much in the magnitude of FA.

No significant pattern in FA magnitude of the skeletal traits was observed with increasing adult age, although the majority of the traits and indices increased in FA with increasing age from middle adults to mature adults (when the small young adult sample is excluded). Markedly smaller sample sizes for the young adult age category (n = 10; see Table 4.1) could possibly have influenced the observed trend in the current study as it may be too small to be representative of the young adult population FA.

However, when all adult age categories are evaluated, the trend in FA with increasing age is less clear. While Storm (2009) noted increasing asymmetry levels with increasing age during adulthood in archaeological English individuals, results from the current study indicated this upward trend for only three cranial and three femoral traits, and for six indices (dentition, mandibular dentition, cranium, the base of the cranium, mandible and the femur). This increasing trend within the indices, pertaining mostly to the cranium, mandible and dentition, was found by Hallgrímsson (1999) for adult cranial and postcranial elements, where the FA values of only the cranial traits increased with increasing age. Moreover, somewhat in line with Hallgrímsson's (1999) findings of a lack of increase in FA with advancing age for the postcranial elements, here there were decreases in FA levels with increasing age groups for tibial and long bone indices. Only one cranial trait (in the upper facial area) followed this trend.

Relating to the increased dental FA with increasing age, Garn *et al.* (1966) suggested that much of the side-to-side discrepancy in tooth size, or the measured FA, might be due to variations in the thickness of the enamel and/or the variations in the size of the dentinal structures. Moreover, increased dental wear with increasing age might increase this side-to-side discrepancy in tooth size and the amount of FA with age. In addition to dental wear, the length of the dental arch has been shown to decrease with age and dental crowding (especially anteriorly) to increase with age (Bishara *et al.*, 1994). It may be possible that this increased crowding affects the bilateral dimensions of the enamel enough to cause an

increase in FA magnitude with age. Additionally, antemortem tooth loss is known to change the shape of the mandible and maxilla due to irreversible alveolar bone resorption. The mandibular angle widens and the supero-inferior diameter of the body decreases. Alveolar bone resorption due to tooth loss increases over time and is usually greater in the mandible (Bodic *et al.*, 2005).

Changes in the shape of the mandible have been associated with changes in the cranial base and related cranial or neural structures (Pirttiniemi, 1998). Changes in the asymmetry of the cranium can also be related to asymmetric changes of the brain with age. Kovalev *et al.* (2003) studied changes in brain asymmetry in healthy individuals aged 18 to 70 years of age and found various regions of the brain to become significantly more asymmetric with age. However, a smaller proportion of the regions included in the study decreased in asymmetry with age. Nevertheless, this study by Kovalev *et al.* (2003) indicated that changes in the asymmetry of the brain, and by inference also the cranium, changes with age – with the majority of regions included in the study to increase in asymmetry with age.

The remaining traits and indices in the current study decreased from young adult to middle adult and increased again from middle adult to mature adults. However, when the young adult age category is not taken into consideration, the majority of traits showed an increase in FA with increasing age, which concurs with the trend observed by Storm (2009) mentioned above.

Because the greatest accumulation of asymmetry occurs from fertilisation to adulthood (Møller and Swaddle, 1997; Hallgrímsson, 1999; Storm, 2009), it can be argued that the increase in FA magnitude with increasing adult age is more likely due to mechanical 'wear and tear' (Palmer and Strobeck, 2003) than it is due to the greater levels of stress during development. The random effects of 'wear and tear', such as due to lifestyle, attrition or preferential usage of the left or right elements, can differentially alter the size and shape of the left and right bones, and thus increase the measured FA. Lastly, the abovementioned differences in asymmetry with age should not be regarded as trends in mean FA with advancing age, but merely as differences that exist in the mean FA between the different age groups. Because the data are of a cross-sectional nature (data are collected at a specific point in time) and not of a longitudinal nature, trends for the change in FA levels over time cannot be inferred (Rindfleisch *et al.*, 2008).

5.5. Lesions indicating pathology and levels of asymmetry

In this study, two skeletal markers and one dental marker of stress were chosen for further analyses in order to provide possible additional information on the observed levels of FA within the Dutch populations. The markers included cribra orbitalia/porotic hyperostosis, subperiosteal bone reactions and enamel hypoplasia (EH). Both the GRK and MeB populations showed signs of these three markers of stress.

The observed frequencies of the pathologies differed between the GRK and MeB populations. The GRK population exhibited higher frequencies of cribra orbitalia/porotic hyperostosis, EH and subperiosteal bone reactions. When the frequencies of all three skeletal lesions were analysed simultaneously and per lesion, no significant differences in the frequency of the lesions were indicated between the populations. No significant difference in the frequencies of pathological lesions between the populations might be an indication that the populations were subjected to the same level or duration of environmental (external) stress, although the type of stress might have differed, or that each population differentially responded to these environmental stresses.

However, mental disorders have been associated with several syndromes and congenital illnesses, of which EH is sometimes a part (Webb *et al.*, 1991; Määttä *et al.*, 2006; Bhatia *et al.*, 2012). While various systemic (hormonal, vitamin or mineral deficiencies) and local (trauma or infection at or surrounding the tooth germs) factors can lead to EH, the hypoplastic defects have also been associated with several congenital or inherited syndromes and illnesses (Goodman and Rose, 1990; Brook, 2009; Schuurs, 2013). Some of these syndromes and illnesses such as Down's syndrome, congenital rubella, tuberous sclerosis, phenylketonuria, and cretinism are also characterised by mental disabilities or mental retardation (Webb *et al.*, 1991; Määttä *et al.*, 2006; Bhatia *et al.*, 2012; Schuurs, 2013). While nutritional deficiencies were likely to contribute to the observed EH frequency within the MeB population, the association of congenital or hereditary syndromes and illnesses with EH and mental deficiencies suggests it to be a feasible cause in this allegedly mentally compromised population. If the enamel hypoplastic defects within the MeB population are assumed to be associated with the mental illnesses and syndromes, the MeB population could be considered to have been subjected to less external stressors relative to the GRK population, but to more internal or genetic stressors due to the association of EH with congenital syndromes and illnesses. However, all possible aetiologies should be considered in any paleopathological analysis.

Each type of pathological lesion is formed in response to different stressors or environmental influences. While all three types of lesions can occur due to nutritional deficiencies, a deficiency of vitamin C is believed to be one of the most common causes of cribra orbitalia and porotic hyperostosis (Ortner, 2003; Brickley and Ives, 2008; Walker *et al.*, 2009). Cribra orbitalia and porotic hyperostosis can occur both during adult- and childhood, although the lesions (especially cribra orbitalia) are more apparent in children, as the lesions are more often active at the time of death (Mann and Murphy, 1990; Walker *et al.*, 2009). Non-specific infectious diseases, among other causes, play a more prominent role in the aetiology of subperiosteal bone reactions. Subperiosteal bone reactions can occur throughout life (Mann and Murphy, 1990; Ortner, 2003).

Taking the above mentioned information into consideration, it could be speculated that the GRK population was possibly subjected to infectious diseases, trauma or nutritional deficiencies throughout life. However, the higher frequencies of subperiosteal bone reactions (25%) and cribra orbitalia/porotic hyperostosis (5.3%) in the GRK population, can also be an indication of illness and hardship in the later stages of life.

Further speculation as to possible specific causes of the observed lesions within the populations was not attempted, as the severity and state (active or healed) of the lesions were not taken into account during data collection. Other disease conditions observable from the skeletal remains were also excluded from the current study.

In an attempt to link the magnitude of stress to the frequency of observed lesions between the two populations, the median FA levels of all the individuals who exhibited a pathological lesion (cribra orbitalia/porotic hyperostosis, subperiosteal bone reaction, EH) were compared between the GRK and MeB populations. The comparison revealed no statistically significant difference between the populations, corresponding to the lack of a significant difference between the (combined) population frequencies of the lesions, discussed above. This indicates that although the GRK population exhibited greater frequencies of pathological lesions than the MeB population, their stressors or noise during development (ontogeny) were likely more or less of a similar magnitude or duration.

However, evidence supporting the use of FA as an indicator of developmental instability and its positive relationship to skeletal indicators of stress (Hoover *et al.*, 2005; DeLeon, 2007; Hoover and Matsumura, 2008) was observed in the comparison of the magnitude of FA between individuals exhibiting a pathological lesion and the rest of the sample (with the populations pooled). That is to say, individuals who exhibited any one of the three lesions (cribra orbitalia/porotic hyperostosis, subperiosteal bone reaction, EH) were

compared to all the individuals who did not exhibit one of the three pathological lesions, in terms of their average median FA. The individuals who exhibited the pathological lesions were significantly more asymmetrical (in magnitude) than the individuals without any of the three lesions. This corresponded to findings by Hoover and Matsumura (2008) on 13 archaeological Japanese populations, in which higher levels of FA were observed in individuals who exhibited EH. It can be inferred that individuals who are better buffered or resistant against environmental stressors, such as nutritional deficiencies or infectious diseases, are also more developmentally stable. However, a lower frequency or absence of skeletal lesions and a lower magnitude of FA could also be an indication that the individuals were less exposed to stressors.

5.6. Population differences in asymmetry

The current study found no significant difference in FA values between the supposedly general GRK population and MeB psychiatric hospital sample. The largest differences in median FA between the populations were only found for two cranial traits located in the cranial vault (bregma-porion length and lambda-frontomalare length), mandibular height, maximum midshaft diameter of the radius and distal epicondylar breadth of the femur. Bregma-porion length and mandibular height exhibited greater FA values in the GRK population while FA in the rest of the aforementioned traits was greater in the MeB population. Although the overall mean FA values per individual were slightly higher in the MeB population, there was no difference between the populations in the magnitude of median FA. However, more traits from the GRK population exhibited higher mean FA values than the MeB population, even though it was only by a few more traits. It seems that no real differences in the magnitude of FA between the two populations were apparent.

These results are in contrast to findings in the literature that mentally impaired or ill individuals exhibit higher levels of FA or are more developmentally unstable than their mentally healthy counterparts (Malina and Buschang, 1984; Markow and Wandler, 1986; Lalumière *et al.*, 2001; Reilly *et al.*, 2001). For example, Malina and Buschang (1984) observed higher levels of FA within the long bones of mentally impaired or ill males compared to mentally healthy males, which were statistically significant for the upper limb traits. In another study, schizophrenic individuals exhibited higher magnitudes of FA, which were directly proportional to the severity of the condition (Markow and Wandler, 1986; Markow and Gottesman, 1989; Reilly *et al.*, 2001). Because no specific information on the

Meerenberg individuals included in the current study was available, an analysis or comparison of the level of FA against the type or degree of mental impairment or illness was not possible.

Due to the lack of significant differences in FA magnitude between the populations, additional factors were considered for possible explanations. One possible factor that could provide an explanation is the frequency of pathological lesions within the two populations. The GRK population exhibited higher frequencies of cribra orbitalia/porotic hyperostosis, EH and subperiosteal bone reactions, although the difference was not significant. When considering the frequencies alone, it seems that both populations were subjected to more or less equal amounts of stress or insults. However, as discussed in Section 5.5, the aetiology and frequencies of each type of lesion within each population may provide additional information regarding the level of stress within each population. An important consideration within the MeB population is their history of apparent mental illness. Some of the conditions are syndromes or congenital illnesses with which EH is sometimes associated (Webb *et al.*, 1991; Bhatia *et al.*, 2012; Schuurs, 2013). Therefore, the observed frequency of EH in the MeB population compared to the GRK population might also be explained by the presence of syndromes and other congenital conditions within MeB.

The historical socio-political information on the different time periods of the two populations supports the finding from the pathological lesions that individuals from the GRK population might have been under greater environmental stress relative to the MeB population. Comparisons of the socio-political environments of the individuals from GRK during the 18th to early 19th century, and individuals from MeB during the early 19th to the early 20th centuries, suggest that the two populations lived in similar economic circumstances, although the socio-economic environment of the GRK individuals seems to have been less stable.

The GRK economy started at an extreme low at the start of the 18th century, followed by a long laborious recovery and an overall decrease in the standard of living, just to end in another recession at the turn of the century (De Vries and Van der Woude, 1997; Allen, 2000). The first half of the 18th century was characterised by chronic unemployment and de-urbanisation as the country struggled to recover from the economic crisis of the late 17th century. Alkmaar, where the Grote Kerk is located, was one of the smaller cities that suffered tremendously during this period. During the second half of the 18th century, the economy improved slightly and the population density increased at a rapid pace, but the rising cost of living, together with infrequent and minor wage increases, lessened this economic

improvement for the general population (Van den Eerenbeemt, 1962; De Vries and Van der Woude, 1997).

A lack of credit-creating institutions, together with the declaration of war by the British in 1780 and the French rule over the Netherlands by the end of the century, sent the Dutch economy into another economic recession, which was at its worst until 1813. While the Meerenberg population might have been born in a poverty stricken nation at the beginning of the 19th century, the Dutch managed to recover their economy by the second half of the 19th century. Despite the slow, albeit improving, state of the economy, high rates of unemployment, rapid urbanisation and commercialisation resulted in a decreased standard of living for the general population and subsequent decrease in adult stature during this time. However, life expectancy at birth, adult stature and population density increased again after the 1870's and continued during the 20th century (Allen, 2000; Haines, 2004; Deneweth *et al.*, 2014). Overall, the socio-economic environment of the MeB individuals seems to have been more stable compared to that of the GRK individuals.

When the linkage between EH and certain mental disorders or deficiencies are taken into consideration, it is possible that the GRK population was subjected to greater amounts (or longer duration) of external stressors than the MeB population, while the MeB population could likely have been subjected to less external stressors, but was also influenced by internal stress due to their mental status. Nevertheless, the possibility remains that despite the accounts of socio-economic history, both populations were subjected to similar amounts or durations of external stress.

Despite the small and insignificant differences in FA between the populations, the indices revealed an interesting pattern. The MeB population exhibited greater magnitudes of asymmetry in the cranium, specifically the facial and vault regions, as well as in the upper limb midshaft dimensions, and the distal long bone elements (radius and tibia). The GRK population exhibited higher levels of asymmetry in the dentition (maxillary and mandibular dentition, permanent dentition), the mandible, the base of the cranium, the humerus and the long bone lengths (upper and lower).

If it is assumed that the two populations were subjected to the same amount of stress, the distribution of differences in FA magnitude of the traits between the populations can be explained by the differential buffering capacity of each trait to different stressors. Each individual's buffering or canalisation ability does not only differ in its response between traits, but also in its response to different types of stress factors for a specific trait (Møller and Swaddle, 1997; Wagner *et al.*, 1997). Whereas the MeB cranial vaults and facial regions, for

example, could have been more susceptible to the stressors causing EH (e.g., congenital syndromes and illnesses, nutritional deficiencies and fevers), the GRK cranial bases could have been more susceptible to the stressors that caused subperiosteal bone reactions (e.g., nutritional deficiencies, infections).

The facial and vault regions of the cranium, as well as the long bone lengths, are possibly the best indicators of developmental instability, while the cranial base and temporal region, as well as the dentition, are weak indicators of developmental instability (Section 5.2). The greater magnitudes of FA within the facial and vault regions of MeB may, therefore, be argued to carry more weight in terms of developmental instability than the cranial base and dentition, which were greater in magnitude within the GRK population. However, within the postcranial skeleton, the long bone lengths can also be argued to carry more weight in terms of developmental instability, and these exhibited greater asymmetry levels in the GRK sample. Therefore, the distribution of differences in FA magnitude of the supposedly better indicators of instability does not indicate that one sample is more developmentally unstable than the other. This corroborates the observed lack of a difference in the magnitude of FA between the two populations, also suggesting that both populations were under the same amount of stress.

In summary, it is suggested from the frequencies of pathological lesions and the socio-political history that the GRK population might have been subjected to more or worse external stressors than the MeB population, even if only slightly. If the enamel hypoplastic defects within the MeB population are assumed to be associated with congenital syndromes or mental illnesses, it can be concluded that although the MeB individuals were subjected to some level of environmental stressors (relatively less than the GRK population), they were also subjected to additional internal or genetic stressors associated with mental conditions. Therefore, as suggested by the observed patterns and similar magnitudes of FA, it seems that both populations were subjected to similar levels of stress, even though the source, timing or duration of stress might have been different.

5.7. Skeletal versus dental developmental stability

The magnitude of fluctuating asymmetry between the skeleton and dentition in the current study differed significantly, both when ages were pooled and for the adult skeleton against the permanent dentition. In both instances, the dentition exhibited higher levels of FA than the skeleton. The inferred greater developmental instability in the dentition as opposed

to the skeleton is contradictory to the literature, which states that the dentition is less sensitive to environmental and genetic stress and should therefore exhibit less FA. Dental development is thought to be less sensitive to developmental noise as it is under greater genetic control relative to the skeleton (Bogin, 1988; Cardoso, 2007).

One possible reason for the greater FA in the dentition is the amount of measurement error (ME) observed for both the intra- and inter-observer repeatability. Measurement error for the dentition was relatively high with 18 out of the 28 permanent dental traits displaying significantly higher ME relative to the between side difference due to FA. The amount of ME for the dentition was also slightly greater than the observed ME of the skeletal traits (refer to Section 4.4). It is reasonable to expect that objects or traits smaller in size will exhibit differences (FA values) that are also smaller in magnitude. Any ME will amplify the differences of FA values, and has the potential to produce inflated FA values, especially when the accuracy or repeatability of measurements are low (Greene, 1984; Palmer, 1994). Another possibility for the increased variance in size, or FA, within the dentition is the likelihood of increased dental wear and change of the shape of the jaws with increasing age, as discussed in Section 5.4. An additional factor that might have increased the amount of measurement error in the FA values of the dentition is the experience of the primary observer and/or the second observer in the measurement of the dental traits.

Within the current study, the repeatability of dental traits per side, assessed by means of the percentage technical error of measurement (%TEM), revealed no permanent dental measurements with a %TEM above the acceptable ranges (Perini *et al.*, 2005) for intra- or inter-observer measurements. Dental traits with a low repeatability (high %TEM) for the intra-observer traits included only five deciduous dental traits. The permanent dental traits are therefore repeatable, which possibly limited its inflationary effect on the magnitude of FA. This is supported by the observed patterns of dental FA magnitudes within the current study, which are in agreement with published studies (refer to Section 5.2.3). This further indicates that, although the FA values might have been inflated by ME, the ME was constant among the dentition and did not conceal the underlying buffering capacity of the dentition. While the possibility exists that the ME could have caused the fluctuating dental asymmetry values to be inflated beyond the observed FA magnitude in the skeleton, the repeatability and observed patterns within the dentition indicates that the observed FA was due to real differences between left and right sides.

No difference in FA magnitude was observed for the deciduous dentition against the subadult skeleton, although the deciduous dentition exhibited a higher mean and median FA.

Small subadult sample sizes might have contributed to this non-significant result (Nunnally, 1960; Guadagnoli and Velicer, 1988).

5.8. Statistical considerations

A study on FA should be meticulous in its removal of outliers in order to ensure that the population FA is not inflated by extreme individual values (Palmer and Strobeck, 1986; Palmer, 1994). However, as pointed out by Storm (2009), outlier values can provide meaningful information on the health status of individuals and populations being studied. Outliers removed in the current study involved 0.8% of the total measurements taken, of which female values constituted a slightly greater percentage than males. The findings of this study are in contrast to Storm's (2009) results where males exhibited a slightly greater percentage of the outlier values. However, this may be attributable to the skewed sex distribution of the two samples within the current study. Both samples are predominantly female, especially the MeB sample (refer to Table 4.1).

All skeletal elements included in this study, except the mandible, exhibited at least one outlier. The values identified as outliers per region of the skeleton were approximately equally represented between the populations. Both populations included outlier values for the cranium, the distal and proximal measurements of the proximal long bone elements, and the midshaft diameters of the long bones. All long bone outliers for GRK belonged to the lower limb while all except one long bone measurement for MeB belonged to the upper limb. Outliers in the dentition of both populations showed no tendency towards a specific crown diameter, tooth class or jaw.

While the type of measurement identified as an outlier is similar between the populations and the median FA values are identical at 15%, the average FA of the outlier values are not. Mean fluctuating asymmetry values within the GRK outliers (29%) were more than two times greater in magnitude than the MeB outliers (12%). The greater magnitude of FA in GRK correlates with findings that GRK might have been subjected to greater amounts of environmental stress due to the precarious state of the economy in the 18th to early 19th century. It could be argued that the exclusion of the outlier values from the between population analyses prevented the detection of a significant difference in the FA values. However, the average median asymmetry values for all the outliers combined (15%) was substantially greater than the median value per individual for the rest of the sample (2.4%) and greater than the greatest median asymmetry value per index (temporal region of the

cranium in MeB, 6%). Although the outlier values provided additional information on the health status of the populations, the immense difference in the average median asymmetry of the outlier values corroborates the claim that outlier values might confound estimates of FA.

5.9. The osteological paradox

The osteological paradox (Wood *et al.*, 1992) states that all archaeological samples are biassed in the sense that the individuals in the sample under study are, in fact, those who died or did not survive. That is to say, those who survived a certain risk of death at each age are not represented in the sample (at that age).

Applied to the current study of FA, it can be argued that the observed levels of FA in these samples are elevated against what would have been the FA of the entire population of Alkmaar or Meerenberg. An increased magnitude of FA in a population has previously been associated with decreased fitness (Clarke, 1995). Therefore, it can be implied that the individuals in these samples with a higher magnitude of FA, and a lower level of fitness, would have had an increased risk of dying – increasing the average magnitude of FA within the skeletal sample above that of the entire population.

Additionally, because FA has been shown to increase with increasing adult age, it can be argued that the observed FA for middle and mature adults are due to more than just developmental instabilities, but are also the result of unequal 'wear and tear' of left and right elements or traits due to lifestyle, attrition and habitual preference for a side (refer to Section 5.4). The imposed underlying developmental stability (or canalisation ability) of these older individuals would therefore be more stable than suggested by the observed FA of the sample.

Besides the problem of the living being represented by the dead, a skeletal sample is also subjected to hidden heterogeneity. This refers to the differential frailty of the individuals within the sample or population, which is unknown to the researcher (Wood *et al.*, 1992; DeWitte and Stojanowski, 2015). This is especially important in the interpretation of skeletal and dental markers of stress. Pathological lesions on bone are more likely markers of chronic stress. Therefore, individuals who suffered from acute stress, or those who succumbed from the disease or illness before any lesions could develop, would not have any skeletal signs of stress. Similarly, individuals who experienced no stress would also not present with a skeletal lesion. Lesions are therefore more likely to form on individuals who experienced moderate amounts of chronic stress, or in 'strong' populations who were able to resist the cause of stress long enough for the lesions to develop. The frequency of pathological lesions within a

sample is therefore not necessarily an accurate estimation of stress within a population, and might be underrepresented in the sample due to the possibility of no lesions on individuals who succumbed to certain stressors or diseases (Wood *et al.*, 1992). Similarly, FA related to a mental illness or deficiency could also be underrepresented or lower in the MeB skeletal sample due to the inclusion of individuals who might have developed a mental illness (such as depression) later in life. The depression, for example, would not necessarily have been due to a developmental instability, but could be a response to a certain life event.

Additionally, the higher magnitude of FA within the individuals who presented with one of the three markers of stress (relative to the individuals who did not present with any of the three lesions) in the current study could also have been related to the chronic stress itself (refer to Section 5.5). That is to say, increased energy was needed for these individuals to survive the chronic stress/illness during development, and therefore less energy was available for the maintenance of homeostasis, resulting in increased asymmetry (Møller and Swaddle, 1997).

DeWitte and Stojanowski (2015) reviewed the impact of each of the components of the osteological paradox within the literature in the past 20 years, and emphasised the need to incorporate the effect of the social and political structures on health disparities into bioarchaeological and anthropological studies. They suggested that this approach might shed some light on how the disparities of heterogeneous frailty arise, and what the consequences of these disparities are, as all aspects of heterogeneous frailty cannot be explained by the study of only the differential health between populations in terms of the frequencies of pathological lesions and differences in status. Fluctuating asymmetry, in combination with the socio-political history of the populations, might therefore be a possible way to detect this hidden frailty or susceptibility to diseases and stress factors within a sample, even though it might not represent the frailty of the entire (living) population.

5.10. Limitations of this study

A study on the minute differences between bilateral anatomical structures is bound to have several limitations, one of which is measurement error and repeatability of the measurements. The repeatability of several measurements within this study was low and the measurement error for asymmetry high, especially for the dental traits. The high ME for the dentition has been discussed in Section 5.7. However, in measures of small differences, such as in studies of FA, ME cannot be excluded, but only minimised (Greene, 1984). Overall

repeatability and accuracy of all measurements might be improved if the entire sample included in the study can be measured at least twice and the average value used for comparisons (Palmer, 1994; Palmer and Strobeck, 2003). One possible way to ensure a greater accuracy and repeatability of dental measurements is to use finer instruments to measure the crown diameters, such as a needle-point dial calliper.

A lack of time and funding is another factor that hampered the current study. For this reason, the principal investigator could not remeasure any outlier values or reassess skeletons or traits with high magnitudes of FA. Also, due to time constraints, it was not possible to collect measurements from all the available individuals from the GRK population. Additionally, because of the lack of an available individual with experience in osteological measurements, it was not possible to conduct interobserver measurements on the GRK and MeB populations. Therefore, the principal investigator was obliged to conduct the interobserver repeatability on another skeletal collection housed at the University of Pretoria, the Pretoria Bone Collection. Although it can be argued that the use of a different population for the interobserver repeatability influenced the results of the current study, the purpose of the repeatability test was to assess the ability of the primary investigator to correctly and accurately measure bones and teeth. The interobserver repeatability, therefore, is more a test of the methodology than it is a test of developmental instability. Except for the removal of a few traits with high measurement error from the analysis of FA, the data and results from the interobserver repeatability do not affect the observed magnitude of FA within the Dutch populations.

A further aspect that should not be overlooked is the limitation of working with archaeological remains. Archaeological remains are usually incomplete and fragmentary (which was also the case in the current study), limiting the amount of information that could be gained from the sample.

Another limitation was the lack of available data on the individuals from Meerenberg. The only known information about the MeB individuals is that they were buried in a graveyard believed to have been part of an old Catholic cemetery of the psychiatric hospital Meerenberg, in the Netherlands. No information regarding the identity or health status of the specific individuals was available, not to mention the type and duration of their mental condition. Because of these factors, the MeB sample was possibly not entirely representative of a “mentally ill” population. Firstly, according to historical information, both patients and employees or caretakers (such as nurses) were buried in the cemeteries. Secondly, not all patients housed at the Meerenberg psychiatric hospital were buried in the MeB cemeteries.

Some patients were collected and buried by their families. (Van Twuyver, 2000). Therefore, the individuals included in the MeB collection might not all have suffered from a mental condition. Additionally, skulls that presented with abnormal shapes or features were gathered by the physicians and curated in various pathology collections (Vijselaar, 1982). These skulls were not buried in the cemeteries and are also not available for analysis. Information on the health status or mental illness of the individuals would have provided a better background against which to assess and compare the magnitude of FA.

The different periods of time during which the GRK and MeB individuals lived could be seen as another limitation, although the difference in socio-political and environmental history also provided useful information in terms of the magnitude of FA and the frequencies of pathological lesions. The GRK individuals lived during the 18th to the early 19th century, while the MeB population was slightly later, from the early 19th to the early 20th century. From the socio-political history alone, it was clear that the individuals were exposed to different external influences. It is possible that the differences due to varying levels of stress during the different time periods could have limited the ability of FA to detect any differences in developmental stability and the effect of mental illness on the magnitude of FA. A comparison between the MeB population and a general population who lived during the same time period might have different results than the current study.

Lastly, the individual effect of each one of the three pathological lesions on the magnitude of FA was not part of the current study (refer to Section 5.5), but this could possibly provide further information in future on the lack of significant differences between the FA levels of the populations despite the difference in lesion frequencies. However, fluctuating asymmetry does not necessarily distinguish between the type of stress during development, partly due to the differential susceptibility or buffering ability of a population (Palmer and Strobeck, 1986; Wagner *et al.*, 1997).

5.11. Future Research

Research possibilities for utilising FA as an indicator of developmental instability are endless. Fluctuating asymmetry provides a means by which to measure and compare the genetic and environmental stressors within and between populations (Van Valen, 1962; Palmer, 1994; DeLeon, 2007; Storm, 2007). However, the results of the current study question the reliability of the sole use of external factors for an explanation of the developmental stability between populations (as observed by the magnitudes of FA), for

which the genetic environment is not controlled. Studies on FA generally focus on the external environmental stressors, such as the economic hardship, the availability of adequate nutrition, and the observed frequency of pathological lesions as an explanation or cause for the observed magnitude of stress between populations. However, as indicated in this study, internal or genetic stresses also contribute to the observed levels of stress. While the GRK population was subjected to greater amounts of environmental stress, as evidenced by the higher frequency of pathological lesions and their socio-political history, the MeB individuals were likely also subjected to additional internal stressors associated with mental illness. Hence the similar levels of FA between the two populations. This supports the need to incorporate genetics and epigenetics (DeWitte and Stojanowski, 2015) for an estimation of internal developmental stressors, in additional to external stressors, in future studies of developmental instability.

Another possible avenue for future studies is to compare the FA levels of MeB, or another sample of known mentally ill individuals, to an archaeological skeletal sample dated to the same time period. If possible, such as comparative sample should be of Dutch origin. In this manner, both the population and environmental effects on the magnitude of FA would be controlled for.

As shown in this study, individuals who showed signs of one of the three skeletal/ dental indicators of stress expressed greater magnitudes of FA than the individuals without any markers of stress. It was also evident that the populations differed in the frequency of observed lesions between each other, and in the frequencies of a specific skeletal lesion within a population - a possible indication of the differential sensitivity of populations to environmental stress and/or to a specific type of stress. However, the consideration of these pathological lesions within the current study was general and incomplete. Future research on how each of these pathological lesions, and perhaps other skeletal indicators of stress, is associated with the magnitude of FA, may provide valuable information as to their association with developmental homeostasis. Furthermore, future research on the socio-political and environmental history of populations, especially during development, might also be able to clarify the reliability of the use of FA as an indicator of developmental stability within skeletal material.

The current study raised concerns regarding the accumulation of FA after adulthood has been reached, due to differential ‘wear and tear’ on the left and right elements or traits as a result of lifestyle, attrition and habitual preference for the use of one side over the other (mechanical influences). It is uncertain whether later asymmetry (at an older age) contributes

anything to the knowledge of stress within a population. The inclusion of older individuals within a study of developmental stability might even increase the average magnitude of FA, increasing the inferred developmental instability of a population to a higher magnitude than it is in reality. While the notion to exclude older adults (> 34 years of age) from future studies on developmental stability might not be unreasonable, the exclusion of these older individuals in samples of an archaeological nature is not always feasible due to limited sample sizes. Nonetheless, more information is needed to address and clarify the effects of 'wear and tear' with increasing age on the magnitude of FA.

Conclusion

The main purpose of the current study was to assess the developmental stability of the presumably mentally ill Meerenberg population against that of the general Grote Kerk population by means of comparing the levels of FA. Results from this study indicated no real difference in the developmental instability, as reflected by FA, between the two populations. Based on the frequency of pathological lesions and historical socio-economic information, the GRK population likely experienced elevated environmental stressors relative to the MeB population. The MeB population seemed to have been subjected to less external or environmental stress, and presented with lower frequencies of pathological lesions relative to the GRK population. However, because EH is also associated with certain congenital and heritable syndromes that also cause mental deficiencies, it can be implied that this marker of stress (EH) can also be an indicator of internal or genetic stress. Fluctuating asymmetry is a non-specific indicator of stress, and therefore the average FA in a population does not distinguish between the type of stress, whether environmental or genetic (Palmer, 1994; Møller and Swaddle, 1997).

The current study also highlights the possibility that, as suggested by previous studies (e.g., Black, 1980; Bjorksten *et al.*, 2000), FA is not a highly sensitive indicator of developmental stress. Mentally ill individuals have previously been shown to be more developmentally unstable, and would therefore exhibit greater magnitudes of asymmetry relative to mentally healthy individuals (Malina and Buschang, 1984; Markow and Wandler, 1986; Reilly *et al.*, 2001; Thoma *et al.*, 2002). Due to their mental status, the MeB population was expected to be more developmentally unstable than the GRK population, and was therefore expected to exhibit increased levels of FA regardless of the similar levels of stress. However, this is not what was observed in the current study. Consequently, it could also be considered that the MeB psychiatric hospital sample was not as developmentally unstable as

suggested by previous research, or that FA is not such a highly sensitive indicator of developmental stress as indicated in the literature (Livshits and Kobyliansky, 1991; DeLeon, 2007; Storm, 2007, 2008; Hoover and Matsumura, 2008). Additionally, it must be noted that the lack of available information on the two populations, especially on the MeB population, does not allow for much deliberation on the developmental stability of the two populations. Consequently, it could also be considered that the MeB psychiatric sample was not as mentally deficient or developmentally unstable as initially suggested.

Further conclusions and observed trends regarding FA between and within the two populations, as well as of the other objectives of the study, such as the level of FA between the dentition and the skeleton, are summarised in Chapter 6.

Chapter 6: Conclusion

This study aimed to assess the fluctuating asymmetry (FA) levels between and within two archaeological Dutch populations, namely the Grote Kerk (GRK) and the Meerenberg (MeB) populations. Bilateral osteometric and odontometric measurements were collected from the cranium, mandible, humerus, radius, femur, tibia and dentition (except third molars) of both samples. The bilateral measurements were utilised to calculate FA values, from which several comparisons were made between and within the two populations. Dental and skeletal stress markers were observed and noted for all individuals. The frequency of these lesions was compared between the populations and was utilised for several comparisons in terms of FA magnitude.

The main conclusions from this study are as follows:

- The average median asymmetry was 2.4% per adult individual and 2.3% per subadult individual. The most informative traits in terms of FA were in the long bone lengths and facial and vault regions of the cranium. The least informative traits in terms of FA were the temporal region and base of the cranium, as well as the majority of dental traits (especially the mandibular dentition). The traits were considered to be more or less informative based on the amount of measurement error (ME), range (standard deviation) and magnitude of average FA, as suggested by Storm (2009). Traits with the least amount of ME, smallest range and smallest magnitude of average FA were considered the most informative, while those with the highest amount of ME, widest range and greatest magnitude of FA were considered the least informative.
- Fluctuating asymmetry varied across traits and indices, although patterns within the skeleton and dentition were discernible. For the cranium, the cranial base was the most asymmetric and the facial area the least asymmetric. Traits of the vault and orbital regions ranged from low to high in terms of FA magnitude, with no clear pattern relative to the cranial base or face.
- Within the mandible and long bones, the lengths exhibited the least FA, while the breadths (of the ramus and at midshaft) exhibited the most asymmetry. The distal element of each limb is more asymmetrical than the proximal element. The observed greater magnitude of FA within the upper limb, as opposed to the lower

limb, is likely due to a greater need for symmetry in locomotion and gait in the lower limbs. Upper limb bones are likely to exhibit high magnitudes of directional asymmetry (DA) in addition to FA. The upper limbs are possibly more susceptible to differential mechanical forces, which may have played a role in their high levels of asymmetry.

- FA magnitudes increased from mesial to distal within a tooth class and correlated with a greater variability in the development and eruption of the later formed teeth. This suggests that crown formation is more stable for the first tooth in each morphogenic class. Within each tooth class, the mesiodistal crown diameters were more asymmetric than the buccolingual crown diameters. Outside of the tooth class, no pattern in FA magnitude was discernible between the dentition or between the jaws.
- Fluctuating asymmetry levels, and therefore also developmental instability, did not differ between males and females.
- No statistically significant differences in FA magnitude of the skeleton and dentition existed between adult and subadults, although skeletal FA was slightly higher in adults. With the exclusion of the small (in sample size) young adult age category, the majority of traits increased in FA magnitude from middle to mature adult age, although not significantly. This increase with increasing age is most likely due to mechanical ‘wear and tear’ with increasing age, rather than due to increased developmental stability or stress.
- Subperiosteal bone reactions, enamel hypoplasia (EH) and cribra orbitalia/porotic hyperostosis occurred more frequently in the GRK population, although not significantly more frequent than in the MeB population. Similarly, the FA levels of the individuals with at least one of the three markers of stress indicated no difference in magnitude between the two populations.
- Evidence supporting the use of FA as an indicator of developmental instability and its positive relationship to indicators of stress was observed in the comparison of the magnitude of FA between individuals exhibiting a pathological lesion and the rest of the sample. Individuals with at least one of the three pathological lesions were more asymmetrical than individuals without any of the three skeletal lesions.

- No significant difference in FA magnitude existed between the general GRK population and the MeB psychiatric hospital population, although the mean FA was slightly higher in MeB. This corresponds to the abovementioned conclusion that the two populations were subjected to similar levels of stress. However, it is suggested that the GRK population was subjected to more external stressors relative to the MeB population (based on socio-economic history), while the MeB population might also have been subjected to internal or genetic stress (due to their mental illness and the association of EH with congenital syndromes and illnesses).
- The magnitude of fluctuating asymmetry was greater in the permanent dentition than in the adult skeleton, although the dental asymmetry values were possibly inflated by higher levels of measurement error. No difference in FA magnitude was found between the deciduous dentition and the subadult skeleton. Small subadult sample sizes might have contributed to this non-significant result.
- Burial practices may have biased the sample of the MeB population.
- The incorporation of genetics and epigenetics as estimators of the internal or genetic stressors is needed in future studies of developmental stability in addition to external indicators of stress. This will provide a better indication of all stressors that may affect the developmental stability of a population. Another avenue for future research is to compare the MeB population to an archaeological skeletal sample dated to the same time period to control the population and environmental effects, in order to focus on the influence of mental illness on developmental stability. Other possibilities for future studies include research on the effect of increasing age, and the association of specific lesions of stress (each lesion separately) on the magnitude of FA.
- The current study also portrays the possibility that FA is not a highly sensitive indicator of developmental stress. Mentally ill or deficient individuals have been associated with increased developmental instability relative to mentally healthy individuals, and would therefore exhibit greater magnitudes of FA. Because the amount of stress was concluded to have been similar between the two populations, the MeB population was expected to exhibit higher levels of FA than the GRK population, which was not the case in the current study.

- The lack of available information on the two populations, especially on the MeB population, does not allow for much deliberation on the developmental stability of the two populations. Consequently, it could also be considered that the MeB psychiatric sample was not as mentally deficient or developmentally unstable as initially suggested.

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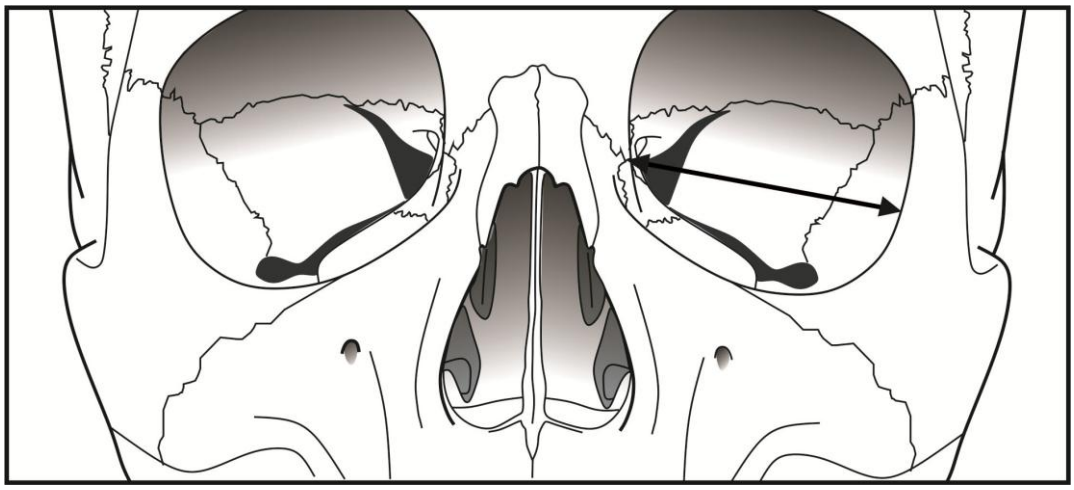
Appendix 1: Measurement guidelines

Cranial measurements*

A 1.1. Orbital breadth (COBB)

The maximum distance from dacryon (d) to ectoconchion (ec), measured parallel to the superior orbital border, on the internal margins of the orbit

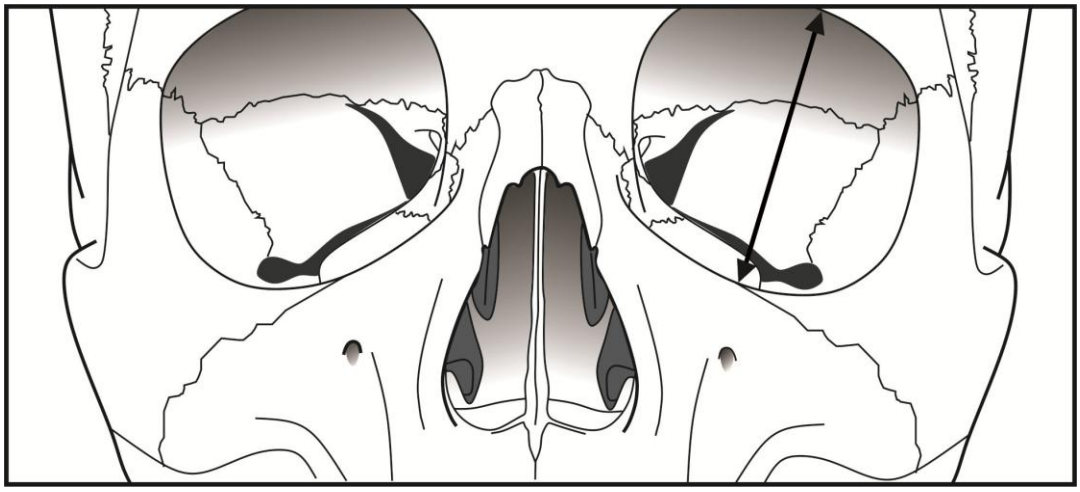
– *Sliding callipers; Adult*



A 1.2. Orbital height (COBH)

The direct distance between the superior and inferior orbital borders, perpendicular to orbital breadth

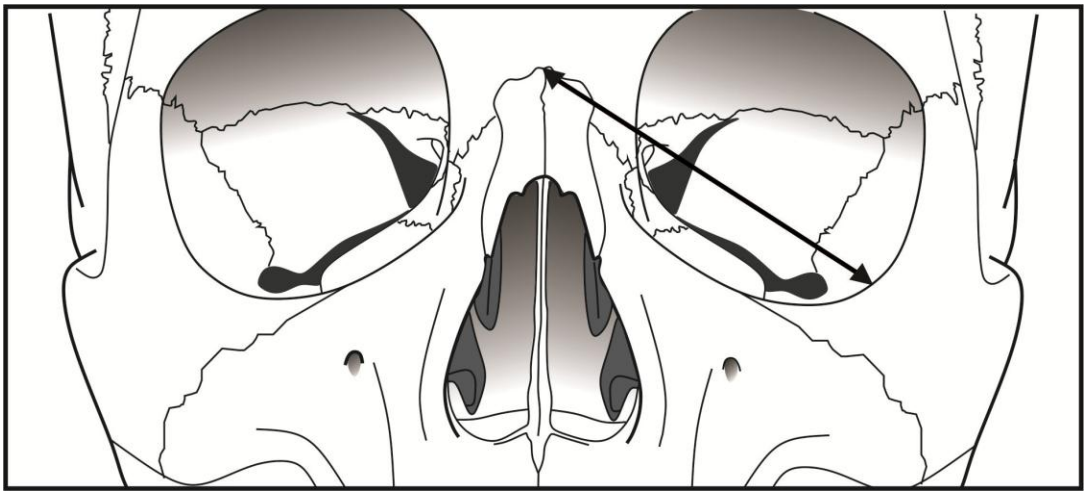
– *Sliding callipers; Adult*



A 1.3. Diagonal orbital breadth (CNOR)

The direct distance from nasion (n) to orbitale (or)

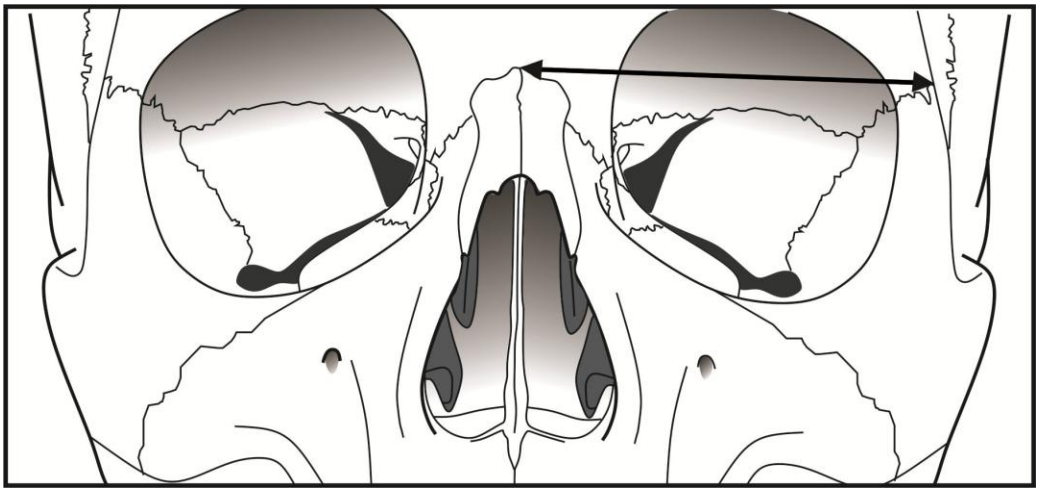
– *Sliding callipers; Adult*



A 1.4. Frontomalare-nasion length (CFMTN)

The direct distance from frontomalare (fmt) to nasion (n)

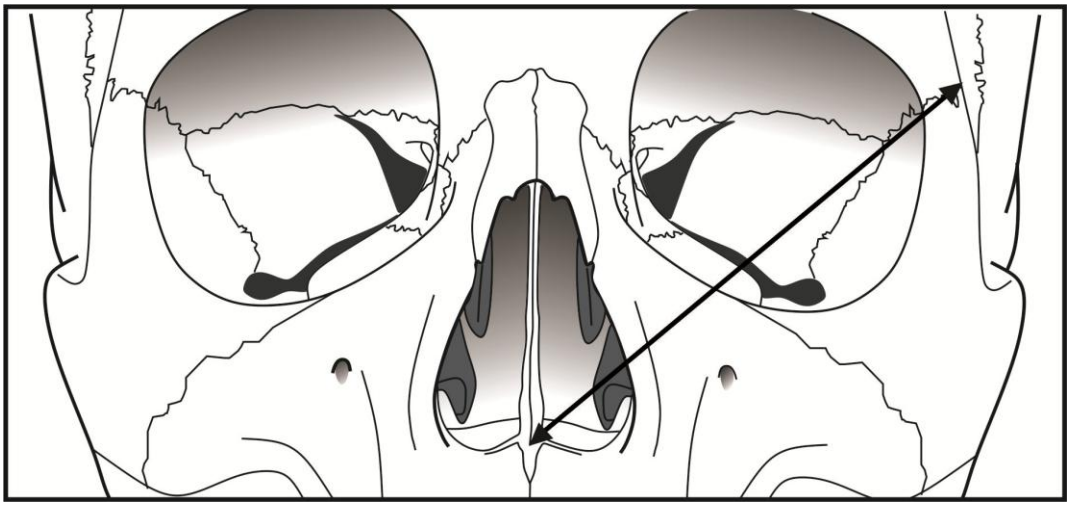
– *Sliding callipers; Foetus to Mature Adult*



A 1.5. Frontomalare-nasospinale length (CFMTNS)

The direct distance from frontomalare (fmt) to nasospinale (ns)

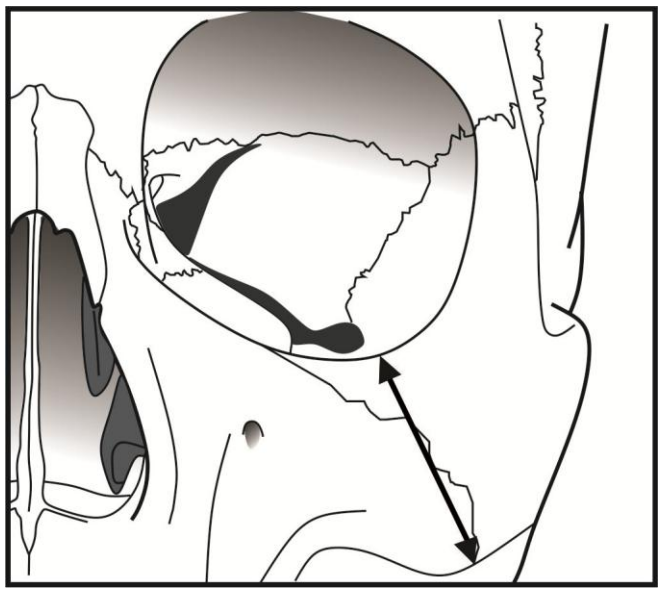
– *Sliding callipers; Adult*



A 1.6. Malar height (CMAH) / cheek height

The least distance from the most inferior point on the lower margin of the orbit to the most superior point on the inferior border of the zygomatic

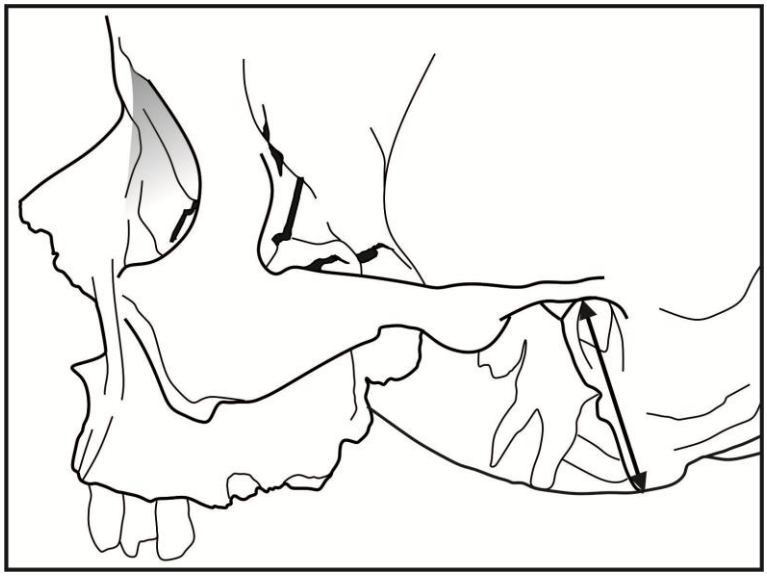
– *Sliding callipers; Foetus to Mature Adult*



A 1.7. Length of mastoid process (CMPL)

The direct distance from porion (po) to mastoidale (ms)

– *Sliding callipers; Early Childhood to Mature Adult*

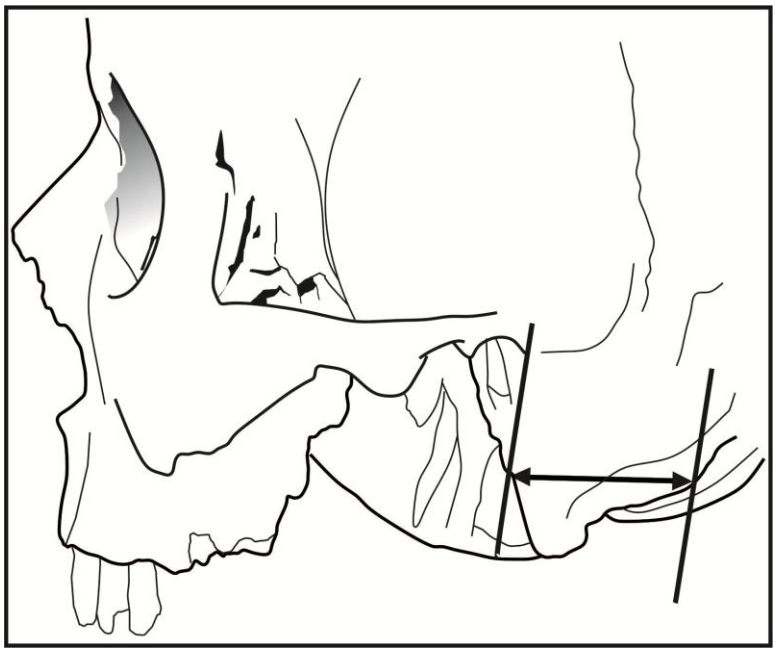


A 1.8. Breadth of mastoid process (CMPB)

The distance from the posterior margin of the external auditory meatus to the most anterior point along the posterior border of the mastoid process

With the cranium in the Frankfort plane, the callipers should be parallel to the external auditory meatus and perpendicular to the Frankfort plane

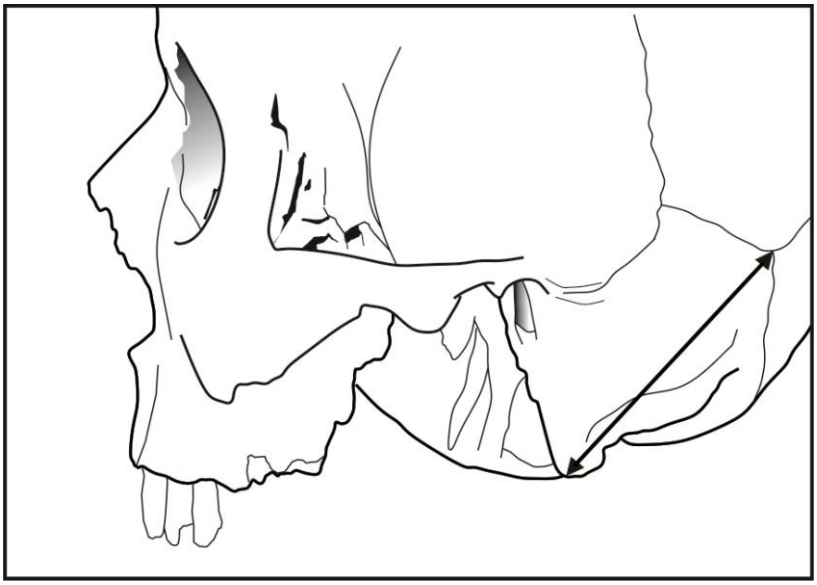
– *Sliding callipers; Early Childhood to Mature Adult*



A 1.9. Mastoidale-asterion length (CMSAST)

The direct distance from mastoidale (ms) to asterion (ast)

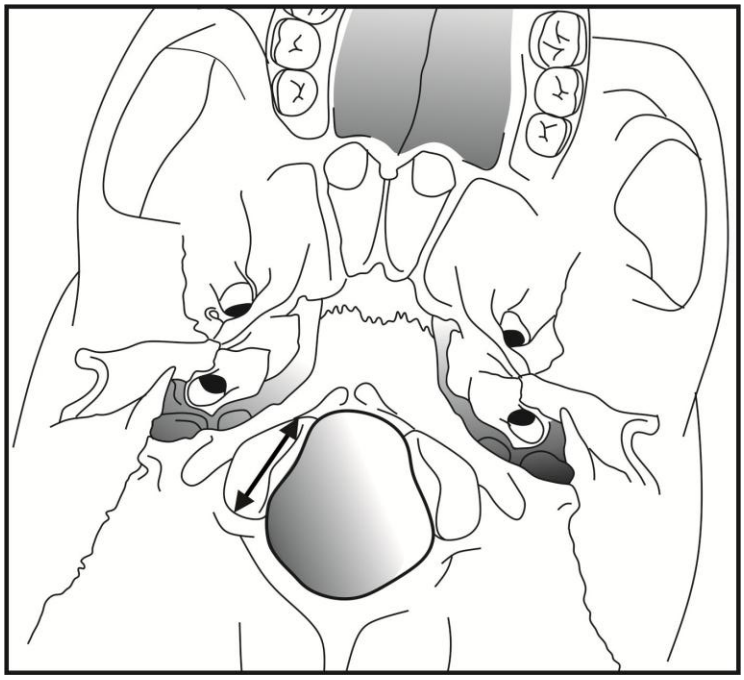
– *Sliding callipers; Early Childhood to Mature Adult*



A 1.10. Occipital condyle length (COCL)

The maximum distance between the most anterior to the most posterior points on the occipital condyles

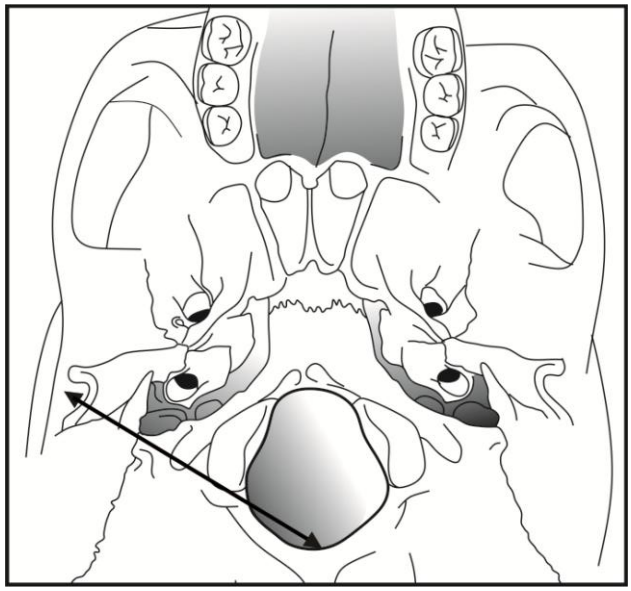
– *Sliding callipers; Foetus to Mature Adult*



A 1.11. Opisthion-porion length (COPO)

The direct distance from opisthion (o) to porion (po)

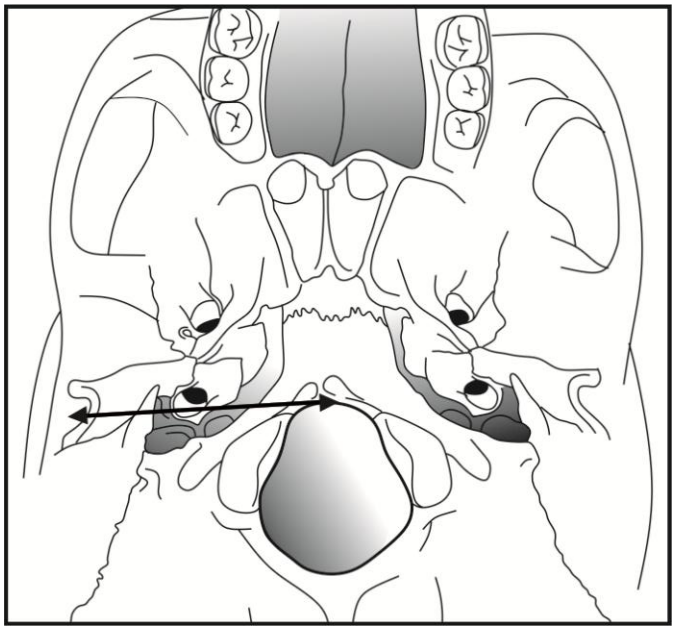
– *Sliding callipers; Adult*



A 1.12. Basion-porion length (CBAPO)

The direct distance from basion (ba) to porion (po)

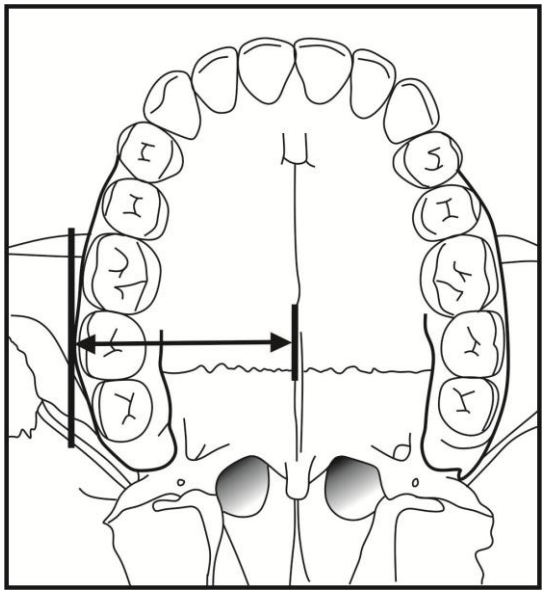
– *Sliding callipers; Adult*



A 1.13. Ectomalare-intermaxillary suture length (CECMIS)

The direct distance from ectomalare (ecm) to the intermaxillary suture, with the cranium in the Frankfort plane and the callipers in the transverse plane

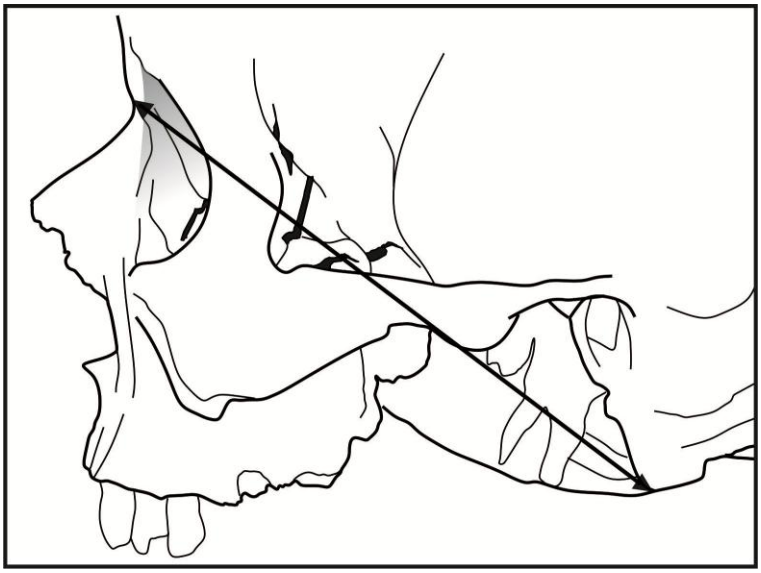
– *Sliding callipers; Early Childhood to Mature Adult*



A 1.14. Nasion-mastoidale length (CNMS)

The direct distance from nasion (n) to mastoidale (ms)

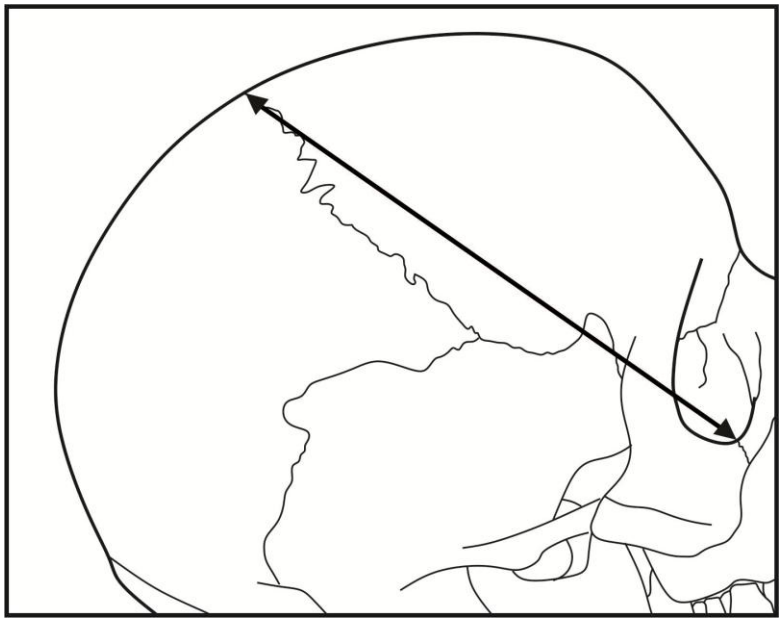
– *Spreading callipers; Adult*



A 1.15. Bregma-zygoorbitale length (CBZO)

The direct distance from bregma (b) to zygoorbitale (zo)

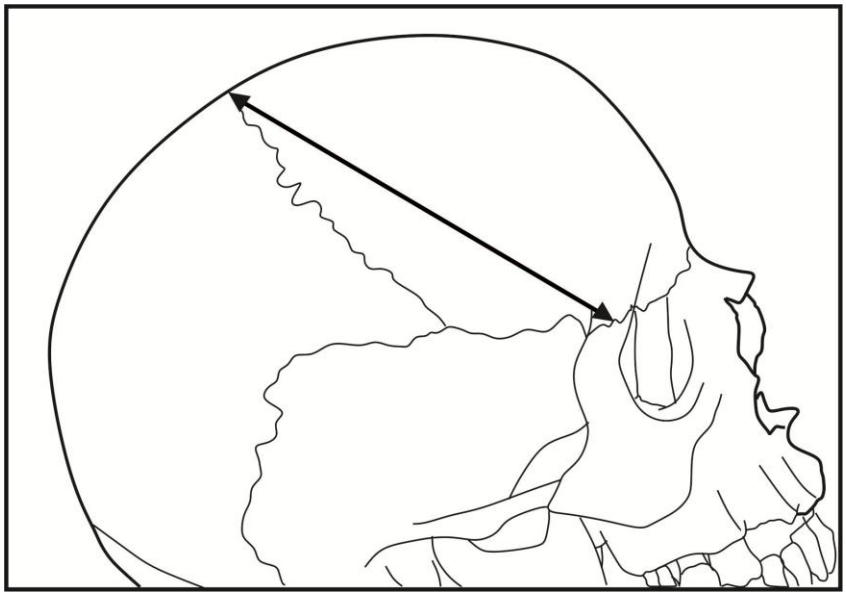
– *Spreading callipers; Adult*



A 1.16. Frontomalare-bregma length (CFMTB)

The direct distance from frontomalare (fmt) to bregma (b)

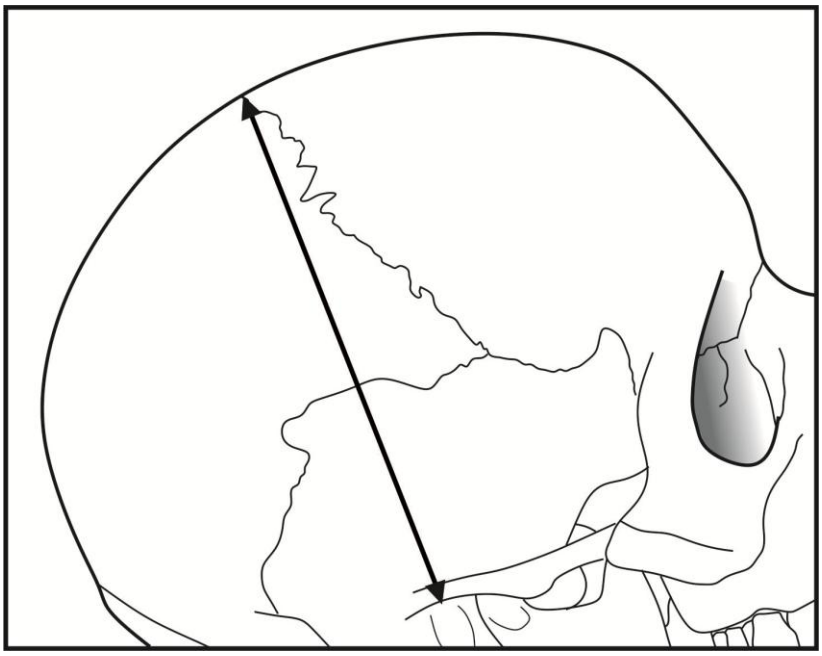
– *Spreading callipers; Adult*



A 1.17. Bregma-porion length (CBPO)

The direct distance from bregma (b) to porion (po)

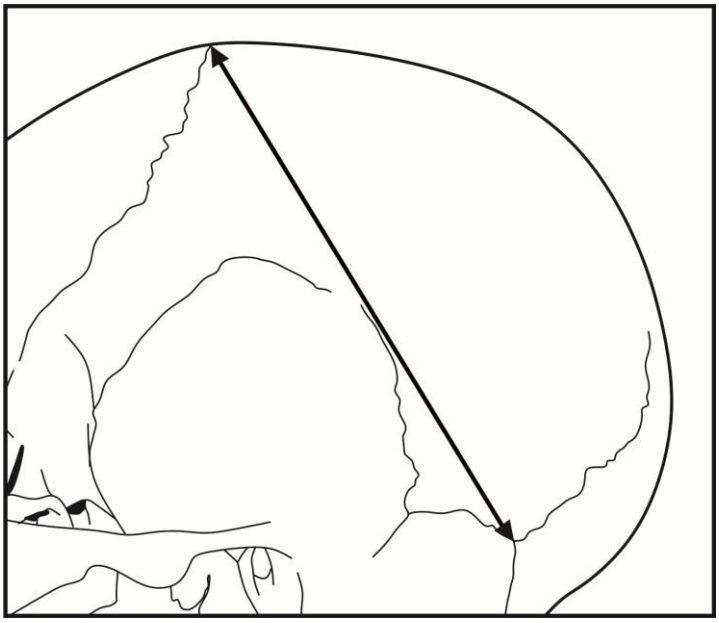
– *Spreading callipers; Adult*



A 1.18. Bregma-asterion length (CBAST)

The direct distance from bregma (b) to asterion (ast)

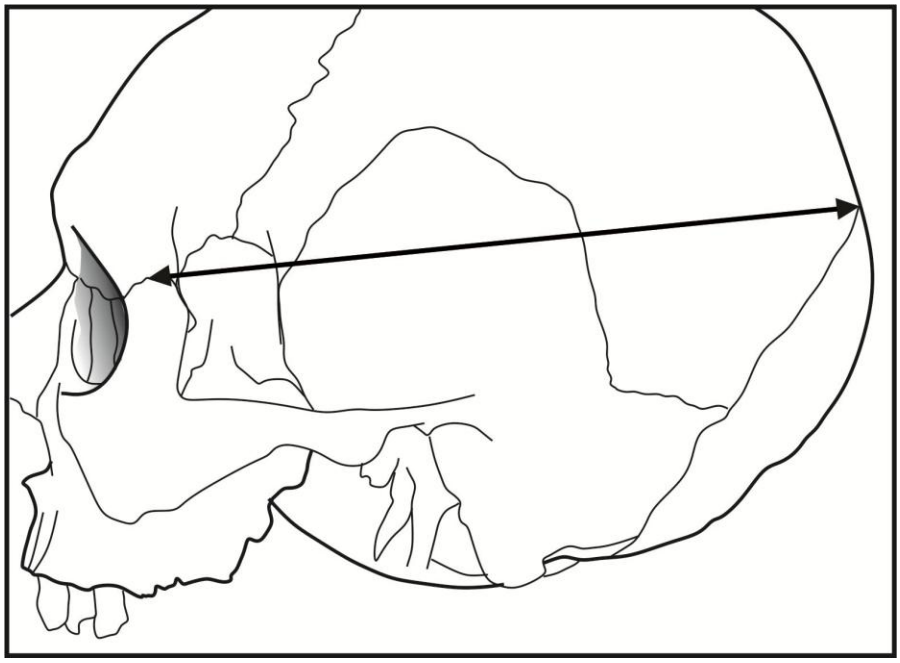
– *Spreading callipers; Adult*



A 1.19. Lambda-frontomalare length (CLFMT)

The direct distance from lambda (l) to fromtomalare (fmt)

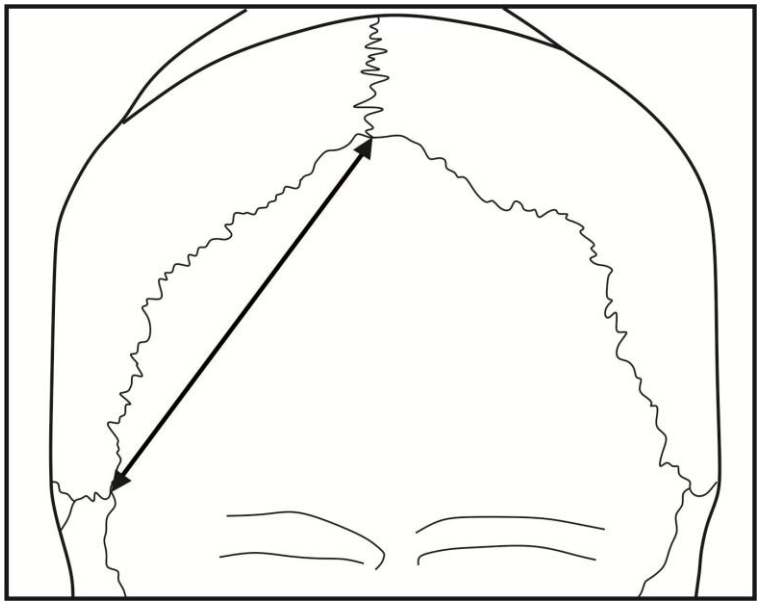
– *Spreading callipers; Adult*



A 1.20. Lambda-asterion length (CLAST)

The direct distance from lambda (l) to asterion (ast)

– *Sliding callipers; Adult*

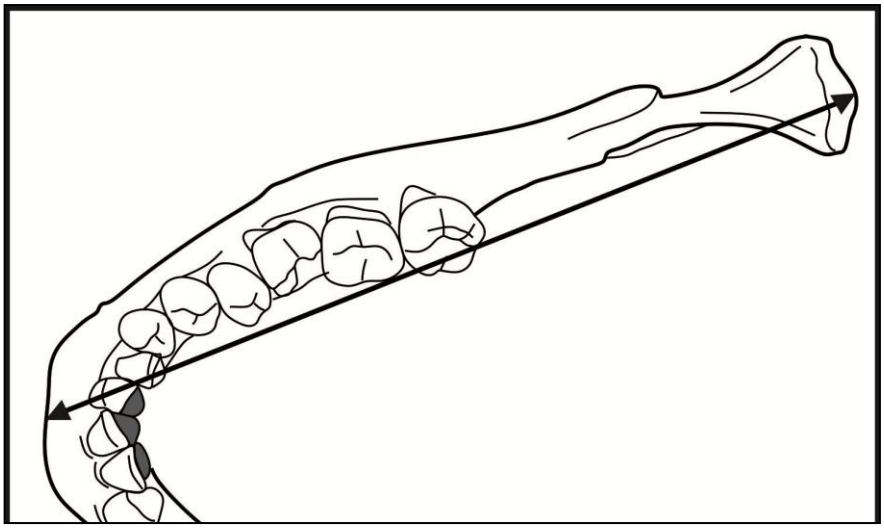


Mandibular measurements*

A 1.21. Mandibular length (MAL)

The direct distance from coronion (cr) to gnathion (gn)

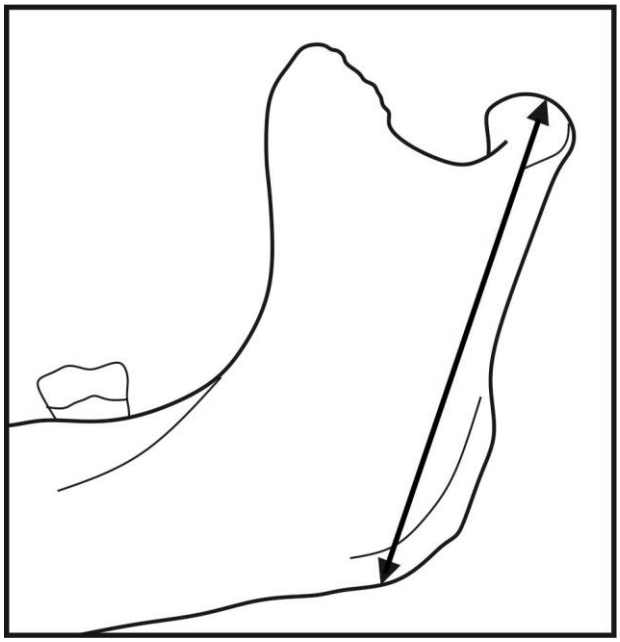
– *Sliding callipers; Foetus to Mature Adult*



A 1.22. Maximum ramus height (MRH)

The direct distance from coronion (cr) to gonion (go)

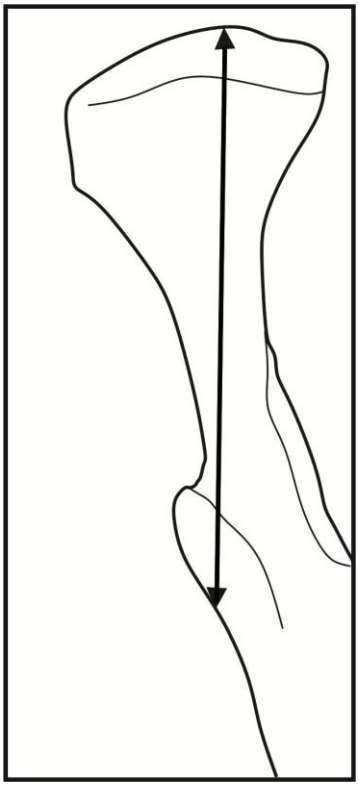
– *Sliding callipers; Foetus to Mature Adult*



A 1.23. Maximum ramus breadth (MXRB)

The maximum distance from the anterior point on the ascending ramus at the coronoid process to the most posterior point on the condyle

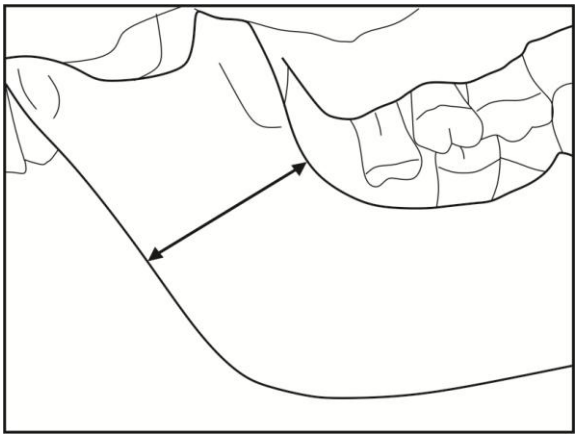
– *Sliding callipers; Foetus to Mature Adult*



A 1.24. Minimum ramus breadth (MIRB)

The least distance from the anterior to the posterior margin of the ascending ramus measured perpendicular to the height of the ramus

– *Sliding callipers; Foetus to Mature Adult*



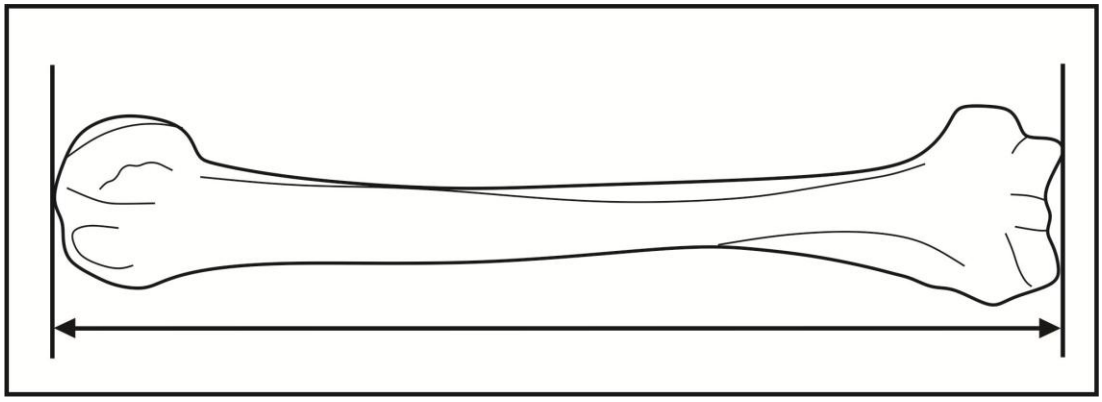
Humeral measurements*

A 1.25. Maximum length of the humerus (HML)

The distance from the most proximal to the most distal point on the humerus

Place the humerus' long axis parallel to the osteometric board and move it up, down and sideways to determine the maximum measurement. For subadults, do not include unfused epiphyses

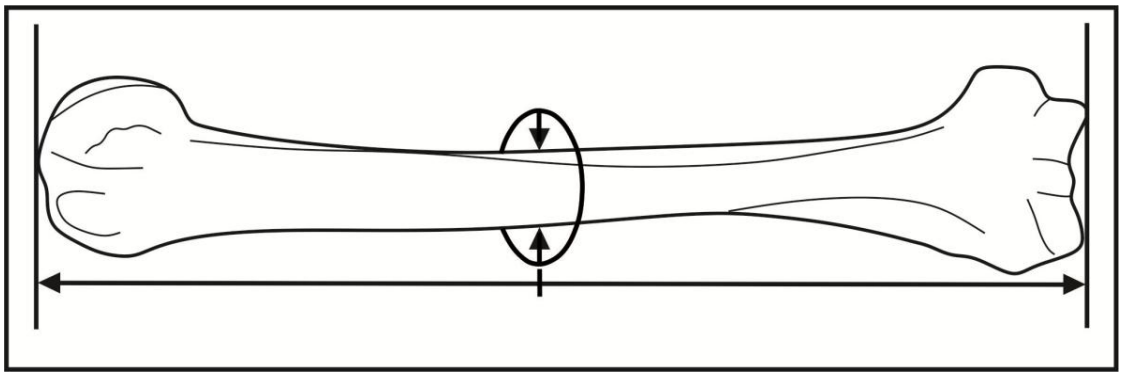
– *Osteometric board (Early Childhood to Mature Adult) OR sliding callipers (Foetus to Infant); Foetus to Mature Adult*



A 1.26. Maximum humeral diameter at midshaft (HXMS)

Determine the midpoint of the shaft (osteometric board) and turn the bone until the maximum midshaft diameter is obtained

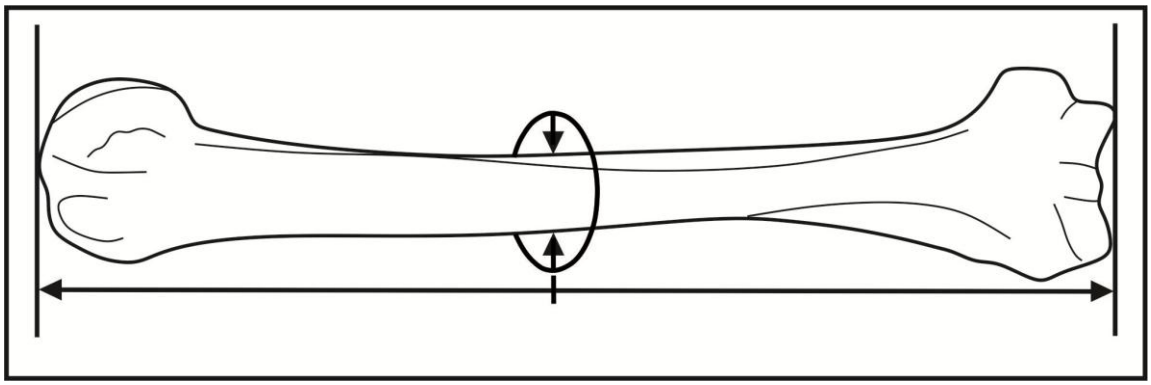
– *Sliding callipers; Foetus to Mature Adult*



A 1.27. Minimum humeral diameter at midshaft (HIMS)

Determine the midpoint of the shaft (osteometric board) and turn the bone until the minimum midshaft diameter is obtained

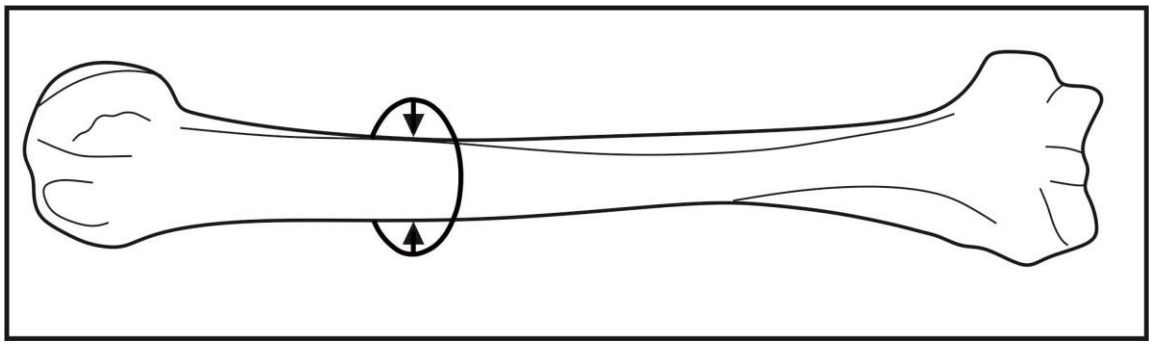
– *Sliding callipers; Foetus to Mature Adult*



A 1.28. Maximum humeral diameter at deltoid tuberosity (HDT)

Move the callipers up and down the area of the deltoid tuberosity while turning the bone to determine the maximum diameter

– *Sliding callipers; Early Childhood to Mature Adult*

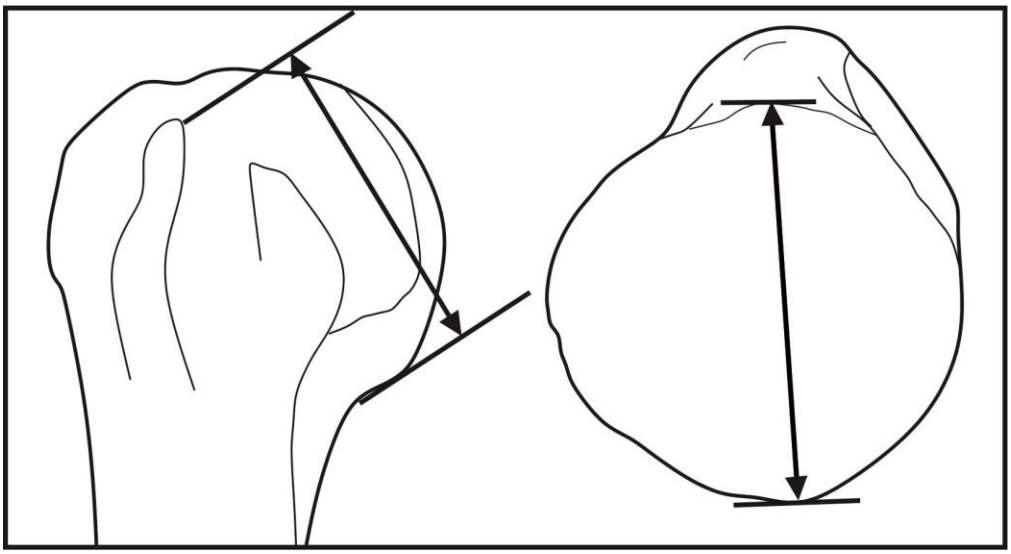


A 1.29. Superoinferior diameter of the humeral head (HSIH)

The maximum distance from the superior to the inferior surface of the humeral head

In unfused subadults, this is an epiphyseal measurement

– *Sliding callipers; Early Childhood to Mature Adult*

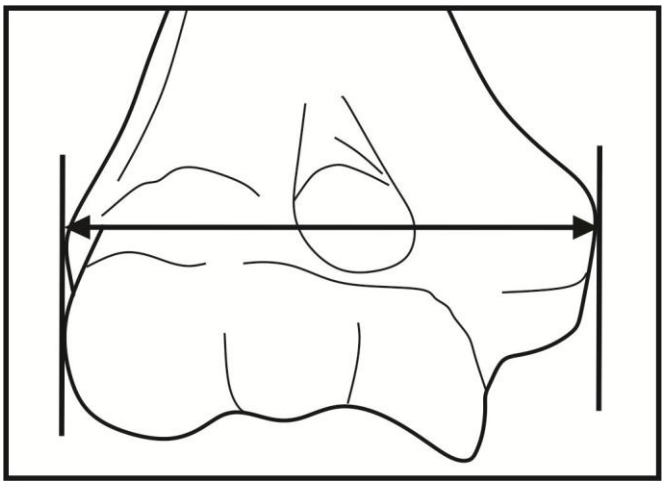


A 1.30. Epicondylar breadth of the humerus (HEB)

The distance from the most medial to the most lateral points of the epicondyle

In unfused subadults, this is an epiphyseal measurement

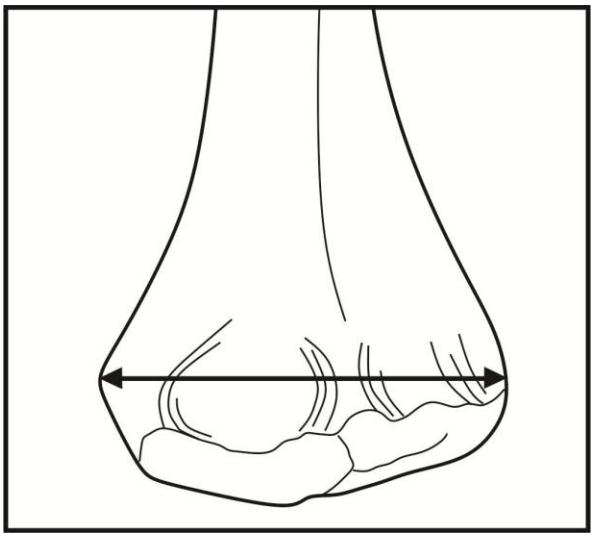
– *Sliding callipers; Adult*



A 1.31. Maximum subadult distal mediolateral width of the humerus (HSMLD)

The distance from the most medial to the most lateral point on the distal end of the humerus. This is a metaphyseal measurement.

– *Sliding callipers; Foetus to Unfused Adolescence*

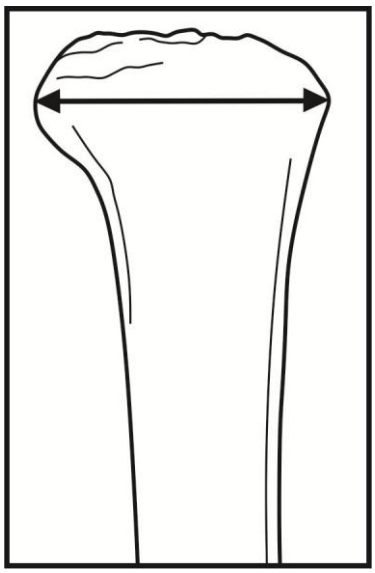


A 1.32. Maximum subadult proximal mediolateral width of the humerus (HSMLP)

The distance from the most medial to the most lateral point of the unfused proximal end of the humerus

This is a metaphyseal measurement.

– *Sliding callipers; Foetus to Unfused Adolescence*

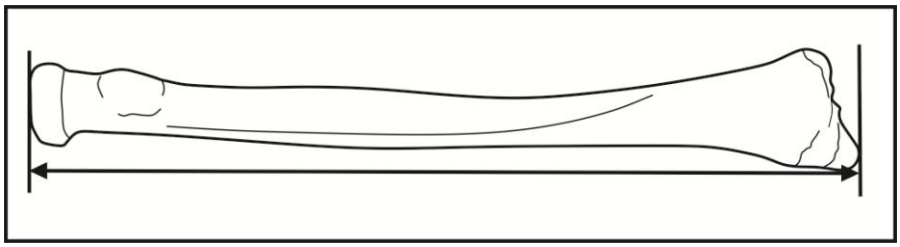


Radial measurements*

A 1.33. Maximum length of the radius (RML)

The distance from the most proximally positioned point on the head of the radius to the tip of the styloid process without regard for the long axis of the bone. Move the bone up, down and sideways to determine the maximum measurement. For subadults, do not include unfused epiphyses

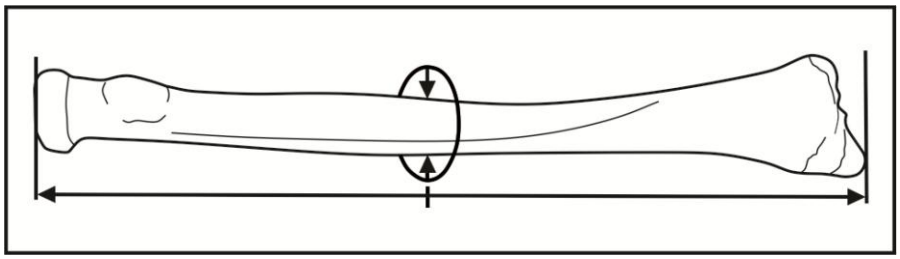
– *Osteometric board (Early Childhood to Mature Adult) OR Sliding callipers (Foetus to Infant); Foetus to Mature Adult*



A 1.34. Maximum midshaft diameter of the radius (RXMS)

Determine the midpoint of the shaft (osteometric board) and turn the bone until the maximum midshaft diameter is obtained

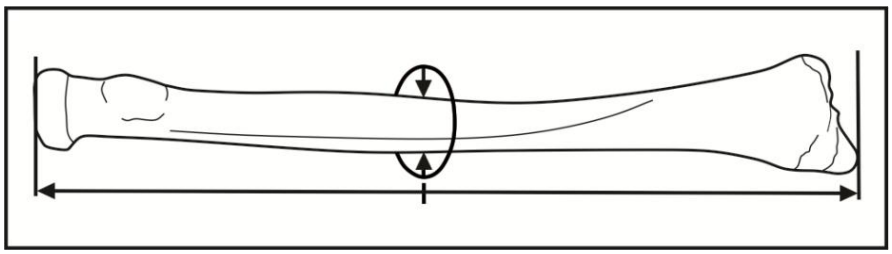
– *Sliding callipers; Foetus to Mature Adult*



A 1.35. Minimum midshaft diameter of the radius (RIMS)

Determine the midpoint of the shaft (osteometric board) and turn the bone until the minimum midshaft diameter is obtained

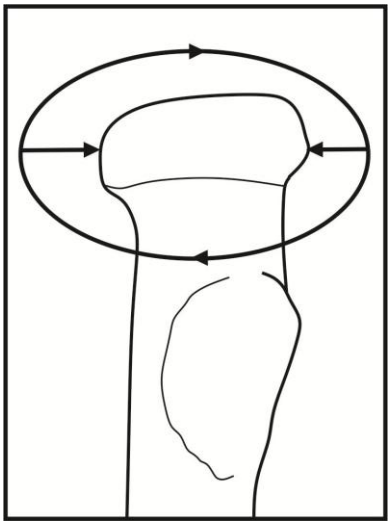
– *Sliding callipers; Foetus to Mature Adult*



A 1.36. Maximum diameter of the radial head (RGH)

Encircle the head or proximal epiphysis with the callipers until the maximum diameter is obtained

– *Sliding callipers; Early Childhood to Mature Adult*

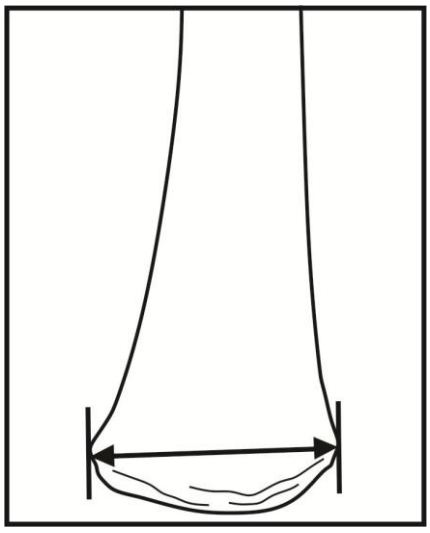


A 1.37. Subadult distal end mediolateral width of the radius (RSMLD)

The distance from the most medial to the most lateral point of the distal end

This is a metaphyseal measurement

- *Sliding callipers; Foetus to unfused Adolescence*

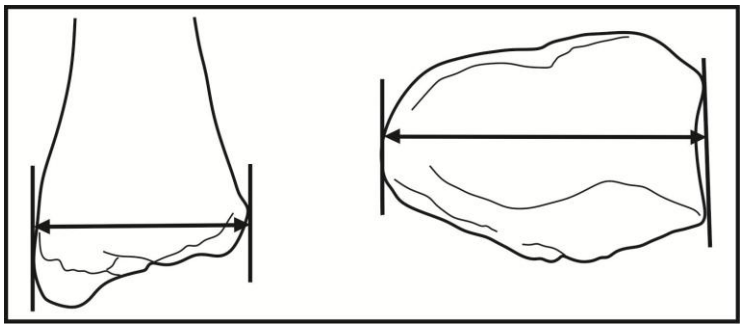


A 1.38. Distal end/epiphysis mediolateral width (RMLD)

The distance from the most medial to the most lateral point of the distal end or the unfused epiphyses

In subadults, this is an epiphyseal measurement.

– *Sliding callipers; Foetus to Mature Adult*

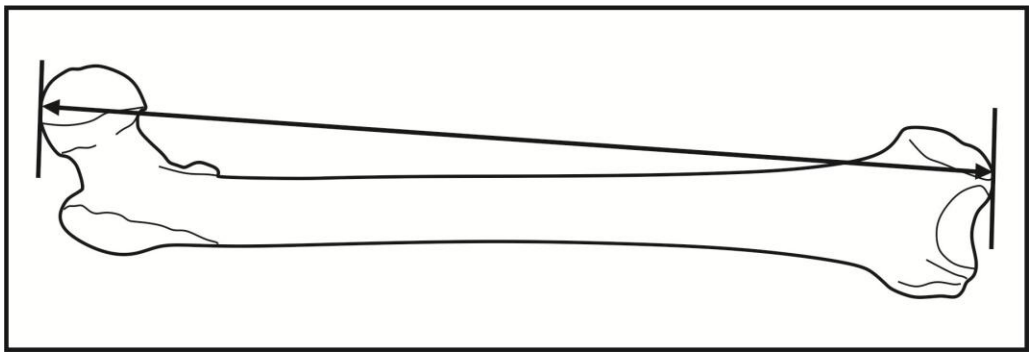


Femoral measurements*

A 1.39. Maximum length of the femur (FML)

The distance from the most proximal point on the head of the femur to the most distal point on the condyles. Place the femur parallel to the long axis of the osteometric board and resting on its posterior surface. move the bone up, down and sideways to determine the maximum measurement. For subadults, do not include unfused epiphyses

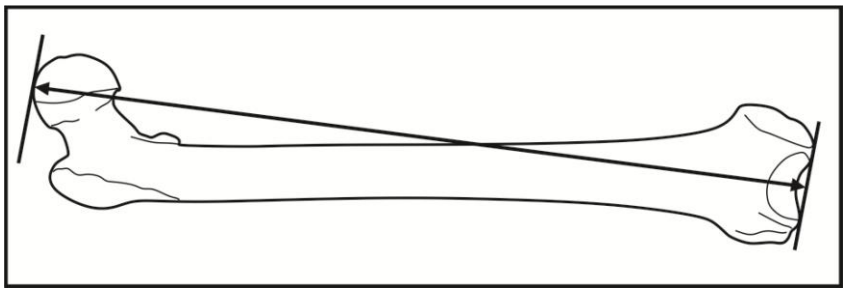
– *Osteometric board (Early Childhood to Mature Adult) OR Sliding callipers (Foetus to Infant); Foetus to Mature Adult*



A 1.40. Physiological length of the femur (FPL)

The distance from the most superior point on the head of the femur to a plane along the inferior surfaces of the distal condyles. Place the femur with its posterior surface resting on the osteometric board. For subadults, do not include unfused epiphyses

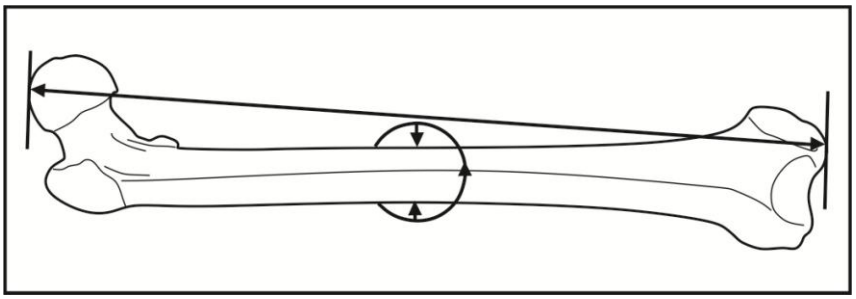
– *Osteometric board Osteometric board (Early Childhood to Mature Adult) OR Sliding callipers (Foetus to Infant); Foetus to Mature Adult*



A 1.41. Maximum midshaft diameter of the femur (FXMS)

Determine the midpoint of the shaft (osteometric board) and turn the bone until the maximum midshaft diameter is obtained

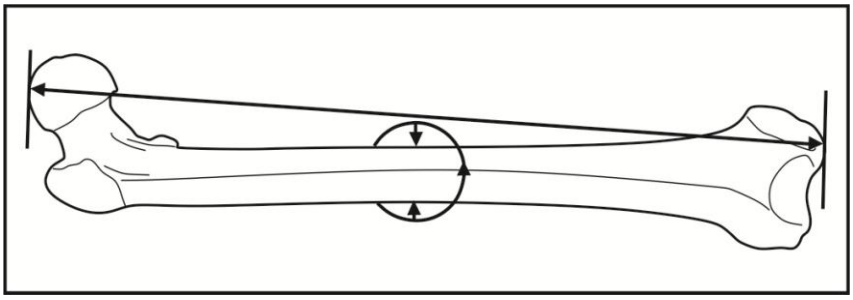
– *Sliding callipers; Foetus to Mature Adult*



A 1.42. Minimum midshaft diameter of the femur (FIMS)

Determine the midpoint of the shaft (osteometric board) and turn the bone until the minimum midshaft diameter is obtained

– *Sliding callipers; Foetus to Mature Adult*

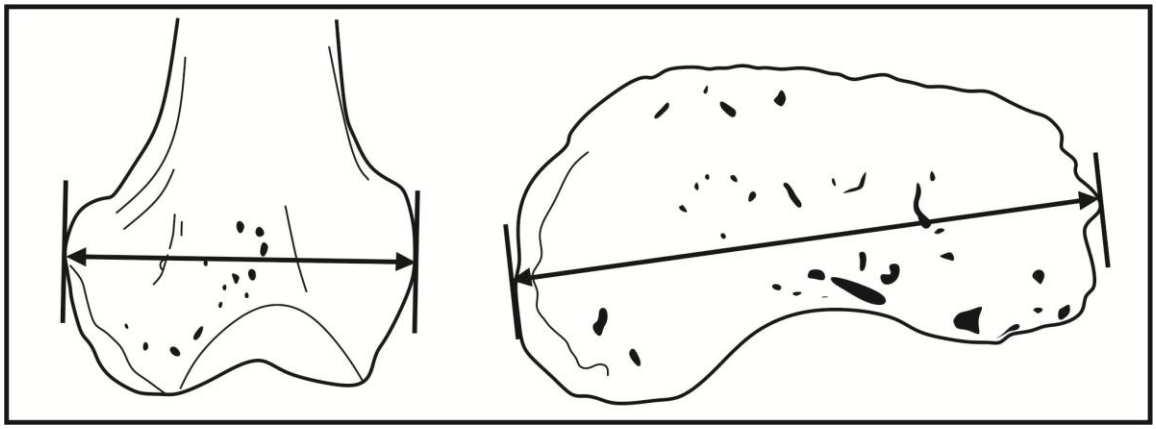


A 1.43. Epicondylar breadth of the femur (FEB)

The distance between the two most laterally projecting points on the epicondyles. Place the femur on the osteometric board so that it is resting on its posterior surface. Press one of the epicondyles against the vertical endboard while applying the movable upright to the other condyle. The measurement is parallel to the distal surfaces of the condyles

In unfused subadults, this is the maximum breadth of the distal epiphysis and should be taken with sliding callipers

– *Osteometric board (Adult) OR Sliding callipers (Subadults); Foetus to Mature Adult*

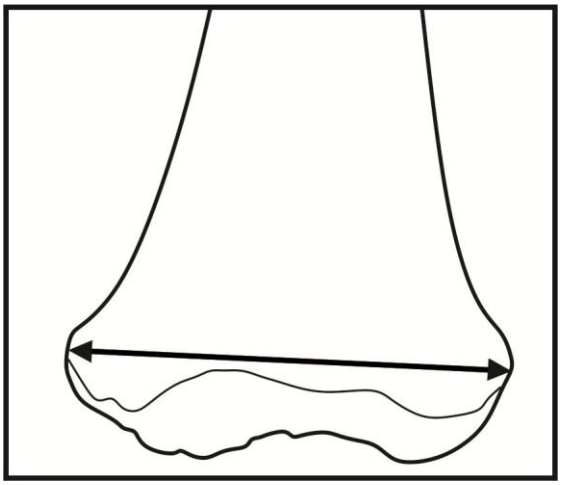


A 1.44. Subadult distal end mediolateral width of the femur (FSMLD)

The distance from the most medial to the most lateral point on the distal end

This is a metaphyseal measurement.

- *Sliding callipers; Foetus to unfused Adolescence*

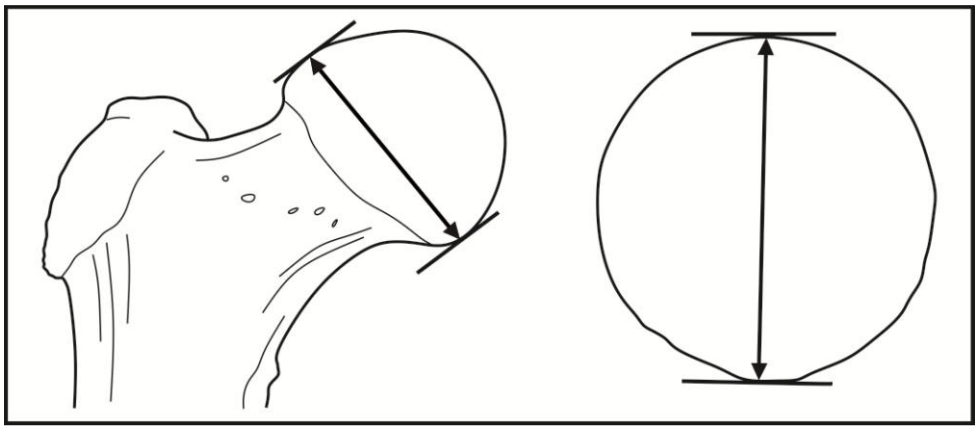


A 1.45. Maximum superoinferior femoral diameter of the femoral head (FSIH)

The maximum distance from the superior to the inferior surface of the femoral head

In subadults, this is an epiphyseal measurement

– *Sliding callipers; Early Childhood to Mature Adult*

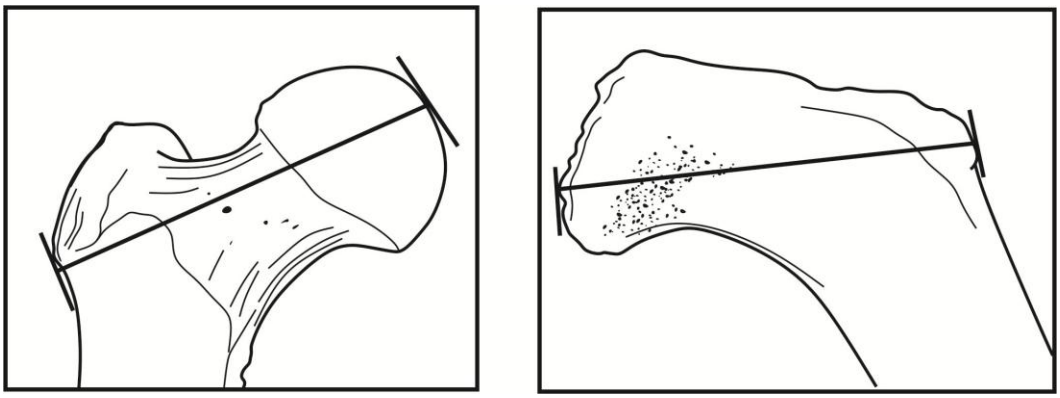


A 1.46. Maximum proximal end with of the femur (FMLP)

The distance from the most medial point on the femoral head to the most lateral point on the greater trochanter

In subadults, this measurement does not include the head

– *Sliding callipers; Foetus to Mature Adult*



Tibial measurements*

A 1.47. Maximum length of the tibia (TML)

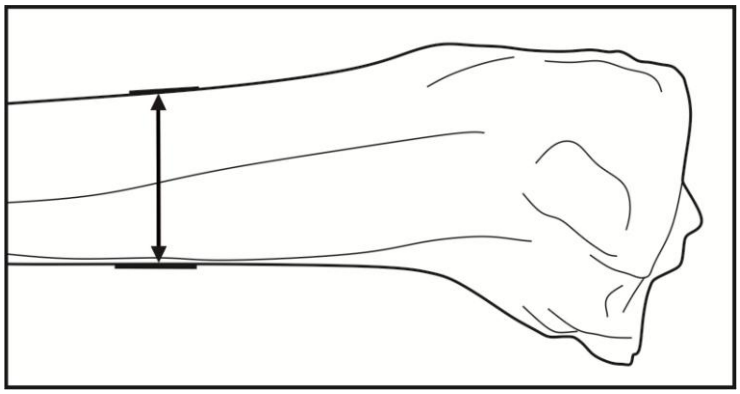
The distance from the superior articular surface of the lateral condyle to the tip of the medial malleolus. Measured with the longitudinal axis parallel to the osteometric board and the tibia resting on its posterior surface. Place the lip of the medial malleolus on the vertical endboard and press the movable upright against the proximal articular surface of the lateral condyle
For subadults, do not include unfused epiphyses

– *Osteometric board Osteometric board (Early Childhood to Mature Adult) OR Sliding callipers (Foetus to Infant); Foetus to Mature Adult*

A 1.48. Maximum diameter at the nutrient foramen of the tibial shaft (TXNF)

Find the nutrient foramen on the proximal shaft and turn the bone to determine the maximum diameter

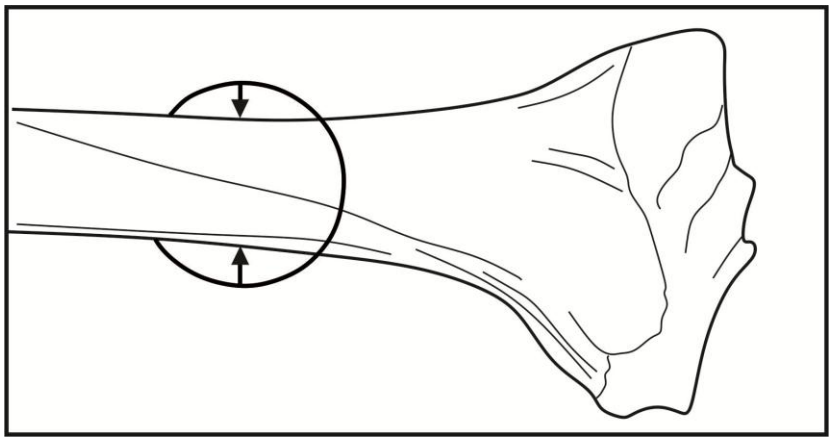
– *Sliding callipers; Foetus to Mature Adult*



A 1.49. Minimum diameter at the nutrient foramen of the tibial shaft (TINF)

Find the nutrient foramen on the proximal shaft and turn the bone to determine the minimum diameter

– *Sliding callipers; Foetus to Mature Adult*

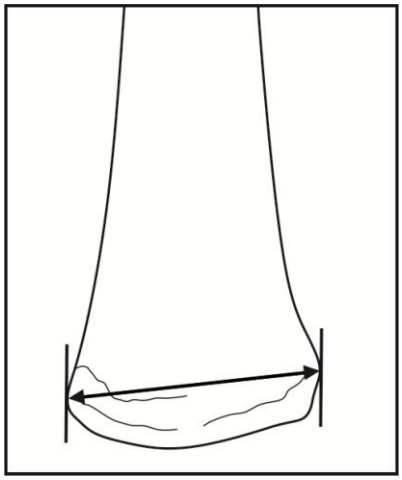


A 1.50. Subadult Maximum Distal End Mediolateral Breadth of the Tibial shaft (TSMLD)

The distance from the most medial to the most lateral point of the unfused distal end

This is a metaphyseal measurement.

- *Sliding callipers; Early Childhood to unfused adolescence*

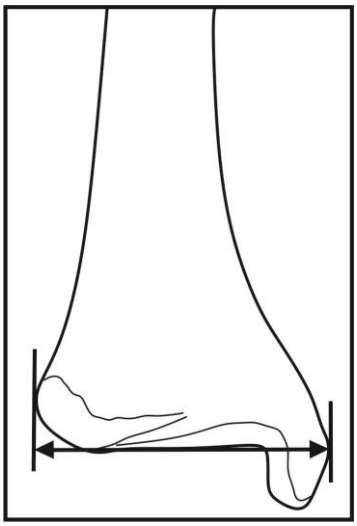


A 1.51. Maximum distal end mediolateral breadth of the tibial shaft (TMLD)

The distance from the most medial to the most lateral point on the distal end

In unfused subadults, this is an epiphyseal measurement

– *Osteometric board (Adults) OR Sliding callipers (Subadults); Foetus to Mature Adult*

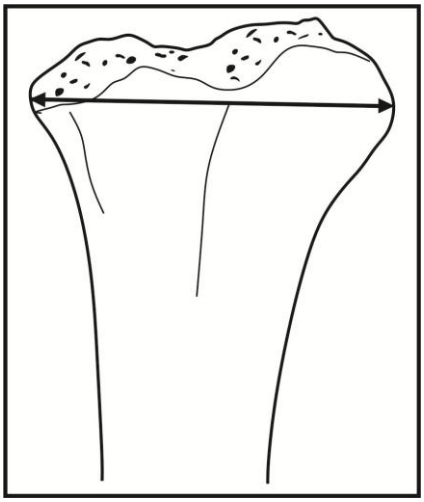


A 1.52. Subadult maximum proximal end mediolateral breadth of the tibial shaft (TSMLP)

The distance from the most medial to the most lateral point of the unfused proximal end

This is a metaphyseal measurement

- *Sliding callipers; Early Childhood to unfused Adolescence*

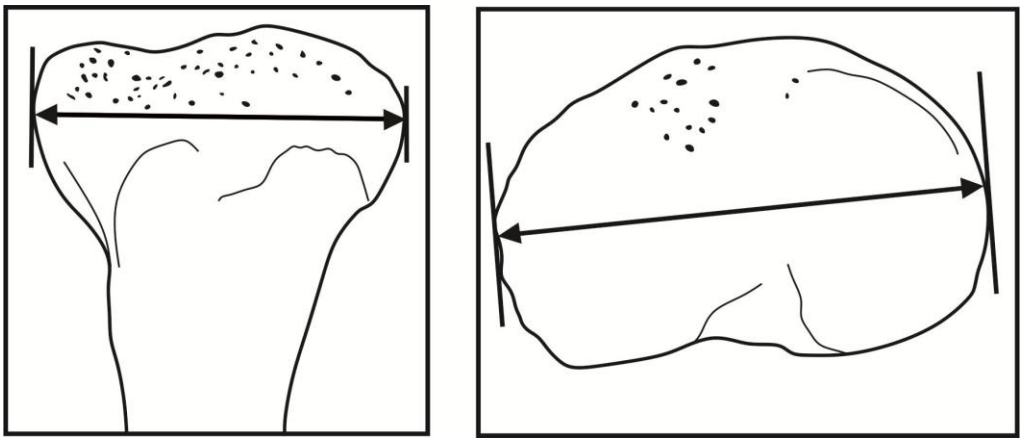


A 1.53. Maximum proximal end mediolateral breadth of the tibial shaft (TMLP)

The distance from the most medial to the most lateral point on the proximal end

In unfused subadults, this is an epiphyseal measurement

– *Osteometric board (Adults) OR Sliding callipers (Subadults); Foetus to Mature Adult*

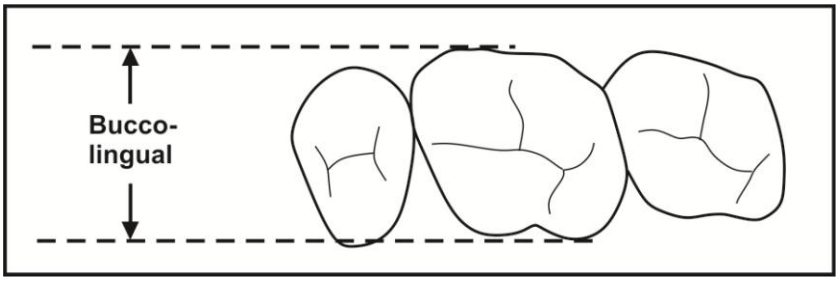


Dental Measurements**

A 1.54. Maximum buccolingual diameter (BL)

The maximum distance between the buccal and lingual surfaces of a tooth, measured perpendicular to the mesio-distal axis

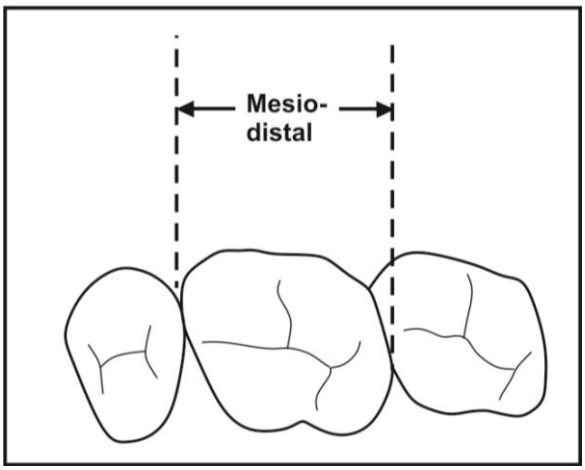
– *Sliding callipers; Early Childhood to Mature Adult*



A 1.55. Maximum mesiodistal diameter (MD)

The maximum distance between the mesial and distal surfaces of a tooth, measured parallel to the occlusal and labial surfaces

– *Sliding callipers; Early Childhood to Mature Adult*



*All skeletal images were modified from Storm (2009)

**All dental images were modified from Kieser (1990)

Appendix 2: Outlier values

Table A2.1. Raw (right - left) and FA8 outliers for both populations, indicating the critical value and p-value for the Grubb's outlier test for FA8 values

Population	Spoor nr	Vonds nr	Trait	Sex	Age	Raw (R-L)	FA8	T_G	p-value
Skeleton									
GRK	NA	510	COCL	F	MA	-7.72	0.34	4.441	< 0.001
GRK	NA	359	COCL	M	MDA	-7.36	0.32	4.468	< 0.001
GRK	NA	942	COCL	F	MA	6.88	0.32	4.468	< 0.001
GRK	NA	493	COPO	F	MDA	9.46	0.15	4.566	< 0.001**
GRK	NA	358	CLAST	M	MA	-13.25	0.13	4.099	0.0019
GRK	NA	826	CLAST	M	MA	-11.14	0.13	4.099	0.0019
GRK	NA	93	FEB	M	MA	-5.00	0.06	4.112	< 0.001**
GRK	NA	562	FSIH	M	MA	4.25	0.08	4.376	< 0.001**
GRK	NA	3	FSIH	F	YA	4.08	0.11	4.980	< 0.001**
GRK	NA	68	TXNF	F	A	9.52	0.37	7.978	< 0.001**
GRK	NA	68	TINF	F	A	-6.27	0.25	5.568	< 0.001**
MeB	1077	370	COBH	F	MDA	3.60	0.11	4.170	< 0.001**
MeB	57	221J	COCL	F	A	5.92	0.26	4.574	< 0.001**
MeB	1039	69	HXMS	F	MDA	3.93	0.20	4.648	< 0.001**
MeB	2031	150	HSIH	F	MDA	5.30	0.14	5.187	< 0.001**
MeB	1039	69	HEB	F	MDA	5.39	0.10	3.729	< 0.001**
MeB	101	199C	RIMS	I	A	1.75	0.16	3.361	0.0144*
MeB	1086	192	TINF	M	MDA	5.00	0.22	4.891	< 0.001**
Dentition									
GRK	NA	75	i2l_bl	M	MDA	-0.77	0.12	3.798	< 0.001
GRK	NA	194	i2l_md	NA	LC	0.76	0.15	4.224	< 0.001**
GRK	NA	573	c1l_md	F	MDA	-5.09	1.22	5.454	< 0.001**
GRK	NA	566	i2u_bl	F	MDA	-0.84	0.13	2.984	0.0155
GRK	NA	4	c1u_bl	F	MDA	-0.43	0.06	2.147	0.7852•
GRK	NA	985	c1u_md	F	A	1.20	0.16	3.404	0.0043
GRK	NA	782	c1u_md	F	A	1.04	0.14	3.801	< 0.001
GRK	NA	964	pm1u_md	F	MA	-1.36	0.22	4.516	< 0.001**
GRK	NA	173	pm2u_bl	M	MA	3.25	0.55	5.243	< 0.001**
GRK	NA	918A	m2u_bl	F	MDA	-1.11	0.10	2.909	0.0090*
MeB	92	219H	i2l_bl	I	A	-1.18	0.17	3.948	< 0.001**
MeB	57	221G	pm2l_bl	M	MA	1.46	0.18	3.325	< 0.001
MeB	2033	67	m1l_md	M	MA	-1.24	0.12	2.665	0.0131*
MeB	1177	2083	m2l_bl	F	MA	0.61	0.06	2.987	0.0011
MeB	2036	140	i2u_bl	F	YA	-0.84	0.15	3.230	0.0020*
MeB	2083	237	pm1u_bl	F	MA	-0.50	0.06	3.217	0.0011
MeB	2083	237	pm2u_md	F	MA	0.79	0.12	2.587	0.0782•
MeB	2035	76	m1u_bl	F	MDA	0.74	0.07	2.932	0.0101
MeB	2133	390	m2u_md	M	MA	-1.51	0.15	2.579	0.0907•

**significant after a Holm's adjustment, •outlier for raw (R-L) only and * outlier for FA8 only; $p < 0.05$
F=female, M=male, I=indeterminate; A=adult, YA-young adult, MDA=middle adult, MA=mature adult; Spoor nr and Vonds nr = excavation numbering system for identification of the individuals buried in each grave; T_G = test statistic for the Grubb's outlier test

Appendix 3: Descriptive results

Table A3.1. Descriptive results for fluctuating asymmetry scores per population

	Grote Kerk						Meerenberg					
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
COBB	81	0.0189	0.0167	0.0200	0.0000	0.0700	38	0.0150	0.0118	0.0100	0.0000	0.0400
COBH	85	0.0208	0.0151	0.0200	0.0000	0.0700	36	0.0217	0.0148	0.0200	0.0000	0.0700
CNOR	84	0.0156	0.0125	0.0100	0.0000	0.0500	35	0.0177	0.0146	0.0100	0.0000	0.0500
CFMTN	94	0.0182	0.0136	0.0150	0.0000	0.0600	38	0.0145	0.0113	0.0100	0.0000	0.0400
CFMTNS	78	0.0169	0.0156	0.0100	0.0000	0.0700	33	0.0142	0.0123	0.0100	0.0000	0.0400
CMAH	90	0.0403	0.0336	0.0300	0.0000	0.1600	37	0.0478	0.0477	0.0400	0.0000	0.2300
CMPL	83	0.0647	0.0558	0.0500	0.0000	0.2500	38	0.0671	0.0536	0.0500	0.0000	0.2300
CMPB	87	0.0551	0.0455	0.0400	0.0000	0.1900	44	0.0686	0.0632	0.0500	0.0000	0.2900
CMSAST	62	0.0402	0.0349	0.0300	0.0000	0.1600	27	0.0370	0.0255	0.0300	0.0000	0.0900
COCL	100	0.0493	0.0460	0.0400	0.0000	0.2400	36	0.0464	0.0282	0.0500	0.0000	0.1100
COPO	100	0.0267	0.0238	0.0200	0.0000	0.1100	43	0.0265	0.0232	0.0200	0.0000	0.0800
CBAPO	107	0.0249	0.0216	0.0200	0.0000	0.1100	45	0.0222	0.0205	0.0200	0.0000	0.1000
CECMIS	35	0.0306	0.0236	0.0300	0.0000	0.0900	18	0.0328	0.0295	0.0250	0.0000	0.1000
CNMS	66	0.0179	0.0159	0.0200	0.0000	0.0800	30	0.0167	0.0132	0.0200	0.0000	0.0500
CBZO	75	0.0112	0.0097	0.0100	0.0000	0.0400	20	0.0125	0.0097	0.0150	0.0000	0.0300
CFMTB	86	0.0173	0.0138	0.0100	0.0000	0.0600	22	0.0177	0.0141	0.0200	0.0000	0.0400
CBPO	104	0.0194	0.0156	0.0200	0.0000	0.0600	24	0.0125	0.0126	0.0100	0.0000	0.0400
CBAST	86	0.0162	0.0138	0.0100	0.0000	0.0700	21	0.0181	0.0125	0.0200	0.0000	0.0400
CLFMT	79	0.0084	0.0074	0.0100	0.0000	0.0200	22	0.0136	0.0085	0.0100	0.0000	0.0300
CLAST	81	0.0221	0.0194	0.0200	0.0000	0.0900	19	0.0342	0.0315	0.0200	0.0000	0.1100
MAL	71	0.0131	0.0126	0.0100	0.0000	0.0500	28	0.0143	0.0126	0.0100	0.0000	0.0400
MRH	57	0.0382	0.0316	0.0300	0.0000	0.1200	27	0.0222	0.0241	0.0100	0.0000	0.0800
MXRB	72	0.0360	0.0265	0.0300	0.0000	0.1400	28	0.0282	0.0189	0.0250	0.0000	0.0700
MIRB	79	0.0395	0.0275	0.0400	0.0000	0.1200	40	0.0348	0.0256	0.0300	0.0000	0.1100
HML	55	0.0131	0.0088	0.0100	0.0000	0.0400	43	0.0119	0.0107	0.0100	0.0000	0.0400
HXMS	94	0.0377	0.0300	0.0300	0.0000	0.1700	50	0.0324	0.0250	0.0300	0.0000	0.0900
HIMS	94	0.0282	0.0234	0.0200	0.0000	0.1300	51	0.0369	0.0293	0.0300	0.0000	0.1300
HDT	87	0.0331	0.0263	0.0300	0.0000	0.1200	49	0.0335	0.0259	0.0200	0.0100	0.1100
HSIH	67	0.0182	0.0153	0.0200	0.0000	0.0700	46	0.0167	0.0137	0.0150	0.0000	0.0500
HSMLD	5	0.0240	0.0378	0.0100	0.0000	0.0900	3	0.0100	0.0100	0.0100	0.0000	0.0200
HSMLP	7	0.0300	0.0265	0.0300	0.0000	0.0700	2	0.0350	0.0071	0.0350	0.0300	0.0400
RML	61	0.0102	0.0083	0.0100	0.0000	0.0300	28	0.0071	0.0071	0.0100	0.0000	0.0300

Table A3.1 continued

	Grote Kerk						Meerenberg					
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
RXMS	77	0.0373	0.0312	0.0300	0.0000	0.1500	49	0.0524	0.0395	0.0500	0.0000	0.1400
RIMS	78	0.0279	0.0237	0.0200	0.0000	0.1000	49	0.0322	0.0311	0.0200	0.0000	0.1200
RGH	35	0.0271	0.0222	0.0200	0.0000	0.0900	18	0.0211	0.0160	0.0200	0.0000	0.0600
RSMLD	9	0.0322	0.0303	0.0200	0.0000	0.1000	1	0.0100	NA	0.0100	0.0100	0.0100
RMLD	59	0.0186	0.0172	0.0100	0.0000	0.0700	36	0.0222	0.0182	0.0200	0.0000	0.0800
FML	67	0.0072	0.0075	0.0100	0.0000	0.0300	32	0.0072	0.0073	0.0100	0.0000	0.0200
FPL	65	0.0080	0.0073	0.0100	0.0000	0.0300	33	0.0055	0.0067	0.0000	0.0000	0.0200
FXMS	113	0.0269	0.0230	0.0200	0.0000	0.1000	52	0.0290	0.0214	0.0200	0.0000	0.1000
FIMS	112	0.0246	0.0209	0.0200	0.0000	0.1200	52	0.0254	0.0207	0.0200	0.0000	0.0800
FEB	46	0.0085	0.0097	0.0100	0.0000	0.0400	23	0.0152	0.0090	0.0100	0.0000	0.0300
FSMLD	9	0.0267	0.0235	0.0200	0.0000	0.0700	0	N A	NA	NA	NA	NA
FSIH	68	0.0151	0.0124	0.0100	0.0000	0.0500	43	0.0137	0.0118	0.0100	0.0000	0.0400
FMLP	55	0.0153	0.0132	0.0100	0.0000	0.0500	27	0.0189	0.0128	0.0100	0.0000	0.0500
TML	78	0.0067	0.0066	0.0100	0.0000	0.0200	34	0.0059	0.0056	0.0100	0.0000	0.0200
TXNF	111	0.0299	0.0250	0.0200	0.0000	0.1300	58	0.0357	0.0321	0.0300	0.0000	0.1500
TINF	111	0.0357	0.0309	0.0300	0.0000	0.1400	59	0.0332	0.0278	0.0300	0.0000	0.1300
TSMLD	10	0.0220	0.0257	0.0150	0.0000	0.0800	1	0.0300	#N/A	0.0300	0.0300	0.0300
TMLD	62	0.0182	0.0149	0.0200	0.0000	0.0700	19	0.0142	0.0150	0.0200	0.0000	0.0500
TSMLP	4	0.0400	0.0082	0.0400	0.0300	0.0500	0	N A	NA	NA	NA	NA
TMLP	39	0.0079	0.0095	0.0100	0.0000	0.0400	17	0.0129	0.0116	0.0100	0.0000	0.0300
di1l_bl	4	0.0200	0.0141	0.0150	0.0100	0.0400	0	NA	NA	NA	NA	NA
di1l_md	3	0.0267	0.0208	0.0200	0.0100	0.0500	0	NA	NA	NA	NA	NA
di2l_bl	5	0.0420	0.0239	0.0400	0.0100	0.0700	0	NA	NA	NA	NA	NA
di2l_md	3	0.0433	0.0321	0.0300	0.0200	0.0800	0	NA	NA	NA	NA	NA
dc1l_bl	4	0.0425	0.0250	0.0300	0.0300	0.0800	0	NA	NA	NA	NA	NA
dc1l_md	5	0.0100	0.0071	0.0100	0.0000	0.0200	0	NA	NA	NA	NA	NA
dm1l_bl	4	0.0375	0.0330	0.0400	0.0000	0.0700	0	NA	NA	NA	NA	NA
dm1l_md	6	0.0367	0.0308	0.0300	0.0100	0.0900	0	NA	NA	NA	NA	NA
dm2l_bl	2	0.0350	0.0354	0.0350	0.0100	0.0600	0	NA	NA	NA	NA	NA
dm2l_md	2	0.0650	0.0212	0.0650	0.0500	0.0800	0	NA	NA	NA	NA	NA
di1u_bl	5	0.0200	0.0122	0.0200	0.0100	0.0400	0	NA	NA	NA	NA	NA
di1u_md	4	0.0200	0.0082	0.0200	0.0100	0.0300	0	NA	NA	NA	NA	NA
di2u_bl	3	0.0433	0.0058	0.0400	0.0400	0.0500	0	NA	NA	NA	NA	NA
di2u_md	3	0.0267	0.0289	0.0100	0.0100	0.0600	0	NA	NA	NA	NA	NA
dc1u_bl	6	0.0217	0.0204	0.0200	0.0000	0.0600	0	NA	NA	NA	NA	NA

Table A3.1 continued

	Grote Kerk						Meerenberg				
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
dc1u_md	6	0.0217	0.0279	0.0100	0.0000	0.0700	0	NA	NA	NA	NA	NA
dm1u_bl	7	0.0343	0.0294	0.0400	0.0000	0.0800	0	NA	NA	NA	NA	NA
dm1u_md	4	0.0525	0.0532	0.0350	0.0100	0.1300	0	NA	NA	NA	NA	NA
dm2u_bl	5	0.0100	0.0173	0.0000	0.0000	0.0400	0	NA	NA	NA	NA	NA
dm2u_md	4	0.0150	0.0300	0.0000	0.0000	0.0600	0	NA	NA	NA	NA	NA
i1l_bl	26	0.0319	0.0264	0.0200	0.0000	0.1100	16	0.0163	0.0136	0.0100	0.0000	0.0500
i1l_md	22	0.0200	0.0160	0.0200	0.0000	0.0700	18	0.0156	0.0120	0.0100	0.0000	0.0400
i2l_bl	29	0.0245	0.0172	0.0200	0.0000	0.0600	17	0.0124	0.0066	0.0100	0.0000	0.0200
i2l_md	24	0.0246	0.0138	0.0200	0.0000	0.0600	19	0.0200	0.0167	0.0100	0.0000	0.0500
c1l_bl	31	0.0239	0.0186	0.0200	0.0000	0.0500	29	0.0262	0.0265	0.0200	0.0000	0.1000
c1l_md	31	0.0235	0.0211	0.0200	0.0000	0.0900	30	0.0220	0.0142	0.0200	0.0000	0.0600
pm1l_bl	41	0.0280	0.0193	0.0300	0.0000	0.0900	32	0.0284	0.0211	0.0250	0.0000	0.0900
pm1l_md	42	0.0386	0.0369	0.0250	0.0000	0.1500	33	0.0303	0.0266	0.0200	0.0000	0.1100
pm2l_bl	34	0.0291	0.0231	0.0200	0.0000	0.0900	20	0.0375	0.0271	0.0400	0.0000	0.1100
pm2l_md	34	0.0338	0.0323	0.0300	0.0000	0.1400	23	0.0435	0.0308	0.0400	0.0000	0.1000
m1l_bl	16	0.0244	0.0167	0.0250	0.0000	0.0500	11	0.0145	0.0093	0.0100	0.0000	0.0300
m1l_md	16	0.0181	0.0164	0.0100	0.0000	0.0500	12	0.0275	0.0201	0.0200	0.0100	0.0800
m2l_bl	20	0.0290	0.0229	0.0350	0.0000	0.0600	13	0.0115	0.0080	0.0100	0.0000	0.0300
m2l_md	24	0.0254	0.0245	0.0150	0.0000	0.0800	16	0.0338	0.0200	0.0300	0.0100	0.0800
i1u_bl	30	0.0200	0.0164	0.0200	0.0000	0.0600	20	0.0260	0.0209	0.0300	0.0000	0.0900
i1u_md	19	0.0200	0.0221	0.0100	0.0000	0.0700	11	0.0164	0.0163	0.0100	0.0000	0.0500
i2u_bl	21	0.0324	0.0239	0.0400	0.0000	0.0800	19	0.0305	0.0234	0.0200	0.0000	0.0700
i2u_md	12	0.0350	0.0268	0.0300	0.0000	0.0900	14	0.0393	0.0448	0.0200	0.0000	0.1600
c1u_bl	29	0.0241	0.0201	0.0200	0.0000	0.0700	27	0.0215	0.0203	0.0100	0.0000	0.0700
c1u_md	29	0.0210	0.0214	0.0100	0.0000	0.0800	26	0.0162	0.0124	0.0150	0.0000	0.0400
pm1u_bl	29	0.0166	0.0180	0.0100	0.0000	0.0700	17	0.0129	0.0085	0.0100	0.0000	0.0300
pm1u_md	28	0.0289	0.0206	0.0250	0.0000	0.0900	19	0.0416	0.0340	0.0400	0.0000	0.1200
pm2u_bl	30	0.0257	0.0227	0.0200	0.0000	0.0800	20	0.0180	0.0182	0.0100	0.0000	0.0600
pm2u_md	29	0.0438	0.0376	0.0400	0.0000	0.1600	18	0.0317	0.0260	0.0300	0.0000	0.1100
m1u_bl	17	0.0176	0.0144	0.0100	0.0000	0.0500	17	0.0106	0.0134	0.0100	0.0000	0.0400
m1u_md	18	0.0333	0.0181	0.0300	0.0100	0.0700	18	0.0417	0.0378	0.0350	0.0000	0.1400
m2u_bl	16	0.0244	0.0167	0.0200	0.0000	0.0600	19	0.0305	0.0255	0.0200	0.0000	0.0800
m2u_md	21	0.0495	0.0385	0.0500	0.0000	0.1400	19	0.0426	0.0323	0.0300	0.0000	0.1300
Individual	171	0.0247	0.0067	0.0239	0.0000	0.0543	106	0.0256	0.0102	0.0237	0.0050	0.0733
Skeleton	168	0.0243	0.0075	0.0233	0.0000	0.0600	105	0.0254	0.0110	0.0228	0.0050	0.0733

Table A3.1 continued

	Grote Kerk						Meerenberg					
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
Dentition	77	0.0286	0.0113	0.0275	0.0050	0.0700	53	0.0267	0.0109	0.0250	0.0092	0.0650
Dentition: permanent	70	0.0286	0.0115	0.0269	0.0050	0.0700	53	0.0267	0.0109	0.0250	0.0092	0.0650
Dentition: deciduous	10	0.0282	0.0105	0.0317	0.0100	0.0400	0	NA	NA	NA	NA	NA
Dentition: mandible	67	0.0290	0.0121	0.0270	0.0100	0.0733	45	0.0263	0.0127	0.0229	0.0100	0.0700
Dentition: maxilla	66	0.0278	0.0128	0.0265	0.0050	0.0700	42	0.0259	0.0125	0.0250	0.0029	0.0650
Cranium	127	0.0228	0.0074	0.0218	0.0050	0.0550	52	0.0240	0.0091	0.0237	0.0100	0.0600
Cranium: orbit	83	0.0187	0.0104	0.0200	0.0000	0.0550	36	0.0192	0.0093	0.0200	0.0000	0.0400
Cranium: facial	103	0.0207	0.0096	0.0200	0.0000	0.0500	41	0.0237	0.0178	0.0200	0.0000	0.1150
Cranium: temporal	86	0.0542	0.0311	0.0467	0.0100	0.1733	45	0.0609	0.0399	0.0600	0.0000	0.1900
Cranium: base	115	0.0299	0.0180	0.0275	0.0000	0.1033	49	0.0271	0.0156	0.0250	0.0050	0.0733
Cranium: vault	109	0.0170	0.0115	0.0150	0.0000	0.0900	27	0.0175	0.0100	0.0150	0.0000	0.0425
Mandible	88	0.0307	0.0154	0.0300	0.0000	0.0850	46	0.0289	0.0157	0.0258	0.0050	0.0800
Humerus	107	0.0279	0.0183	0.0267	0.0000	0.1500	54	0.0271	0.0133	0.0258	0.0000	0.0700
Radius	88	0.0256	0.0153	0.0223	0.0000	0.0900	56	0.0327	0.0230	0.0233	0.0000	0.1150
Femur	121	0.0190	0.0135	0.0157	0.0000	0.0800	56	0.0187	0.0098	0.0169	0.0025	0.0550
Tibia	123	0.0257	0.0173	0.0233	0.0000	0.1050	60	0.0287	0.0212	0.0250	0.0000	0.1050
Upper limb	124	0.0272	0.0162	0.0250	0.0000	0.1500	67	0.0293	0.0142	0.0250	0.0000	0.0733
Lower Limb	140	0.0225	0.0126	0.0195	0.0000	0.0725	65	0.0224	0.0113	0.0200	0.0050	0.0675
Midshafts	145	0.0308	0.0138	0.0283	0.0050	0.0817	77	0.0343	0.0187	0.0313	0.0050	0.1400
Upper limb: midshafts	109	0.0326	0.0181	0.0300	0.0000	0.1500	63	0.0390	0.0228	0.0350	0.0050	0.1400
Lower limb: midshafts	138	0.0296	0.0157	0.0263	0.0050	0.0800	65	0.0300	0.0138	0.0325	0.0050	0.0675
Lengths	114	0.0092	0.0072	0.0100	0.0000	0.0400	64	0.0089	0.0079	0.0088	0.0000	0.0400
Upper limb: lengths	78	0.0119	0.0083	0.0100	0.0000	0.0400	51	0.0102	0.0097	0.0100	0.0000	0.0400
Lower limb: lengths	94	0.0071	0.0058	0.0075	0.0000	0.0200	41	0.0063	0.0056	0.0050	0.0000	0.0200

Table A3.2. Descriptive results for adult fluctuating asymmetry scores per population group (permanent dentition also includes subadult individuals)

	Grote Kerk						Meerenberg					
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
COBB	81	0.0189	0.0167	0.0200	0.0000	0.0700	38	0.0150	0.0118	0.0100	0.0000	0.0400
COBH	85	0.0208	0.0151	0.0200	0.0000	0.0700	36	0.0217	0.0148	0.0200	0.0000	0.0700
CNOR	84	0.0156	0.0125	0.0100	0.0000	0.0500	35	0.0177	0.0146	0.0100	0.0000	0.0500
CFMTN	89	0.0185	0.0136	0.0200	0.0000	0.0600	38	0.0145	0.0113	0.0100	0.0000	0.0400
CFMTNS	78	0.0169	0.0156	0.0100	0.0000	0.0700	33	0.0142	0.0123	0.0100	0.0000	0.0400
CMAH	86	0.0412	0.0339	0.0350	0.0000	0.1600	37	0.0478	0.0477	0.0400	0.0000	0.2300
CMPL	80	0.0648	0.0558	0.0500	0.0000	0.2500	36	0.0694	0.0541	0.0550	0.0000	0.2300
CMPB	84	0.0555	0.0462	0.0400	0.0000	0.1900	42	0.0643	0.0542	0.0500	0.0000	0.2000
CMSAST	61	0.0407	0.0349	0.0300	0.0000	0.1600	27	0.0370	0.0255	0.0300	0.0000	0.0900
COCL	99	0.0493	0.0462	0.0400	0.0000	0.2400	35	0.0463	0.0286	0.0500	0.0000	0.1100
COPO	100	0.0267	0.0238	0.0200	0.0000	0.1100	43	0.0265	0.0232	0.0200	0.0000	0.0800
CBAPO	107	0.0249	0.0216	0.0200	0.0000	0.1100	45	0.0222	0.0205	0.0200	0.0000	0.1000
CECMIS	30	0.0280	0.0225	0.0250	0.0000	0.0800	18	0.0328	0.0295	0.0250	0.0000	0.1000
CNMS	66	0.0179	0.0159	0.0200	0.0000	0.0800	30	0.0167	0.0132	0.0200	0.0000	0.0500
CBZO	75	0.0112	0.0097	0.0100	0.0000	0.0400	20	0.0125	0.0097	0.0150	0.0000	0.0300
CFMTB	86	0.0173	0.0138	0.0100	0.0000	0.0600	22	0.0177	0.0141	0.0200	0.0000	0.0400
CBPO	104	0.0194	0.0156	0.0200	0.0000	0.0600	24	0.0125	0.0126	0.0100	0.0000	0.0400
CBAST	86	0.0162	0.0138	0.0100	0.0000	0.0700	21	0.0181	0.0125	0.0200	0.0000	0.0400
CLFMT	79	0.0084	0.0074	0.0100	0.0000	0.0200	22	0.0136	0.0085	0.0100	0.0000	0.0300
CLAST	81	0.0221	0.0194	0.0200	0.0000	0.0900	19	0.0342	0.0315	0.0200	0.0000	0.1100
MAL	66	0.0136	0.0128	0.0100	0.0000	0.0500	28	0.0143	0.0126	0.0100	0.0000	0.0400
MRH	52	0.0394	0.0327	0.0300	0.0000	0.1200	27	0.0222	0.0241	0.0100	0.0000	0.0800
MXRB	67	0.0363	0.0273	0.0300	0.0000	0.1400	28	0.0282	0.0189	0.0250	0.0000	0.0700
MIRB	68	0.0406	0.0284	0.0400	0.0000	0.1200	40	0.0348	0.0256	0.0300	0.0000	0.1100
HML	49	0.0139	0.0089	0.0100	0.0000	0.0400	41	0.0122	0.0108	0.0100	0.0000	0.0400
HXMS	84	0.0395	0.0310	0.0300	0.0000	0.1700	47	0.0328	0.0250	0.0300	0.0000	0.0900
HIMS	84	0.0295	0.0239	0.0250	0.0000	0.1300	48	0.0363	0.0294	0.0300	0.0000	0.1300
HDT	83	0.0330	0.0261	0.0300	0.0000	0.1200	46	0.0335	0.0258	0.0250	0.0100	0.1100
HSIH	66	0.0183	0.0154	0.0200	0.0000	0.0700	45	0.0169	0.0138	0.0200	0.0000	0.0500
HEB	40	0.0185	0.0185	0.0100	0.0000	0.0700	21	0.0162	0.0112	0.0100	0.0000	0.0400
RML	55	0.0107	0.0084	0.0100	0.0000	0.0300	27	0.0070	0.0072	0.0100	0.0000	0.0300
RXMS	67	0.0381	0.0320	0.0300	0.0000	0.1500	46	0.0524	0.0401	0.0450	0.0000	0.1400
RIMS	68	0.0269	0.0231	0.0200	0.0000	0.0900	46	0.0317	0.0318	0.0200	0.0000	0.1200
RGH	35	0.0271	0.0222	0.0200	0.0000	0.0900	18	0.0211	0.0160	0.0200	0.0000	0.0600

Table A3.2 continued

	Grote Kerk						Meerenberg					
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
RMLD	59	0.0186	0.0172	0.0100	0.0000	0.0700	35	0.0223	0.0185	0.0200	0.0000	0.0800
FML	58	0.0081	0.0076	0.0100	0.0000	0.0300	32	0.0072	0.0073	0.0100	0.0000	0.0200
FPL	60	0.0083	0.0074	0.0100	0.0000	0.0300	33	0.0055	0.0067	0.0000	0.0000	0.0200
FXMS	102	0.0272	0.0235	0.0200	0.0000	0.1000	50	0.0290	0.0209	0.0200	0.0000	0.1000
FIMS	101	0.0246	0.0217	0.0200	0.0000	0.1200	50	0.0248	0.0200	0.0200	0.0000	0.0800
FEB	45	0.0084	0.0098	0.0100	0.0000	0.0400	22	0.0150	0.0091	0.0100	0.0000	0.0300
FSIH	65	0.0148	0.0124	0.0100	0.0000	0.0500	43	0.0137	0.0118	0.0100	0.0000	0.0400
FMLP	49	0.0155	0.0126	0.0100	0.0000	0.0400	26	0.0192	0.0129	0.0150	0.0000	0.0500
TML	69	0.0064	0.0066	0.0100	0.0000	0.0200	33	0.0058	0.0056	0.0100	0.0000	0.0200
TXNF	100	0.0292	0.0251	0.0200	0.0000	0.1300	55	0.0360	0.0328	0.0300	0.0000	0.1500
TINF	101	0.0371	0.0314	0.0300	0.0000	0.1400	56	0.0330	0.0277	0.0300	0.0000	0.1300
TMLD	61	0.0182	0.0150	0.0200	0.0000	0.0700	19	0.0142	0.0150	0.0200	0.0000	0.0500
TMLP	38	0.0079	0.0096	0.0100	0.0000	0.0400	16	0.0125	0.0118	0.0100	0.0000	0.0300
i1l_bl	26	0.0319	0.0264	0.0200	0.0000	0.1100	16	0.0163	0.0136	0.0100	0.0000	0.0500
i1l_md	22	0.0200	0.0160	0.0200	0.0000	0.0700	18	0.0156	0.0120	0.0100	0.0000	0.0400
i2l_bl	29	0.0245	0.0172	0.0200	0.0000	0.0600	17	0.0124	0.0066	0.0100	0.0000	0.0200
i2l_md	24	0.0246	0.0138	0.0200	0.0000	0.0600	19	0.0200	0.0167	0.0100	0.0000	0.0500
c1l_bl	31	0.0239	0.0186	0.0200	0.0000	0.0500	29	0.0262	0.0265	0.0200	0.0000	0.1000
c1l_md	31	0.0235	0.0211	0.0200	0.0000	0.0900	30	0.0220	0.0142	0.0200	0.0000	0.0600
pm1l_bl	41	0.0280	0.0193	0.0300	0.0000	0.0900	32	0.0284	0.0211	0.0250	0.0000	0.0900
pm1l_md	42	0.0386	0.0369	0.0250	0.0000	0.1500	33	0.0303	0.0266	0.0200	0.0000	0.1100
pm2l_bl	34	0.0291	0.0231	0.0200	0.0000	0.0900	20	0.0375	0.0271	0.0400	0.0000	0.1100
pm2l_md	34	0.0338	0.0323	0.0300	0.0000	0.1400	23	0.0435	0.0308	0.0400	0.0000	0.1000
m1l_bl	16	0.0244	0.0167	0.0250	0.0000	0.0500	11	0.0145	0.0093	0.0100	0.0000	0.0300
m1l_md	16	0.0181	0.0164	0.0100	0.0000	0.0500	12	0.0275	0.0201	0.0200	0.0100	0.0800
m2l_bl	20	0.0290	0.0229	0.0350	0.0000	0.0600	13	0.0115	0.0080	0.0100	0.0000	0.0300
m2l_md	24	0.0254	0.0245	0.0150	0.0000	0.0800	16	0.0338	0.0200	0.0300	0.0100	0.0800
i1u_bl	30	0.0200	0.0164	0.0200	0.0000	0.0600	20	0.0260	0.0209	0.0300	0.0000	0.0900
i1u_md	19	0.0200	0.0221	0.0100	0.0000	0.0700	11	0.0164	0.0163	0.0100	0.0000	0.0500
i2u_bl	21	0.0324	0.0239	0.0400	0.0000	0.0800	19	0.0305	0.0234	0.0200	0.0000	0.0700
i2u_md	12	0.0350	0.0268	0.0300	0.0000	0.0900	14	0.0393	0.0448	0.0200	0.0000	0.1600
c1u_bl	29	0.0241	0.0201	0.0200	0.0000	0.0700	27	0.0215	0.0203	0.0100	0.0000	0.0700
c1u_md	29	0.0210	0.0214	0.0100	0.0000	0.0800	26	0.0162	0.0124	0.0150	0.0000	0.0400
pm1u_bl	29	0.0166	0.0180	0.0100	0.0000	0.0700	17	0.0129	0.0085	0.0100	0.0000	0.0300
pm1u_md	28	0.0289	0.0206	0.0250	0.0000	0.0900	19	0.0416	0.0340	0.0400	0.0000	0.1200

Table A3.2 continued

	Grote Kerk						Meerenberg					
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
pm2u_bl	30	0.0257	0.0227	0.0200	0.0000	0.0800	20	0.0180	0.0182	0.0100	0.0000	0.0600
pm2u_md	29	0.0438	0.0376	0.0400	0.0000	0.1600	18	0.0317	0.0260	0.0300	0.0000	0.1100
m1u_bl	17	0.0176	0.0144	0.0100	0.0000	0.0500	17	0.0106	0.0134	0.0100	0.0000	0.0400
m1u_md	18	0.0333	0.0181	0.0300	0.0100	0.0700	18	0.0417	0.0378	0.0350	0.0000	0.1400
m2u_bl	16	0.0244	0.0167	0.0200	0.0000	0.0600	19	0.0305	0.0255	0.0200	0.0000	0.0800
m2u_md	21	0.0495	0.0385	0.0500	0.0000	0.1400	19	0.0426	0.0323	0.0300	0.0000	0.1300
Individual	148	0.0247	0.0066	0.0240	0.0000	0.0543	103	0.0256	0.0103	0.0238	0.0050	0.0733
Skeleton	147	0.0244	0.0075	0.0236	0.0000	0.0600	102	0.0252	0.0110	0.0228	0.0050	0.0733
Dentition	64	0.0290	0.0118	0.0269	0.0050	0.0700	51	0.0272	0.0108	0.0250	0.0115	0.0650
Dentition: permanent	70	0.0286	0.0115	0.0269	0.0050	0.0700	53	0.0267	0.0109	0.0250	0.0092	0.0650
Dentition: mandible	56	0.0285	0.0128	0.0267	0.0100	0.0733	43	0.0268	0.0128	0.0230	0.0100	0.0700
Dentition: maxilla	53	0.0292	0.0129	0.0267	0.0050	0.0700	40	0.0266	0.0123	0.0250	0.0029	0.0650
Cranium	121	0.0230	0.0072	0.0220	0.0100	0.0550	51	0.0235	0.0084	0.0236	0.0100	0.0600
Cranium: orbit	83	0.0187	0.0104	0.0200	0.0000	0.0550	36	0.0192	0.0093	0.0200	0.0000	0.0400
Cranium: facial	97	0.0211	0.0094	0.0200	0.0025	0.0500	41	0.0237	0.0178	0.0200	0.0000	0.1150
Cranium: temporal	83	0.0546	0.0314	0.0467	0.0100	0.1733	43	0.0595	0.0378	0.0600	0.0000	0.1900
Cranium: base	114	0.0297	0.0180	0.0275	0.0000	0.1033	48	0.0267	0.0154	0.0238	0.0050	0.0733
Cranium: vault	109	0.0170	0.0115	0.0150	0.0000	0.0900	27	0.0175	0.0100	0.0150	0.0000	0.0425
Mandible	77	0.0313	0.0159	0.0300	0.0000	0.0850	46	0.0289	0.0157	0.0258	0.0050	0.0800
Humerus	97	0.0286	0.0189	0.0267	0.0000	0.1500	51	0.0270	0.0133	0.0250	0.0000	0.0700
Radius	77	0.0252	0.0160	0.0200	0.0000	0.0900	53	0.0324	0.0234	0.0233	0.0000	0.1150
Femur	108	0.0192	0.0138	0.0157	0.0000	0.0800	53	0.0182	0.0098	0.0167	0.0025	0.0550
Tibia	111	0.0260	0.0176	0.0233	0.0000	0.1050	57	0.0285	0.0213	0.0250	0.0000	0.1050
Upper limb	110	0.0274	0.0169	0.0255	0.0000	0.1500	64	0.0292	0.0144	0.0250	0.0000	0.0733
Lower Limb	124	0.0225	0.0126	0.0190	0.0000	0.0725	62	0.0221	0.0110	0.0200	0.0050	0.0675
Midshafts	125	0.0313	0.0141	0.0288	0.0050	0.0817	74	0.0342	0.0189	0.0306	0.0050	0.1400
Upper limb: midshafts	96	0.0335	0.0187	0.0325	0.0000	0.1500	60	0.0388	0.0230	0.0350	0.0050	0.1400
Lower limb: midshafts	123	0.0296	0.0159	0.0250	0.0050	0.0800	62	0.0300	0.0138	0.0313	0.0050	0.0675
Lengths	99	0.0098	0.0073	0.0100	0.0000	0.0400	62	0.0089	0.0080	0.0088	0.0000	0.0400
Upper limb: lengths	69	0.0127	0.0084	0.0100	0.0000	0.0400	49	0.0104	0.0098	0.0100	0.0000	0.0400
Lower limb: lengths	81	0.0073	0.0058	0.0100	0.0000	0.0200	40	0.0063	0.0056	0.0050	0.0000	0.0200

Table A3.3. Descriptive results for adult fluctuating asymmetry scores stratified by age

	YA						MDA				
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
COBB	4	0.0175	0.0050	0.0200	0.0100	0.0200	62	0.0185	0.0158	0.0150	0.0000	0.0700
COBH	4	0.0225	0.0096	0.0250	0.0100	0.0300	66	0.0194	0.0138	0.0200	0.0000	0.0500
CNOR	2	0.0100	0.0141	0.0100	0.0000	0.0200	67	0.0148	0.0119	0.0100	0.0000	0.0500
CFMTN	2	0.0250	0.0071	0.0250	0.0200	0.0300	70	0.0173	0.0126	0.0100	0.0000	0.0500
CFMTNS	3	0.0133	0.0058	0.0100	0.0100	0.0200	55	0.0151	0.0143	0.0100	0.0000	0.0700
CMAH	4	0.0450	0.0129	0.0450	0.0300	0.0600	65	0.0431	0.0386	0.0300	0.0000	0.1600
CMPL	1	0.1600	NA	0.1600	0.1600	0.1600	70	0.0569	0.0505	0.0400	0.0000	0.2500
CMPB	0	NA	NA	NA	NA	NA	76	0.0557	0.0461	0.0500	0.0000	0.2000
CMSAST	1	0.0900	NA	0.0900	0.0900	0.0900	49	0.0376	0.0289	0.0300	0.0000	0.1600
COCL	2	0.0550	0.0495	0.0550	0.0200	0.0900	78	0.0436	0.0390	0.0400	0.0000	0.2200
COPO	4	0.0125	0.0250	0.0000	0.0000	0.0500	85	0.0264	0.0223	0.0200	0.0000	0.1000
CBAPO	4	0.0225	0.0096	0.0250	0.0100	0.0300	88	0.0213	0.0172	0.0200	0.0000	0.0800
CECMIS	2	0.0400	0.0566	0.0400	0.0000	0.0800	17	0.0276	0.0205	0.0300	0.0000	0.0700
CNMS	0	NA	NA	NA	NA	NA	59	0.0176	0.0159	0.0200	0.0000	0.0800
CBZO	4	0.0100	0.0115	0.0100	0.0000	0.0200	51	0.0120	0.0096	0.0100	0.0000	0.0300
CFMTB	4	0.0175	0.0206	0.0150	0.0000	0.0400	60	0.0155	0.0127	0.0100	0.0000	0.0500
CBPO	4	0.0150	0.0129	0.0150	0.0000	0.0300	74	0.0191	0.0158	0.0200	0.0000	0.0600
CBAST	4	0.0100	0.0141	0.0050	0.0000	0.0300	57	0.0174	0.0128	0.0100	0.0000	0.0500
CLFMT	4	0.0075	0.0096	0.0050	0.0000	0.0200	53	0.0091	0.0084	0.0100	0.0000	0.0300
CLAST	4	0.0275	0.0236	0.0200	0.0100	0.0600	51	0.0241	0.0223	0.0200	0.0000	0.1100
MAL	2	0.0050	0.0071	0.0050	0.0000	0.0100	47	0.0138	0.0134	0.0100	0.0000	0.0500
MRH	1	0.0000	NA	0.0000	0.0000	0.0000	43	0.0388	0.0327	0.0300	0.0000	0.1200
MXRB	2	0.0400	0.0141	0.0400	0.0300	0.0500	46	0.0339	0.0244	0.0300	0.0000	0.0900
MIRB	2	0.0000	0.0000	0.0000	0.0000	0.0000	55	0.0400	0.0288	0.0400	0.0000	0.1200
HML	5	0.0200	0.0158	0.0200	0.0000	0.0400	37	0.0130	0.0100	0.0100	0.0000	0.0400
HXMS	6	0.0433	0.0314	0.0550	0.0000	0.0800	63	0.0397	0.0263	0.0300	0.0000	0.1100
HIMS	6	0.0367	0.0339	0.0350	0.0000	0.0800	63	0.0295	0.0208	0.0200	0.0000	0.0800
HDT	5	0.0300	0.0235	0.0200	0.0100	0.0600	63	0.0327	0.0262	0.0300	0.0000	0.1200
HSIH	4	0.0175	0.0096	0.0150	0.0100	0.0300	49	0.0173	0.0158	0.0200	0.0000	0.0700
HEB	2	0.0100	0.0000	0.0100	0.0100	0.0100	28	0.0171	0.0172	0.0100	0.0000	0.0700
RML	3	0.0100	0.0000	0.0100	0.0100	0.0100	42	0.0110	0.0082	0.0100	0.0000	0.0300
RXMS	5	0.0380	0.0192	0.0400	0.0100	0.0600	55	0.0375	0.0303	0.0300	0.0000	0.1400
RIMS	5	0.0320	0.0507	0.0100	0.0000	0.1200	57	0.0279	0.0238	0.0200	0.0000	0.1000
RGH	1	0.0100	NA	0.0100	0.0100	0.0100	27	0.0315	0.0220	0.0300	0.0000	0.0900
RMLD	2	0.0250	0.0071	0.0250	0.0200	0.0300	43	0.0207	0.0176	0.0200	0.0000	0.0700

Table A3.3 continued

	YA						MDA				
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
FML	2	0.0050	0.0071	0.0050	0.0000	0.0100	48	0.0083	0.0081	0.0100	0.0000	0.0300
FPL	2	0.0050	0.0071	0.0050	0.0000	0.0100	49	0.0073	0.0070	0.0100	0.0000	0.0200
FXMS	4	0.0300	0.0141	0.0350	0.0100	0.0400	81	0.0260	0.0222	0.0200	0.0000	0.0800
FIMS	4	0.0100	0.0082	0.0100	0.0000	0.0200	80	0.0225	0.0185	0.0200	0.0000	0.1100
FEB	1	0.0200	NA	0.0200	0.0200	0.0200	41	0.0105	0.0097	0.0100	0.0000	0.0400
FSIH	3	0.0067	0.0058	0.0100	0.0000	0.0100	57	0.0147	0.0124	0.0100	0.0000	0.0500
FMLP	3	0.0133	0.0058	0.0100	0.0100	0.0200	36	0.0147	0.0116	0.0100	0.0000	0.0400
TML	2	0.0150	0.0071	0.0150	0.0100	0.0200	53	0.0064	0.0068	0.0100	0.0000	0.0200
TXNF	7	0.0500	0.0503	0.0300	0.0100	0.1400	76	0.0303	0.0262	0.0200	0.0000	0.1300
TINF	7	0.0486	0.0449	0.0400	0.0000	0.1300	78	0.0378	0.0323	0.0300	0.0000	0.1400
TMLD	3	0.0167	0.0208	0.0100	0.0000	0.0400	39	0.0164	0.0131	0.0200	0.0000	0.0500
TMLP	0	NA	NA	NA	NA	NA	29	0.0069	0.0085	0.0100	0.0000	0.0300
i1l_bl	4	0.0225	0.0206	0.0200	0.0000	0.0500	10	0.0220	0.0148	0.0250	0.0000	0.0500
i1l_md	4	0.0100	0.0082	0.0100	0.0000	0.0200	9	0.0167	0.0224	0.0100	0.0000	0.0700
i2l_bl	5	0.0100	0.0071	0.0100	0.0000	0.0200	15	0.0173	0.0128	0.0100	0.0100	0.0500
i2l_md	6	0.0217	0.0147	0.0150	0.0100	0.0400	9	0.0200	0.0141	0.0200	0.0000	0.0400
c1l_bl	6	0.0100	0.0126	0.0050	0.0000	0.0300	18	0.0211	0.0175	0.0200	0.0000	0.0500
c1l_md	7	0.0300	0.0231	0.0300	0.0000	0.0600	15	0.0213	0.0168	0.0200	0.0000	0.0500
pm1l_bl	6	0.0300	0.0303	0.0200	0.0000	0.0800	21	0.0257	0.0157	0.0200	0.0000	0.0600
pm1l_md	6	0.0350	0.0251	0.0300	0.0100	0.0800	22	0.0300	0.0253	0.0200	0.0000	0.1000
pm2l_bl	6	0.0283	0.0075	0.0300	0.0200	0.0400	18	0.0250	0.0201	0.0200	0.0000	0.0600
pm2l_md	6	0.0317	0.0426	0.0150	0.0000	0.1100	18	0.0428	0.0369	0.0300	0.0000	0.1400
m1l_bl	2	0.0050	0.0071	0.0050	0.0000	0.0100	9	0.0256	0.0174	0.0300	0.0000	0.0500
m1l_md	2	0.0250	0.0212	0.0250	0.0100	0.0400	9	0.0200	0.0141	0.0200	0.0000	0.0400
m2l_bl	5	0.0100	0.0100	0.0100	0.0000	0.0200	8	0.0250	0.0207	0.0200	0.0000	0.0600
m2l_md	5	0.0160	0.0114	0.0200	0.0000	0.0300	11	0.0327	0.0280	0.0300	0.0000	0.0800
i1u_bl	5	0.0120	0.0130	0.0100	0.0000	0.0300	15	0.0200	0.0100	0.0200	0.0000	0.0300
i1u_md	5	0.0240	0.0241	0.0100	0.0000	0.0500	6	0.0250	0.0259	0.0150	0.0000	0.0700
i2u_bl	2	0.0450	0.0071	0.0450	0.0400	0.0500	13	0.0392	0.0281	0.0500	0.0000	0.0700
i2u_md	4	0.0875	0.0574	0.0850	0.0200	0.1600	5	0.0380	0.0259	0.0300	0.0100	0.0800
c1u_bl	6	0.0283	0.0194	0.0350	0.0000	0.0500	16	0.0163	0.0150	0.0100	0.0000	0.0500
c1u_md	7	0.0171	0.0138	0.0100	0.0000	0.0400	14	0.0164	0.0122	0.0100	0.0000	0.0400
pm1u_bl	5	0.0120	0.0084	0.0100	0.0000	0.0200	12	0.0217	0.0217	0.0150	0.0000	0.0700
pm1u_md	5	0.0240	0.0055	0.0200	0.0200	0.0300	10	0.0510	0.0303	0.0500	0.0100	0.1100
pm2u_bl	3	0.0100	0.0100	0.0100	0.0000	0.0200	18	0.0211	0.0188	0.0200	0.0000	0.0600

Table A3.3 continued

	YA						MDA				
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
pm2u_md	3	0.0267	0.0252	0.0300	0.0000	0.0500	13	0.0462	0.0417	0.0300	0.0100	0.1400
m1u_bl	3	0.0133	0.0115	0.0200	0.0000	0.0200	9	0.0144	0.0133	0.0200	0.0000	0.0400
m1u_md	3	0.0333	0.0153	0.0300	0.0200	0.0500	7	0.0300	0.0231	0.0300	0.0100	0.0700
m2u_bl	3	0.0200	0.0100	0.0200	0.0100	0.0300	9	0.0467	0.0224	0.0500	0.0100	0.0800
m2u_md	5	0.0560	0.0498	0.0600	0.0100	0.1300	9	0.0467	0.0324	0.0400	0.0000	0.1000
Individual	10	0.0272	0.0129	0.0235	0.0172	0.0625	118	0.0243	0.0067	0.0237	0.0000	0.0543
Skeleton	9	0.0287	0.0150	0.0229	0.0134	0.0625	118	0.0242	0.0075	0.0230	0.0000	0.0600
Dentition	7	0.0243	0.0047	0.0233	0.0187	0.0325	41	0.0280	0.0125	0.0260	0.0050	0.0700
Dentition: mandible	7	0.0217	0.0057	0.0200	0.0150	0.0300	35	0.0264	0.0115	0.0233	0.0100	0.0500
Dentition: maxilla	7	0.0255	0.0106	0.0267	0.0100	0.0378	33	0.0296	0.0148	0.0257	0.0050	0.0700
Cranium	4	0.0215	0.0054	0.0218	0.0153	0.0269	99	0.0226	0.0073	0.0221	0.0100	0.0550
Cranium: orbit	4	0.0200	0.0108	0.0225	0.0050	0.0300	64	0.0175	0.0087	0.0150	0.0000	0.0400
Cranium: facial	4	0.0235	0.0079	0.0250	0.0140	0.0300	76	0.0209	0.0098	0.0200	0.0025	0.0500
Cranium: temporal	1	0.1250	#N/A	0.1250	0.1250	0.1250	75	0.0514	0.0304	0.0400	0.0000	0.1400
Cranium: base	4	0.0246	0.0181	0.0267	0.0050	0.0400	94	0.0267	0.0168	0.0250	0.0000	0.1033
Cranium: vault	4	0.0150	0.0089	0.0175	0.0025	0.0225	79	0.0174	0.0127	0.0150	0.0000	0.0900
Mandible	2	0.0138	0.0088	0.0138	0.0075	0.0200	61	0.0314	0.0167	0.0275	0.0000	0.0850
Humerus	6	0.0331	0.0148	0.0350	0.0067	0.0467	72	0.0277	0.0144	0.0267	0.0000	0.0600
Radius	5	0.0330	0.0256	0.0275	0.0075	0.0750	64	0.0263	0.0167	0.0223	0.0000	0.0900
Femur	5	0.0141	0.0096	0.0100	0.0050	0.0300	85	0.0179	0.0117	0.0150	0.0000	0.0700
Tibia	7	0.0469	0.0355	0.0367	0.0033	0.1050	85	0.0265	0.0173	0.0233	0.0000	0.1050
Upper limb	6	0.0342	0.0177	0.0354	0.0071	0.0575	85	0.0272	0.0116	0.0267	0.0000	0.0600
Lower Limb	7	0.0291	0.0208	0.0220	0.0033	0.0675	97	0.0222	0.0122	0.0189	0.0000	0.0700
Midshafts	7	0.0376	0.0159	0.0400	0.0125	0.0625	97	0.0311	0.0131	0.0286	0.0050	0.0800
Upper limb: midshafts	6	0.0383	0.0182	0.0438	0.0050	0.0575	75	0.0333	0.0130	0.0350	0.0050	0.0700
Lower limb: midshafts	7	0.0361	0.0198	0.0375	0.0050	0.0675	96	0.0294	0.0155	0.0275	0.0075	0.0800
Lengths	5	0.0165	0.0136	0.0125	0.0050	0.0400	78	0.0101	0.0075	0.0100	0.0000	0.0400
Upper limb: lengths	5	0.0180	0.0135	0.0150	0.0050	0.0400	55	0.0125	0.0089	0.0100	0.0000	0.0400
Lower limb: lengths	2	0.0100	0.0000	0.0100	0.0100	0.0100	63	0.0075	0.0061	0.0100	0.0000	0.0200

Table A3.3 continued

	MA						A				
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
COBB	44	0.0159	0.0144	0.0100	0.0000	0.0500	9	0.0200	0.0206	0.0100	0.0000	0.0700
COBH	42	0.0226	0.0170	0.0200	0.0000	0.0700	9	0.0256	0.0151	0.0200	0.0100	0.0500
CNOR	41	0.0183	0.0153	0.0100	0.0000	0.0500	9	0.0189	0.0117	0.0200	0.0000	0.0400
CFMTN	46	0.0167	0.0143	0.0100	0.0000	0.0600	9	0.0189	0.0117	0.0200	0.0000	0.0400
CFMTNS	45	0.0171	0.0158	0.0100	0.0000	0.0700	8	0.0188	0.0146	0.0150	0.0000	0.0400
CMAH	45	0.0429	0.0398	0.0400	0.0000	0.2300	9	0.0444	0.0439	0.0400	0.0000	0.1400
CMPL	40	0.0790	0.0555	0.0600	0.0000	0.2000	5	0.0760	0.0888	0.0400	0.0100	0.2300
CMPB	42	0.0640	0.0562	0.0400	0.0000	0.1900	8	0.0550	0.0363	0.0600	0.0100	0.1100
CMSAST	35	0.0417	0.0371	0.0300	0.0000	0.1500	3	0.0300	0.0100	0.0300	0.0200	0.0400
COCL	44	0.0548	0.0492	0.0500	0.0000	0.2400	10	0.0580	0.0316	0.0650	0.0200	0.1100
COPO	45	0.0262	0.0238	0.0200	0.0000	0.1100	9	0.0378	0.0323	0.0300	0.0000	0.1000
CBAPO	51	0.0276	0.0240	0.0200	0.0000	0.1000	9	0.0322	0.0373	0.0200	0.0000	0.1100
CECMIS	24	0.0321	0.0260	0.0250	0.0000	0.1000	5	0.0220	0.0295	0.0100	0.0000	0.0700
CNMS	34	0.0174	0.0144	0.0150	0.0000	0.0600	3	0.0167	0.0058	0.0200	0.0100	0.0200
CBZO	38	0.0113	0.0099	0.0100	0.0000	0.0400	2	0.0050	0.0071	0.0050	0.0000	0.0100
CFMTB	42	0.0198	0.0146	0.0200	0.0000	0.0600	2	0.0250	0.0212	0.0250	0.0100	0.0400
CBPO	48	0.0171	0.0147	0.0100	0.0000	0.0600	2	0.0150	0.0212	0.0150	0.0000	0.0300
CBAST	44	0.0155	0.0130	0.0100	0.0000	0.0700	2	0.0300	0.0424	0.0300	0.0000	0.0600
CLFMT	41	0.0107	0.0072	0.0100	0.0000	0.0200	3	0.0033	0.0058	0.0000	0.0000	0.0100
CLAST	42	0.0252	0.0238	0.0200	0.0000	0.0900	3	0.0133	0.0058	0.0100	0.0100	0.0200
MAL	32	0.0138	0.0124	0.0100	0.0000	0.0500	13	0.0154	0.0120	0.0100	0.0000	0.0400
MRH	26	0.0323	0.0304	0.0200	0.0000	0.1100	9	0.0156	0.0142	0.0100	0.0000	0.0400
MXRB	36	0.0347	0.0289	0.0300	0.0000	0.1400	11	0.0300	0.0195	0.0300	0.0000	0.0600
MIRB	38	0.0392	0.0264	0.0300	0.0000	0.1100	13	0.0354	0.0237	0.0300	0.0000	0.0800
HML	33	0.0127	0.0088	0.0100	0.0000	0.0300	15	0.0120	0.0094	0.0100	0.0000	0.0300
HXMS	42	0.0364	0.0359	0.0300	0.0000	0.1700	20	0.0285	0.0193	0.0300	0.0000	0.0600
HIMS	43	0.0358	0.0322	0.0300	0.0000	0.1300	20	0.0300	0.0253	0.0250	0.0000	0.1100
HDT	41	0.0351	0.0266	0.0300	0.0000	0.1100	20	0.0315	0.0258	0.0200	0.0100	0.1000
HSIH	39	0.0187	0.0156	0.0200	0.0000	0.0500	19	0.0168	0.0111	0.0200	0.0000	0.0400
HEB	19	0.0163	0.0142	0.0100	0.0000	0.0500	12	0.0225	0.0186	0.0200	0.0000	0.0700
RML	27	0.0089	0.0089	0.0100	0.0000	0.0300	10	0.0050	0.0053	0.0050	0.0000	0.0100
RXMS	35	0.0477	0.0415	0.0300	0.0000	0.1500	18	0.0578	0.0415	0.0550	0.0000	0.1400
RIMS	34	0.0300	0.0257	0.0250	0.0000	0.1100	18	0.0289	0.0323	0.0200	0.0000	0.1200
RGH	20	0.0175	0.0171	0.0150	0.0000	0.0600	5	0.0240	0.0152	0.0300	0.0000	0.0400
RMLD	34	0.0188	0.0153	0.0200	0.0000	0.0600	15	0.0200	0.0239	0.0100	0.0000	0.0800

Table A3.3 continued

	MA						A				
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
FML	31	0.0068	0.0070	0.0100	0.0000	0.0200	9	0.0089	0.0060	0.0100	0.0000	0.0200
FPL	31	0.0077	0.0072	0.0100	0.0000	0.0200	11	0.0064	0.0092	0.0000	0.0000	0.0300
FXMS	47	0.0274	0.0222	0.0200	0.0000	0.1000	20	0.0350	0.0267	0.0300	0.0000	0.1000
FIMS	47	0.0319	0.0239	0.0300	0.0000	0.1200	20	0.0190	0.0213	0.0100	0.0000	0.0800
FEB	17	0.0112	0.0122	0.0100	0.0000	0.0300	8	0.0088	0.0064	0.0100	0.0000	0.0200
FSIH	36	0.0153	0.0125	0.0100	0.0000	0.0400	12	0.0117	0.0103	0.0100	0.0000	0.0300
FMLP	27	0.0181	0.0130	0.0200	0.0000	0.0500	9	0.0222	0.0172	0.0100	0.0000	0.0400
TML	36	0.0061	0.0049	0.0100	0.0000	0.0100	11	0.0036	0.0067	0.0000	0.0000	0.0200
TXNF	50	0.0326	0.0296	0.0250	0.0000	0.1500	22	0.0282	0.0213	0.0200	0.0000	0.0800
TINF	49	0.0320	0.0235	0.0300	0.0000	0.1200	23	0.0322	0.0301	0.0300	0.0000	0.1100
TMLD	30	0.0187	0.0185	0.0200	0.0000	0.0700	8	0.0163	0.0074	0.0200	0.0000	0.0200
TMLP	20	0.0110	0.0117	0.0100	0.0000	0.0400	5	0.0160	0.0134	0.0100	0.0000	0.0300
i1l_bl	15	0.0280	0.0293	0.0200	0.0000	0.1100	8	0.0213	0.0217	0.0100	0.0000	0.0600
i1l_md	13	0.0246	0.0097	0.0200	0.0100	0.0400	8	0.0113	0.0064	0.0100	0.0000	0.0200
i2l_bl	17	0.0224	0.0148	0.0200	0.0000	0.0600	7	0.0271	0.0236	0.0200	0.0000	0.0600
i2l_md	17	0.0253	0.0142	0.0200	0.0000	0.0600	9	0.0244	0.0188	0.0200	0.0000	0.0500
c1l_bl	24	0.0263	0.0195	0.0200	0.0000	0.0700	10	0.0380	0.0365	0.0300	0.0000	0.1000
c1l_md	24	0.0221	0.0186	0.0200	0.0000	0.0900	12	0.0217	0.0180	0.0150	0.0000	0.0600
pm1l_bl	30	0.0280	0.0163	0.0300	0.0000	0.0600	12	0.0392	0.0271	0.0300	0.0100	0.0900
pm1l_md	31	0.0348	0.0363	0.0200	0.0000	0.1500	12	0.0467	0.0425	0.0300	0.0100	0.1500
pm2l_bl	21	0.0324	0.0247	0.0300	0.0000	0.0800	8	0.0488	0.0372	0.0450	0.0000	0.1100
pm2l_md	22	0.0241	0.0217	0.0200	0.0000	0.0900	10	0.0600	0.0216	0.0550	0.0300	0.1000
m1l_bl	6	0.0167	0.0151	0.0100	0.0000	0.0400	3	0.0167	0.0115	0.0100	0.0100	0.0300
m1l_md	6	0.0267	0.0163	0.0250	0.0100	0.0500	4	0.0325	0.0320	0.0200	0.0100	0.0800
m2l_bl	13	0.0262	0.0229	0.0200	0.0000	0.0600	6	0.0233	0.0197	0.0150	0.0100	0.0600
m2l_md	16	0.0275	0.0221	0.0300	0.0000	0.0600	7	0.0329	0.0243	0.0300	0.0100	0.0800
i1u_bl	20	0.0275	0.0217	0.0300	0.0000	0.0900	4	0.0200	0.0183	0.0200	0.0000	0.0400
i1u_md	10	0.0100	0.0067	0.0100	0.0000	0.0200	3	0.0300	0.0265	0.0400	0.0000	0.0500
i2u_bl	16	0.0300	0.0239	0.0250	0.0000	0.0800	5	0.0160	0.0055	0.0200	0.0100	0.0200
i2u_md	9	0.0378	0.0268	0.0300	0.0000	0.0900	4	0.0125	0.0050	0.0100	0.0100	0.0200
c1u_bl	24	0.0250	0.0227	0.0200	0.0000	0.0700	9	0.0278	0.0205	0.0200	0.0000	0.0600
c1u_md	24	0.0229	0.0227	0.0100	0.0000	0.0800	9	0.0133	0.0122	0.0100	0.0000	0.0300
pm1u_bl	22	0.0114	0.0121	0.0100	0.0000	0.0500	2	0.0150	0.0071	0.0150	0.0100	0.0200
pm1u_md	25	0.0332	0.0284	0.0300	0.0000	0.1200	2	0.0350	0.0212	0.0350	0.0200	0.0500
pm2u_bl	20	0.0270	0.0243	0.0200	0.0000	0.0800	6	0.0167	0.0225	0.0100	0.0000	0.0600

Table A3.3 continued

	MA						A				
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
pm2u_md	22	0.0436	0.0333	0.0400	0.0000	0.1600	6	0.0317	0.0172	0.0300	0.0100	0.0600
m1u_bl	11	0.0091	0.0083	0.0100	0.0000	0.0300	4	0.0025	0.0050	0.0000	0.0000	0.0100
m1u_md	14	0.0436	0.0247	0.0450	0.0100	0.0900	5	0.0520	0.0593	0.0400	0.0000	0.1400
m2u_bl	17	0.0229	0.0193	0.0200	0.0000	0.0700	5	0.0180	0.0192	0.0100	0.0000	0.0500
m2u_md	19	0.0463	0.0390	0.0300	0.0000	0.1400	6	0.0367	0.0207	0.0350	0.0100	0.0600
Individual	68	0.0253	0.0061	0.0243	0.0100	0.0481	55	0.0263	0.0120	0.0244	0.0050	0.0733
Skeleton	68	0.0245	0.0069	0.0237	0.0100	0.0493	54	0.0256	0.0128	0.0233	0.0050	0.0733
Dentition	46	0.0286	0.0112	0.0273	0.0100	0.0650	21	0.0290	0.0113	0.0257	0.0115	0.0520
Dentition: mandible	39	0.0275	0.0118	0.0267	0.0100	0.0733	18	0.0335	0.0170	0.0325	0.0133	0.0700
Dentition: maxilla	40	0.0286	0.0116	0.0271	0.0100	0.0650	13	0.0240	0.0111	0.0217	0.0029	0.0514
Cranium	56	0.0232	0.0067	0.0221	0.0100	0.0389	13	0.0282	0.0118	0.0300	0.0150	0.0600
Cranium: orbit	42	0.0200	0.0117	0.0200	0.0000	0.0550	9	0.0222	0.0103	0.0200	0.0050	0.0400
Cranium: facial	49	0.0227	0.0159	0.0220	0.0000	0.1150	9	0.0253	0.0139	0.0233	0.0133	0.0567
Cranium: temporal	42	0.0636	0.0357	0.0600	0.0000	0.1900	8	0.0542	0.0419	0.0433	0.0100	0.1450
Cranium: base	53	0.0312	0.0171	0.0250	0.0050	0.0875	11	0.0370	0.0195	0.0333	0.0100	0.0767
Cranium: vault	50	0.0170	0.0088	0.0150	0.0000	0.0500	3	0.0133	0.0104	0.0100	0.0050	0.0250
Mandible	43	0.0315	0.0162	0.0300	0.0000	0.0800	17	0.0256	0.0097	0.0267	0.0100	0.0450
Humerus	47	0.0299	0.0227	0.0250	0.0033	0.1500	23	0.0239	0.0118	0.0250	0.0000	0.0433
Radius	41	0.0275	0.0200	0.0220	0.0000	0.0900	20	0.0342	0.0255	0.0233	0.0100	0.1150
Femur	49	0.0209	0.0146	0.0186	0.0000	0.0800	22	0.0190	0.0119	0.0169	0.0025	0.0550
Tibia	52	0.0259	0.0184	0.0233	0.0000	0.0950	24	0.0244	0.0167	0.0200	0.0000	0.0550
Upper limb	53	0.0283	0.0217	0.0233	0.0000	0.1500	30	0.0289	0.0152	0.0250	0.0050	0.0733
Lower Limb	55	0.0228	0.0112	0.0200	0.0075	0.0725	27	0.0205	0.0106	0.0200	0.0050	0.0450
Midshafts	57	0.0330	0.0148	0.0317	0.0117	0.0817	38	0.0337	0.0234	0.0300	0.0050	0.1400
Upper limb: midshafts	47	0.0376	0.0271	0.0300	0.0000	0.1500	28	0.0376	0.0247	0.0325	0.0100	0.1400
Lower limb: midshafts	55	0.0307	0.0134	0.0300	0.0075	0.0725	27	0.0276	0.0166	0.0275	0.0050	0.0750
Lengths	49	0.0082	0.0061	0.0067	0.0000	0.0300	29	0.0084	0.0086	0.0100	0.0000	0.0300
Upper limb: lengths	38	0.0111	0.0086	0.0100	0.0000	0.0300	20	0.0095	0.0090	0.0100	0.0000	0.0300
Lower limb: lengths	40	0.0063	0.0046	0.0050	0.0000	0.0150	16	0.0059	0.0069	0.0050	0.0000	0.0200

A=adult, YA-young adult, MDA=middle adult, MA=mature adult

Table A3.4. Descriptive results for subadult fluctuating asymmetry scores stratified by age

	FI						EC				
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
CFMTN	0	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
CMAH	0	NA	NA	NA	NA	NA	1	0.0100	NA	0.0100	0.0100	0.0100
CMPL	NA	NA	NA	NA	NA	NA	2	0.0250	0.0071	0.0250	0.0200	0.0300
CMPB	NA	NA	NA	NA	NA	NA	2	0.0350	0.0071	0.0350	0.0300	0.0400
CMSAST	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
COCL	0	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
CECMIS	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
CFMTB	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
MAL	0	NA	NA	NA	NA	NA	3	0.0067	0.0058	0.0100	0.0000	0.0100
MRH	1	0.0400	NA	0.0400	0.0400	0.0400	2	0.0300	0.0141	0.0300	0.0200	0.0400
MXRB	2	0.0350	0.0071	0.0350	0.0300	0.0400	1	0.0300	NA	0.0300	0.0300	0.0300
MIRB	4	0.0325	0.0050	0.0300	0.0300	0.0400	5	0.0340	0.0251	0.0300	0.0000	0.0700
HML	3	0.0067	0.0058	0.0100	0.0000	0.0100	2	0.0100	0.0000	0.0100	0.0100	0.0100
HXMS	4	0.0250	0.0129	0.0250	0.0100	0.0400	3	0.0233	0.0058	0.0200	0.0200	0.0300
HIMS	4	0.0200	0.0216	0.0150	0.0000	0.0500	3	0.0133	0.0058	0.0100	0.0100	0.0200
HDT	NA	NA	NA	NA	NA	NA	2	0.0350	0.0495	0.0350	0.0000	0.0700
HSIH	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
HSMLD	3	0.0300	0.0520	0.0000	0.0000	0.0900	1	0.0200	NA	0.0200	0.0200	0.0200
HSMLP	3	0.0367	0.0306	0.0300	0.0100	0.0700	2	0.0450	0.0212	0.0450	0.0300	0.0600
RML	2	0.0050	0.0071	0.0050	0.0000	0.0100	2	0.0000	0.0000	0.0000	0.0000	0.0000
RXMS	6	0.0267	0.0163	0.0300	0.0000	0.0500	2	0.0450	0.0636	0.0450	0.0000	0.0900
RIMS	6	0.0350	0.0345	0.0250	0.0000	0.1000	2	0.0300	0.0283	0.0300	0.0100	0.0500
RGH	0	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
RSMLD	6	0.0350	0.0356	0.0300	0.0000	0.1000	1	0.0500	NA	0.0500	0.0500	0.0500
RMLD	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
FML	5	0.0000	0.0000	0.0000	0.0000	0.0000	2	0.0000	0.0000	0.0000	0.0000	0.0000
FPL	3	0.0000	0.0000	0.0000	0.0000	0.0000	1	0.0100	NA	0.0100	0.0100	0.0100
FXMS	6	0.0317	0.0214	0.0300	0.0100	0.0600	2	0.0150	0.0071	0.0150	0.0100	0.0200
FIMS	6	0.0267	0.0082	0.0250	0.0200	0.0400	2	0.0300	0.0283	0.0300	0.0100	0.0500
FEB	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
FSMLD	5	0.0260	0.0219	0.0200	0.0000	0.0600	1	0.0200	NA	0.0200	0.0200	0.0200
FSIH	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
FMLP	2	0.0100	0.0000	0.0100	0.0100	0.0100	1	0.0000	NA	0.0000	0.0000	0.0000
TML	5	0.0080	0.0045	0.0100	0.0000	0.0100	1	0.0000	NA	0.0000	0.0000	0.0000
TXNF	5	0.0340	0.0207	0.0300	0.0100	0.0600	1	0.0800	NA	0.0800	0.0800	0.0800

Table A3.4 continued

	FI						EC				
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
TINF	5	0.0140	0.0261	0.0000	0.0000	0.0600	1	0.0400	NA	0.0400	0.0400	0.0400
TSMLD	5	0.0240	0.0167	0.0200	0.0100	0.0500	1	0.0200	NA	0.0200	0.0200	0.0200
TMLD	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
TSMLP	3	0.0400	0.0100	0.0400	0.0300	0.0500	0	NA	NA	NA	NA	NA
TMLP	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
di1l_bl	NA	NA	NA	NA	NA	NA	4	0.0200	0.0141	0.0150	0.0100	0.0400
di1l_md	NA	NA	NA	NA	NA	NA	3	0.0267	0.0208	0.0200	0.0100	0.0500
di2l_bl	NA	NA	NA	NA	NA	NA	5	0.0420	0.0239	0.0400	0.0100	0.0700
di2l_md	NA	NA	NA	NA	NA	NA	3	0.0433	0.0321	0.0300	0.0200	0.0800
dc1l_bl	NA	NA	NA	NA	NA	NA	2	0.0550	0.0354	0.0550	0.0300	0.0800
dc1l_md	NA	NA	NA	NA	NA	NA	3	0.0067	0.0058	0.0100	0.0000	0.0100
dm1l_bl	NA	NA	NA	NA	NA	NA	2	0.0400	0.0283	0.0400	0.0200	0.0600
dm1l_md	NA	NA	NA	NA	NA	NA	4	0.0275	0.0206	0.0250	0.0100	0.0500
dm2l_bl	NA	NA	NA	NA	NA	NA	1	0.0600	NA	0.0600	0.0600	0.0600
dm2l_md	NA	NA	NA	NA	NA	NA	1	0.0500	NA	0.0500	0.0500	0.0500
di1u_bl	NA	NA	NA	NA	NA	NA	5	0.0200	0.0122	0.0200	0.0100	0.0400
di1u_md	NA	NA	NA	NA	NA	NA	4	0.0200	0.0082	0.0200	0.0100	0.0300
di2u_bl	NA	NA	NA	NA	NA	NA	3	0.0433	0.0058	0.0400	0.0400	0.0500
di2u_md	NA	NA	NA	NA	NA	NA	3	0.0267	0.0289	0.0100	0.0100	0.0600
dc1u_bl	NA	NA	NA	NA	NA	NA	4	0.0225	0.0263	0.0150	0.0000	0.0600
dc1u_md	NA	NA	NA	NA	NA	NA	4	0.0225	0.0320	0.0100	0.0000	0.0700
dm1u_bl	NA	NA	NA	NA	NA	NA	5	0.0300	0.0245	0.0400	0.0000	0.0600
dm1u_md	NA	NA	NA	NA	NA	NA	3	0.0667	0.0551	0.0400	0.0300	0.1300
dm2u_bl	NA	NA	NA	NA	NA	NA	2	0.0200	0.0283	0.0200	0.0000	0.0400
dm2u_md	NA	NA	NA	NA	NA	NA	3	0.0200	0.0346	0.0000	0.0000	0.0600
i1l_bl	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
i1l_md	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
i2l_bl	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
i2l_md	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
c1l_bl	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
c1l_md	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
pm1l_bl	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
pm1l_md	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
pm2l_bl	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
pm2l_md	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA

Table A3.4 continued

	FI						EC					
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
m1l_bl	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
m1l_md	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
m2l_bl	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
m2l_md	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
i1u_bl	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
i1u_md	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
i2u_bl	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
i2u_md	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
c1u_bl	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
c1u_md	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
pm1u_bl	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
pm1u_md	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
pm2u_bl	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
pm2u_md	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
m1u_bl	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
m1u_md	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
m2u_bl	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
m2u_md	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
Individual	9	0.0258	0.0096	0.0248	0.0113	0.0440	7	0.0243	0.0089	0.0262	0.0100	0.0368
Skeleton	9	0.0258	0.0096	0.0248	0.0113	0.0440	6	0.0214	0.0074	0.0228	0.0100	0.0317
Dentition	NA	NA	NA	NA	NA	NA	7	0.0270	0.0107	0.0300	0.0100	0.0392
Dentition: permanent	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
Dentition: deciduous	NA	NA	NA	NA	NA	NA	7	0.0270	0.0107	0.0300	0.0100	0.0392
Dentition: mandible	NA	NA	NA	NA	NA	NA	5	0.0332	0.0063	0.0333	0.0250	0.0417
Dentition: maxilla	NA	NA	NA	NA	NA	NA	7	0.0242	0.0119	0.0220	0.0100	0.0413
Cranium	0	NA	NA	NA	NA	NA	1	0.0100	NA	0.0100	0.0100	0.0100
Cranium: facial	NA	NA	NA	NA	NA	NA	1	0.0100	NA	0.0100	0.0100	0.0100
Cranium: temporal	NA	NA	NA	NA	NA	NA	2	0.0300	0.0000	0.0300	0.0300	0.0300
Mandible	4	0.0346	0.0042	0.0342	0.0300	0.0400	5	0.0233	0.0149	0.0267	0.0000	0.0400
Humerus	4	0.0256	0.0094	0.0250	0.0150	0.0375	3	0.0242	0.0038	0.0250	0.0200	0.0275
Radius	6	0.0308	0.0117	0.0333	0.0125	0.0433	2	0.0292	0.0059	0.0292	0.0250	0.0333
Femur	7	0.0209	0.0135	0.0167	0.0100	0.0500	2	0.0125	0.0035	0.0125	0.0100	0.0150
Tibia	5	0.0218	0.0101	0.0220	0.0100	0.0360	1	0.0350	NA	0.0350	0.0350	0.0350
Upper limb	6	0.0284	0.0108	0.0277	0.0125	0.0400	4	0.0272	0.0045	0.0263	0.0229	0.0333
Lower Limb	8	0.0234	0.0135	0.0200	0.0100	0.0500	2	0.0196	0.0066	0.0196	0.0150	0.0243

Table A3.4 continued

	FI						EC				
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
Midshafts	9	0.0288	0.0127	0.0275	0.0175	0.0600	5	0.0275	0.0109	0.0250	0.0150	0.0400
Upper limb: midshafts	6	0.0250	0.0121	0.0238	0.0100	0.0400	4	0.0275	0.0155	0.0225	0.0150	0.0500
Lower limb: midshafts	8	0.0297	0.0167	0.0250	0.0150	0.0600	2	0.0338	0.0053	0.0338	0.0300	0.0375
Lengths	7	0.0050	0.0041	0.0050	0.0000	0.0100	4	0.0038	0.0048	0.0025	0.0000	0.0100
Upper limb: lengths	4	0.0063	0.0048	0.0075	0.0000	0.0100	3	0.0050	0.0050	0.0050	0.0000	0.0100
Lower limb: lengths	7	0.0043	0.0045	0.0050	0.0000	0.0100	2	0.0000	0.0000	0.0000	0.0000	0.0000
	LC						**AD**					
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
CFMTN	4	0.0075	0.0096	0.0050	0.0000	0.0200	1	0.0300	NA	0.0300	0.0300	0.0300
CMAH	2	0.0250	0.0354	0.0250	0.0000	0.0500	1	0.0300	NA	0.0300	0.0300	0.0300
CMPL	2	0.0800	0.0849	0.0800	0.0200	0.1400	1	0.0300	NA	0.0300	0.0300	0.0300
CMPB	2	0.1750	0.1626	0.1750	0.0600	0.2900	1	0.0300	NA	0.0300	0.0300	0.0300
CMSAST	1	0.0100	NA	0.0100	0.0100	0.0100	0	NA	NA	NA	NA	NA
COCL	1	0.0500	NA	0.0500	0.0500	0.0500	1	0.0500	NA	0.0500	0.0500	0.0500
CECMIS	4	0.0450	0.0311	0.0350	0.0200	0.0900	1	0.0500	NA	0.0500	0.0500	0.0500
CFMTB	0	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
MAL	2	0.0050	0.0071	0.0050	0.0000	0.0100	0	NA	NA	NA	NA	NA
MRH	2	0.0150	0.0071	0.0150	0.0100	0.0200	0	NA	NA	NA	NA	NA
MXRB	2	0.0300	0.0141	0.0300	0.0200	0.0400	0	NA	NA	NA	NA	NA
MIRB	2	0.0300	0.0424	0.0300	0.0000	0.0600	0	NA	NA	NA	NA	NA
HML	1	0.0000	NA	0.0000	0.0000	0.0000	2	0.0050	0.0071	0.0050	0.0000	0.0100
HXMS	3	0.0167	0.0153	0.0200	0.0000	0.0300	3	0.0267	0.0306	0.0200	0.0000	0.0600
HIMS	3	0.0233	0.0208	0.0300	0.0000	0.0400	3	0.0400	0.0346	0.0200	0.0200	0.0800
HDT	2	0.0350	0.0354	0.0350	0.0100	0.0600	3	0.0333	0.0321	0.0200	0.0100	0.0700
HSIH	1	0.0100	NA	0.0100	0.0100	0.0100	1	0.0100	NA	0.0100	0.0100	0.0100
HSMLD	2	0.0150	0.0071	0.0150	0.0100	0.0200	2	0.0050	0.0071	0.0050	0.0000	0.0100
HSMLP	2	0.0050	0.0071	0.0050	0.0000	0.0100	2	0.0350	0.0071	0.0350	0.0300	0.0400
RML	2	0.0100	0.0000	0.0100	0.0100	0.0100	1	0.0100	NA	0.0100	0.0100	0.0100
RXMS	3	0.0533	0.0351	0.0500	0.0200	0.0900	2	0.0350	0.0212	0.0350	0.0200	0.0500
RIMS	3	0.0333	0.0153	0.0300	0.0200	0.0500	2	0.0500	0.0141	0.0500	0.0400	0.0600
RGH	0	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
RSMLD	2	0.0150	0.0071	0.0150	0.0100	0.0200	1	0.0100	NA	0.0100	0.0100	0.0100
RMLD	0	NA	NA	NA	NA	NA	1	0.0200	NA	0.0200	0.0200	0.0200
FML	1	0.0100	NA	0.0100	0.0100	0.0100	1	0.0000	NA	0.0000	0.0000	0.0000
FPL	1	0.0100	NA	0.0100	0.0100	0.0100	0	NA	NA	NA	NA	NA

Table A3.4 continued

	LC						AD				
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
FXMS	3	0.0133	0.0115	0.0200	0.0000	0.0200	2	0.0350	0.0354	0.0350	0.0100	0.0600
FIMS	3	0.0333	0.0321	0.0200	0.0100	0.0700	2	0.0150	0.0071	0.0150	0.0100	0.0200
FEB	1	0.0100	NA	0.0100	0.0100	0.0100	1	0.0200	NA	0.0200	0.0200	0.0200
FSMLD	2	0.0400	0.0424	0.0400	0.0100	0.0700	1	0.0100	NA	0.0100	0.0100	0.0100
FSIH	3	0.0233	0.0115	0.0300	0.0100	0.0300	0	NA	NA	NA	NA	NA
FMLP	2	0.0300	0.0283	0.0300	0.0100	0.0500	2	0.0050	0.0071	0.0050	0.0000	0.0100
TML	2	0.0150	0.0071	0.0150	0.0100	0.0200	2	0.0100	0.0000	0.0100	0.0100	0.0100
TXNF	5	0.0300	0.0235	0.0400	0.0000	0.0500	3	0.0300	0.0173	0.0200	0.0200	0.0500
TINF	4	0.0325	0.0287	0.0250	0.0100	0.0700	3	0.0267	0.0231	0.0400	0.0000	0.0400
TSMLD	1	0.0800	NA	0.0800	0.0800	0.0800	3	0.0100	0.0173	0.0000	0.0000	0.0300
TMLD	1	0.0200	NA	0.0200	0.0200	0.0200	0	NA	NA	NA	NA	NA
TSMLP	0	NA	NA	NA	NA	NA	1	0.0400	NA	0.0400	0.0400	0.0400
TMLP	1	0.0100	NA	0.0100	0.0100	0.0100	1	0.0200	NA	0.0200	0.0200	0.0200
di1l_bl	0	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
di1l_md	0	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
di2l_bl	0	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
di2l_md	0	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
dc1l_bl	2	0.0300	0.0000	0.0300	0.0300	0.0300	0	NA	NA	NA	NA	NA
dc1l_md	2	0.0150	0.0071	0.0150	0.0100	0.0200	0	NA	NA	NA	NA	NA
dm1l_bl	2	0.0350	0.0495	0.0350	0.0000	0.0700	0	NA	NA	NA	NA	NA
dm1l_md	2	0.0550	0.0495	0.0550	0.0200	0.0900	0	NA	NA	NA	NA	NA
dm2l_bl	1	0.0100	NA	0.0100	0.0100	0.0100	0	NA	NA	NA	NA	NA
dm2l_md	1	0.0800	NA	0.0800	0.0800	0.0800	0	NA	NA	NA	NA	NA
di1u_bl	0	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
di1u_md	0	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
di2u_bl	0	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
di2u_md	0	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
dc1u_bl	2	0.0200	0.0000	0.0200	0.0200	0.0200	0	NA	NA	NA	NA	NA
dc1u_md	2	0.0200	0.0283	0.0200	0.0000	0.0400	0	NA	NA	NA	NA	NA
dm1u_bl	2	0.0450	0.0495	0.0450	0.0100	0.0800	0	NA	NA	NA	NA	NA
dm1u_md	1	0.0100	NA	0.0100	0.0100	0.0100	0	NA	NA	NA	NA	NA
dm2u_bl	3	0.0033	0.0058	0.0000	0.0000	0.0100	0	NA	NA	NA	NA	NA
dm2u_md	1	0.0000	NA	0.0000	0.0000	0.0000	0	NA	NA	NA	NA	NA
i1l_bl	5	0.0380	0.0268	0.0500	0.0100	0.0700	0	NA	NA	NA	NA	NA
i1l_md	4	0.0200	0.0183	0.0200	0.0000	0.0400	2	0.0200	0.0141	0.0200	0.0100	0.0300

Table A3.4 continued

	LC						AD				
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
i2l_bl	1	0.0300	NA	0.0300	0.0300	0.0300	1	0.0100	NA	0.0100	0.0100	0.0100
i2l_md	1	0.0100	NA	0.0100	0.0100	0.0100	1	0.0000	NA	0.0000	0.0000	0.0000
c1l_bl	1	0.0200	NA	0.0200	0.0200	0.0200	1	0.0300	NA	0.0300	0.0300	0.0300
c1l_md	2	0.0200	0.0000	0.0200	0.0200	0.0200	1	0.0300	NA	0.0300	0.0300	0.0300
pm1l_bl	2	0.0100	0.0000	0.0100	0.0100	0.0100	2	0.0050	0.0071	0.0050	0.0000	0.0100
pm1l_md	2	0.0300	0.0141	0.0300	0.0200	0.0400	2	0.0250	0.0354	0.0250	0.0000	0.0500
pm2l_bl	0	NA	NA	NA	NA	NA	1	0.0500	NA	0.0500	0.0500	0.0500
pm2l_md	0	NA	NA	NA	NA	NA	1	0.0600	NA	0.0600	0.0600	0.0600
m1l_bl	5	0.0200	0.0122	0.0200	0.0100	0.0400	2	0.0300	0.0141	0.0300	0.0200	0.0400
m1l_md	5	0.0120	0.0130	0.0100	0.0000	0.0300	2	0.0200	0.0283	0.0200	0.0000	0.0400
m2l_bl	0	NA	NA	NA	NA	NA	1	0.0000	NA	0.0000	0.0000	0.0000
m2l_md	0	NA	NA	NA	NA	NA	1	0.0400	NA	0.0400	0.0400	0.0400
i1u_bl	4	0.0225	0.0287	0.0150	0.0000	0.0600	2	0.0200	0.0283	0.0200	0.0000	0.0400
i1u_md	4	0.0050	0.0058	0.0050	0.0000	0.0100	2	0.0400	0.0283	0.0400	0.0200	0.0600
i2u_bl	2	0.0150	0.0071	0.0150	0.0100	0.0200	2	0.0350	0.0071	0.0350	0.0300	0.0400
i2u_md	2	0.0050	0.0071	0.0050	0.0000	0.0100	2	0.0150	0.0071	0.0150	0.0100	0.0200
c1u_bl	0	NA	NA	NA	NA	NA	1	0.0000	NA	0.0000	0.0000	0.0000
c1u_md	0	NA	NA	NA	NA	NA	1	0.0100	NA	0.0100	0.0100	0.0100
pm1u_bl	3	0.0133	0.0115	0.0200	0.0000	0.0200	2	0.0300	0.0141	0.0300	0.0200	0.0400
pm1u_md	3	0.0133	0.0153	0.0100	0.0000	0.0300	2	0.0150	0.0071	0.0150	0.0100	0.0200
pm2u_bl	1	0.0100	NA	0.0100	0.0100	0.0100	2	0.0350	0.0212	0.0350	0.0200	0.0500
pm2u_md	1	0.0100	NA	0.0100	0.0100	0.0100	2	0.0000	0.0000	0.0000	0.0000	0.0000
m1u_bl	5	0.0240	0.0195	0.0100	0.0100	0.0500	2	0.0400	0.0000	0.0400	0.0400	0.0400
m1u_md	5	0.0240	0.0167	0.0200	0.0100	0.0500	2	0.0250	0.0212	0.0250	0.0100	0.0400
m2u_bl	0	NA	NA	NA	NA	NA	1	0.0100	NA	0.0100	0.0100	0.0100
m2u_md	0	NA	NA	NA	NA	NA	1	0.0500	NA	0.0500	0.0500	0.0500
Individual	6	0.0222	0.0018	0.0226	0.0190	0.0237	4	0.0245	0.0074	0.0234	0.0180	0.0333
Skeleton	5	0.0258	0.0109	0.0208	0.0164	0.0422	4	0.0226	0.0072	0.0196	0.0180	0.0333
Dentition	6	0.0222	0.0082	0.0233	0.0092	0.0308	2	0.0243	0.0080	0.0243	0.0187	0.0300
Dentition: permanent	6	0.0207	0.0070	0.0200	0.0092	0.0288	2	0.0243	0.0080	0.0243	0.0187	0.0300
Dentition: deciduous	3	0.0308	0.0118	0.0350	0.0175	0.0400	0	NA	NA	NA	NA	NA
Dentition: mandible	6	0.0272	0.0111	0.0235	0.0140	0.0414	2	0.0251	0.0110	0.0251	0.0173	0.0329
Dentition: maxilla	6	0.0160	0.0095	0.0144	0.0063	0.0338	2	0.0242	0.0059	0.0242	0.0200	0.0283
Cranium	4	0.0175	0.0087	0.0200	0.0050	0.0250	2	0.0400	0.0141	0.0400	0.0300	0.0500
Cranium: facial	4	0.0125	0.0119	0.0125	0.0000	0.0250	1	0.0300	NA	0.0300	0.0300	0.0300

Table A3.4 continued

	LC						AD				
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
Cranium: temporal	2	0.1125	0.0601	0.1125	0.0700	0.1550	1	0.0300	NA	0.0300	0.0300	0.0300
Mandible	2	0.0200	0.0106	0.0200	0.0125	0.0275	0	NA	NA	NA	NA	NA
Humerus	3	0.0164	0.0125	0.0200	0.0025	0.0267	3	0.0263	0.0164	0.0200	0.0140	0.0450
Radius	4	0.0319	0.0160	0.0263	0.0200	0.0550	2	0.0300	0.0000	0.0300	0.0300	0.0300
Femur	4	0.0221	0.0112	0.0218	0.0100	0.0350	3	0.0182	0.0095	0.0200	0.0080	0.0267
Tibia	5	0.0328	0.0235	0.0400	0.0067	0.0600	4	0.0170	0.0145	0.0190	0.0000	0.0300
Upper limb	4	0.0237	0.0107	0.0221	0.0125	0.0380	3	0.0251	0.0101	0.0200	0.0186	0.0367
Lower Limb	5	0.0313	0.0156	0.0250	0.0125	0.0475	4	0.0147	0.0118	0.0153	0.0000	0.0283
Midshafts	5	0.0304	0.0149	0.0383	0.0138	0.0450	4	0.0285	0.0139	0.0250	0.0167	0.0475
Upper limb: midshafts	3	0.0317	0.0128	0.0350	0.0175	0.0425	3	0.0342	0.0245	0.0200	0.0200	0.0625
Lower limb: midshafts	5	0.0315	0.0176	0.0400	0.0100	0.0475	3	0.0242	0.0123	0.0300	0.0100	0.0325
Lengths	3	0.0106	0.0042	0.0100	0.0067	0.0150	3	0.0067	0.0029	0.0050	0.0050	0.0100
Upper limb: lengths	2	0.0075	0.0035	0.0075	0.0050	0.0100	2	0.0050	0.0071	0.0050	0.0000	0.0100
Lower limb: lengths	3	0.0133	0.0058	0.0100	0.0100	0.0200	2	0.0075	0.0035	0.0075	0.0050	0.0100

FI=foetal age to infant, EC=early childhood, LC=late childhood, AD=adolescence

Table A3.5. Descriptive results for adult fluctuating asymmetry scores stratified by sex

	Male						Female						Indeterminate					
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
COBB	51	0.0186	0.0150	0.0200	0.0000	0.0600	63	0.0170	0.0160	0.0100	0.0000	0.0700	5	0.0160	0.0114	0.0200	0.0000	0.0300
COBH	52	0.0229	0.0156	0.0200	0.0000	0.0700	64	0.0197	0.0140	0.0200	0.0000	0.0700	5	0.0200	0.0200	0.0100	0.0000	0.0500
CNOR	54	0.0154	0.0114	0.0100	0.0000	0.0400	60	0.0168	0.0143	0.0100	0.0000	0.0500	5	0.0180	0.0179	0.0200	0.0000	0.0400
CFMTN	55	0.0160	0.0127	0.0100	0.0000	0.0500	66	0.0183	0.0138	0.0150	0.0000	0.0600	6	0.0183	0.0075	0.0200	0.0100	0.0300
CFMTNS	44	0.0148	0.0127	0.0100	0.0000	0.0400	61	0.0170	0.0165	0.0100	0.0000	0.0700	6	0.0167	0.0082	0.0150	0.0100	0.0300
CMAH	55	0.0427	0.0403	0.0300	0.0000	0.1600	63	0.0429	0.0365	0.0400	0.0000	0.2300	5	0.0520	0.0507	0.0400	0.0100	0.1400
CMPL	44	0.0557	0.0512	0.0400	0.0000	0.2500	69	0.0736	0.0572	0.0600	0.0000	0.2300	3	0.0500	0.0458	0.0600	0.0000	0.0900
CMPB	47	0.0477	0.0391	0.0400	0.0000	0.2000	74	0.0655	0.0541	0.0550	0.0000	0.1900	5	0.0540	0.0416	0.0700	0.0100	0.1000
CMSAST	32	0.0431	0.0242	0.0450	0.0000	0.1100	54	0.0365	0.0362	0.0300	0.0000	0.1600	2	0.0650	0.0212	0.0650	0.0500	0.0800
COCL	55	0.0484	0.0417	0.0400	0.0000	0.2200	73	0.0495	0.0438	0.0400	0.0000	0.2400	6	0.0383	0.0293	0.0250	0.0100	0.0800
COPO	62	0.0316	0.0238	0.0300	0.0000	0.1100	77	0.0230	0.0233	0.0100	0.0000	0.1000	4	0.0200	0.0082	0.0200	0.0100	0.0300
CBAPO	64	0.0238	0.0216	0.0200	0.0000	0.0800	83	0.0248	0.0211	0.0200	0.0000	0.1100	5	0.0160	0.0195	0.0100	0.0000	0.0500
CECMIS	17	0.0312	0.0203	0.0300	0.0000	0.0700	28	0.0300	0.0287	0.0200	0.0000	0.1000	3	0.0200	0.0173	0.0100	0.0100	0.0400
CNMS	40	0.0188	0.0174	0.0200	0.0000	0.0800	54	0.0167	0.0135	0.0150	0.0000	0.0600	2	0.0150	0.0071	0.0150	0.0100	0.0200
CBZO	41	0.0127	0.0095	0.0100	0.0000	0.0300	53	0.0108	0.0098	0.0100	0.0000	0.0400	1	0.0000	NA	0.0000	0.0000	0.0000
CFMTB	49	0.0190	0.0145	0.0200	0.0000	0.0500	57	0.0165	0.0133	0.0100	0.0000	0.0600	2	0.0050	0.0071	0.0050	0.0000	0.0100
CBPO	57	0.0200	0.0166	0.0200	0.0000	0.0600	68	0.0169	0.0143	0.0200	0.0000	0.0600	3	0.0100	0.0000	0.0100	0.0100	0.0100
CBAST	46	0.0189	0.0151	0.0200	0.0000	0.0700	59	0.0151	0.0121	0.0100	0.0000	0.0600	2	0.0050	0.0071	0.0050	0.0000	0.0100
CLFMT	43	0.0088	0.0082	0.0100	0.0000	0.0300	55	0.0100	0.0077	0.0100	0.0000	0.0300	3	0.0100	0.0100	0.0100	0.0000	0.0200
CLAST	41	0.0266	0.0236	0.0200	0.0000	0.1100	57	0.0230	0.0219	0.0200	0.0000	0.0900	2	0.0200	0.0283	0.0200	0.0000	0.0400
MAL	34	0.0118	0.0087	0.0100	0.0000	0.0300	48	0.0156	0.0149	0.0100	0.0000	0.0500	12	0.0125	0.0129	0.0100	0.0000	0.0400
MRH	27	0.0359	0.0304	0.0300	0.0000	0.1000	44	0.0348	0.0332	0.0200	0.0000	0.1200	8	0.0188	0.0136	0.0150	0.0000	0.0400
MXRB	32	0.0325	0.0278	0.0300	0.0000	0.1400	53	0.0364	0.0247	0.0300	0.0000	0.0900	10	0.0250	0.0196	0.0250	0.0000	0.0600
MIRB	39	0.0359	0.0263	0.0300	0.0000	0.1100	59	0.0419	0.0273	0.0400	0.0000	0.1200	10	0.0280	0.0316	0.0200	0.0000	0.0900
HML	43	0.0126	0.0103	0.0100	0.0000	0.0400	47	0.0136	0.0094	0.0100	0.0000	0.0300	0	NA	NA	NA	NA	NA
HXMS	59	0.0402	0.0295	0.0300	0.0000	0.1700	72	0.0346	0.0287	0.0300	0.0000	0.1700	0	NA	NA	NA	NA	NA
HIMS	59	0.0329	0.0244	0.0300	0.0000	0.1000	73	0.0312	0.0276	0.0200	0.0000	0.1300	0	NA	NA	NA	NA	NA
HDT	57	0.0360	0.0269	0.0300	0.0000	0.1200	72	0.0310	0.0251	0.0200	0.0000	0.1100	0	NA	NA	NA	NA	NA
HSIH	48	0.0167	0.0145	0.0200	0.0000	0.0700	62	0.0189	0.0148	0.0200	0.0000	0.0500	1	0.0000	NA	0.0000	0.0000	0.0000
HEB	28	0.0157	0.0132	0.0100	0.0000	0.0500	32	0.0197	0.0187	0.0150	0.0000	0.0700	1	0.0100	NA	0.0100	0.0100	0.0100
RML	34	0.0094	0.0089	0.0100	0.0000	0.0300	45	0.0100	0.0077	0.0100	0.0000	0.0300	3	0.0033	0.0058	0.0000	0.0000	0.0100
RXMS	47	0.0404	0.0333	0.0300	0.0000	0.1400	63	0.0457	0.0366	0.0400	0.0000	0.1500	3	0.0600	0.0693	0.0200	0.0200	0.1400
RIMS	48	0.0277	0.0225	0.0200	0.0000	0.1000	64	0.0298	0.0302	0.0200	0.0000	0.1200	2	0.0250	0.0212	0.0250	0.0100	0.0400
RGH	23	0.0291	0.0254	0.0200	0.0000	0.0900	30	0.0220	0.0152	0.0200	0.0000	0.0600	0	NA	NA	NA	NA	NA
RMLD	39	0.0208	0.0169	0.0200	0.0000	0.0600	53	0.0177	0.0160	0.0200	0.0000	0.0700	2	0.0650	0.0212	0.0650	0.0500	0.0800

Table A3.5 continued

	Male						Female						Indeterminate					
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
FML	40	0.0080	0.0085	0.0100	0.0000	0.0300	50	0.0076	0.0066	0.0100	0.0000	0.0200	0	NA	NA	NA	NA	NA
FPL	42	0.0081	0.0080	0.0100	0.0000	0.0300	51	0.0067	0.0065	0.0100	0.0000	0.0200	0	NA	NA	NA	NA	NA
FXMS	64	0.0305	0.0243	0.0200	0.0000	0.0800	88	0.0258	0.0213	0.0200	0.0000	0.1000	0	NA	NA	NA	NA	NA
FIMS	64	0.0228	0.0208	0.0200	0.0000	0.1100	87	0.0260	0.0213	0.0200	0.0000	0.1200	0	NA	NA	NA	NA	NA
FEB	36	0.0114	0.0099	0.0100	0.0000	0.0400	31	0.0097	0.0102	0.0100	0.0000	0.0300	0	NA	NA	NA	NA	NA
FSIH	50	0.0134	0.0115	0.0100	0.0000	0.0500	58	0.0152	0.0126	0.0100	0.0000	0.0400	0	NA	NA	NA	NA	NA
FMLP	36	0.0144	0.0118	0.0100	0.0000	0.0400	39	0.0190	0.0133	0.0100	0.0000	0.0500	0	NA	NA	NA	NA	NA
TML	47	0.0064	0.0067	0.0100	0.0000	0.0200	55	0.0060	0.0060	0.0100	0.0000	0.0200	0	NA	NA	NA	NA	NA
TXNF	58	0.0333	0.0272	0.0200	0.0000	0.1300	97	0.0306	0.0288	0.0200	0.0000	0.1500	0	NA	NA	NA	NA	NA
TINF	58	0.0360	0.0281	0.0300	0.0000	0.1300	99	0.0355	0.0313	0.0300	0.0000	0.1400	0	NA	NA	NA	NA	NA
TMLD	38	0.0161	0.0128	0.0150	0.0000	0.0500	42	0.0183	0.0168	0.0200	0.0000	0.0700	0	NA	NA	NA	NA	NA
TMLP	29	0.0086	0.0103	0.0100	0.0000	0.0400	25	0.0100	0.0108	0.0100	0.0000	0.0300	0	NA	NA	NA	NA	NA
i1l_bl	8	0.0188	0.0113	0.0200	0.0000	0.0300	24	0.0258	0.0260	0.0200	0.0000	0.1100	5	0.0260	0.0230	0.0200	0.0000	0.0500
i1l_md	7	0.0114	0.0135	0.0100	0.0000	0.0300	23	0.0196	0.0152	0.0200	0.0000	0.0700	4	0.0175	0.0096	0.0150	0.0100	0.0300
i2l_bl	14	0.0186	0.0117	0.0150	0.0100	0.0500	26	0.0212	0.0184	0.0100	0.0000	0.0600	4	0.0175	0.0050	0.0200	0.0100	0.0200
i2l_md	8	0.0213	0.0210	0.0150	0.0000	0.0600	29	0.0241	0.0138	0.0200	0.0000	0.0500	4	0.0225	0.0126	0.0200	0.0100	0.0400
c1l_bl	17	0.0235	0.0221	0.0200	0.0000	0.0700	35	0.0231	0.0210	0.0200	0.0000	0.1000	6	0.0400	0.0341	0.0350	0.0000	0.1000
c1l_md	14	0.0221	0.0172	0.0200	0.0000	0.0600	38	0.0239	0.0199	0.0200	0.0000	0.0900	6	0.0167	0.0082	0.0150	0.0100	0.0300
pm1l_bl	20	0.0260	0.0198	0.0200	0.0000	0.0900	42	0.0293	0.0185	0.0300	0.0000	0.0800	7	0.0400	0.0265	0.0300	0.0100	0.0900
pm1l_md	22	0.0400	0.0352	0.0300	0.0100	0.1500	43	0.0333	0.0343	0.0200	0.0000	0.1500	6	0.0333	0.0207	0.0300	0.0100	0.0700
pm2l_bl	17	0.0247	0.0207	0.0200	0.0000	0.0600	31	0.0323	0.0228	0.0300	0.0000	0.0900	5	0.0540	0.0404	0.0500	0.0000	0.1100
pm2l_md	19	0.0400	0.0354	0.0300	0.0000	0.1400	32	0.0338	0.0318	0.0300	0.0000	0.1100	5	0.0500	0.0141	0.0500	0.0300	0.0700
m1l_bl	11	0.0236	0.0157	0.0300	0.0000	0.0500	7	0.0157	0.0172	0.0100	0.0000	0.0400	2	0.0100	0.0000	0.0100	0.0100	0.0100
m1l_md	10	0.0250	0.0143	0.0250	0.0100	0.0400	8	0.0188	0.0155	0.0150	0.0000	0.0500	3	0.0400	0.0346	0.0200	0.0200	0.0800
m2l_bl	11	0.0245	0.0225	0.0100	0.0000	0.0600	18	0.0222	0.0207	0.0150	0.0000	0.0600	3	0.0200	0.0100	0.0200	0.0100	0.0300
m2l_md	15	0.0293	0.0255	0.0300	0.0000	0.0800	20	0.0270	0.0239	0.0200	0.0000	0.0800	4	0.0325	0.0096	0.0350	0.0200	0.0400
i1u_bl	14	0.0271	0.0230	0.0250	0.0000	0.0900	26	0.0196	0.0148	0.0200	0.0000	0.0500	4	0.0250	0.0100	0.0300	0.0100	0.0300
i1u_md	5	0.0200	0.0292	0.0100	0.0000	0.0700	18	0.0194	0.0180	0.0100	0.0000	0.0500	1	0.0100	NA	0.0100	0.0100	0.0100
i2u_bl	9	0.0167	0.0212	0.0100	0.0000	0.0700	25	0.0396	0.0226	0.0400	0.0100	0.0800	2	0.0100	0.0141	0.0100	0.0000	0.0200
i2u_md	1	0.0800	#N/A	0.0800	0.0800	0.0800	20	0.0405	0.0390	0.0300	0.0000	0.1600	1	0.0400	NA	0.0400	0.0400	0.0400
c1u_bl	17	0.0206	0.0185	0.0200	0.0000	0.0700	36	0.0247	0.0208	0.0200	0.0000	0.0700	2	0.0200	0.0283	0.0200	0.0000	0.0400
c1u_md	13	0.0162	0.0126	0.0100	0.0000	0.0400	39	0.0203	0.0197	0.0100	0.0000	0.0800	2	0.0100	0.0000	0.0100	0.0100	0.0100
pm1u_bl	11	0.0145	0.0151	0.0100	0.0000	0.0500	27	0.0152	0.0163	0.0100	0.0000	0.0700	3	0.0100	0.0100	0.0100	0.0000	0.0200
pm1u_md	10	0.0540	0.0295	0.0400	0.0200	0.1100	29	0.0286	0.0200	0.0300	0.0000	0.0700	3	0.0533	0.0577	0.0200	0.0200	0.1200
pm2u_bl	17	0.0206	0.0182	0.0200	0.0000	0.0600	28	0.0243	0.0236	0.0200	0.0000	0.0800	2	0.0100	0.0141	0.0100	0.0000	0.0200
pm2u_md	13	0.0354	0.0215	0.0300	0.0100	0.0700	29	0.0407	0.0318	0.0400	0.0000	0.1400	2	0.0950	0.0919	0.0950	0.0300	0.1600

Table A3.5 continued

	Male						Female						Indeterminate					
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
m1u_bl	8	0.0100	0.0141	0.0050	0.0000	0.0400	17	0.0112	0.0093	0.0100	0.0000	0.0300	2	0.0050	0.0071	0.0050	0.0000	0.0100
m1u_md	9	0.0256	0.0142	0.0300	0.0100	0.0500	18	0.0489	0.0363	0.0500	0.0000	0.1400	2	0.0350	0.0071	0.0350	0.0300	0.0400
m2u_bl	10	0.0340	0.0232	0.0350	0.0000	0.0800	22	0.0268	0.0221	0.0200	0.0000	0.0700	2	0.0150	0.0071	0.0150	0.0100	0.0200
m2u_md	11	0.0409	0.0239	0.0400	0.0000	0.0800	26	0.0488	0.0409	0.0350	0.0000	0.1400	2	0.0400	0.0283	0.0400	0.0200	0.0600
Individual	90	0.0246	0.0052	0.0238	0.0133	0.0400	140	0.0254	0.0088	0.0243	0.0000	0.0625	21	0.0255	0.0139	0.0233	0.0050	0.0733
Skeleton	90	0.0250	0.0075	0.0231	0.0133	0.0600	139	0.0247	0.0092	0.0236	0.0000	0.0625	20	0.0242	0.0139	0.0200	0.0050	0.0733
Dentition	40	0.0277	0.0123	0.0246	0.0100	0.0700	65	0.0276	0.0101	0.0101	0.0050	0.0540	10	0.0339	0.0145	0.0315	0.0182	0.0650
Dentition: mandible	34	0.0270	0.0124	0.0262	0.0100	0.0520	57	0.0276	0.0131	0.0089	0.0100	0.0733	8	0.0326	0.0122	0.0305	0.0150	0.0500
Dentition: maxilla	32	0.0270	0.0134	0.0250	0.0050	0.0700	56	0.0282	0.0118	0.0104	0.0029	0.0550	5	0.0335	0.0182	0.0293	0.0182	0.0650
Cranium	70	0.0240	0.0072	0.0235	0.0100	0.0600	95	0.0227	0.0079	0.0213	0.0100	0.0550	7	0.0214	0.0075	0.0233	0.0100	0.0322
Cranium: orbit	51	0.0187	0.0087	0.0200	0.0000	0.0400	64	0.0186	0.0109	0.0200	0.0000	0.0550	4	0.0238	0.0144	0.0250	0.0050	0.0400
Cranium: facial	60	0.0215	0.0104	0.0200	0.0025	0.0500	72	0.0219	0.0138	0.0200	0.0000	0.1150	6	0.0253	0.0160	0.0204	0.0133	0.0567
Cranium: temporal	47	0.0490	0.0246	0.0433	0.0000	0.1033	74	0.0612	0.0382	0.0371	0.0000	0.1900	5	0.0497	0.0268	0.0600	0.0100	0.0733
Cranium: base	66	0.0307	0.0173	0.0300	0.0000	0.1033	89	0.0279	0.0175	0.0148	0.0000	0.0875	7	0.0219	0.0116	0.0200	0.0100	0.0400
Cranium: vault	57	0.0178	0.0111	0.0175	0.0000	0.0500	76	0.0168	0.0115	0.0074	0.0000	0.0900	3	0.0108	0.0038	0.0100	0.0075	0.0150
Mandible	43	0.0303	0.0158	0.0267	0.0067	0.0800	67	0.0321	0.0164	0.0185	0.0000	0.0850	13	0.0215	0.0083	0.0200	0.0100	0.0400
Humerus	65	0.0282	0.0143	0.0267	0.0000	0.0625	82	0.0282	0.0192	0.0250	0.0000	0.1500	1	0.0050	NA	0.0050	0.0050	0.0050
Radius	54	0.0273	0.0179	0.0229	0.0000	0.0900	73	0.0283	0.0206	0.0111	0.0000	0.1150	3	0.0389	0.0299	0.0233	0.0200	0.0733
Femur	67	0.0186	0.0129	0.0157	0.0000	0.0700	94	0.0190	0.0125	0.0085	0.0000	0.0800	0	NA	NA	NA	NA	NA
Tibia	67	0.0257	0.0179	0.0233	0.0000	0.1050	101	0.0276	0.0195	0.0233	0.0000	0.1050	0	NA	NA	NA	NA	NA
Upper limb	71	0.0273	0.0106	0.0260	0.0000	0.0600	99	0.0285	0.0186	0.0250	0.0000	0.1500	4	0.0304	0.0297	0.0217	0.0050	0.0733
Lower Limb	72	0.0220	0.0118	0.0200	0.0067	0.0700	114	0.0226	0.0123	0.0200	0.0000	0.0725	0	NA	NA	NA	NA	NA
Midshafts	76	0.0328	0.0133	0.0300	0.0100	0.0700	120	0.0314	0.0147	0.0127	0.0050	0.0817	3	0.0617	0.0683	0.0300	0.0150	0.1400
Upper limb: midshafts	65	0.0348	0.0143	0.0325	0.0050	0.0700	88	0.0352	0.0217	0.0148	0.0000	0.1500	3	0.0617	0.0683	0.0300	0.0150	0.1400

Table A3.5 continued

	Male						Female						Indeterminate					
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
Lower limb: midshafts	72	0.0306	0.0152	0.0300	0.0075	0.0800	113	0.0292	0.0152	0.0148	0.0050	0.0800	0	NA	NA	NA	NA	NA
Lengths	68	0.0102	0.0087	0.0100	0.0000	0.0400	90	0.0091	0.0067	0.0074	0.0000	0.0300	3	0.0033	0.0058	0.0000	0.0000	0.0100
Upper limb: lengths	53	0.0119	0.0097	0.0100	0.0000	0.0400	62	0.0120	0.0085	0.0074	0.0000	0.0300	3	0.0033	0.0058	0.0000	0.0000	0.0100
Lower limb: lengths	53	0.0073	0.0063	0.0050	0.0000	0.0200	68	0.0067	0.0052	0.0074	0.0000	0.0200	0	NA	NA	NA	NA	NA

Table A3.6. Descriptive results for fluctuating asymmetry scores per sex and population groups

	Grote Kerk																	
	Male						Female						Indeterminate					
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
COBB	39	0.0177	0.0156	0.0200	0.0000	0.0600	40	0.0198	0.0180	0.0100	0.0000	0.0700	2	0.0250	0.0071	0.0250	0.0200	0.0300
COBH	41	0.0232	0.0144	0.0200	0.0000	0.0500	42	0.0188	0.0155	0.0200	0.0000	0.0700	2	0.0150	0.0212	0.0150	0.0000	0.0300
CNOR	43	0.0142	0.0110	0.0100	0.0000	0.0400	39	0.0174	0.0141	0.0200	0.0000	0.0500	2	0.0100	0.0141	0.0100	0.0000	0.0200
CFMTN	44	0.0164	0.0131	0.0100	0.0000	0.0500	43	0.0207	0.0140	0.0200	0.0000	0.0600	2	0.0200	0.0141	0.0200	0.0100	0.0300
CFMTNS	35	0.0160	0.0119	0.0200	0.0000	0.0400	41	0.0178	0.0185	0.0100	0.0000	0.0700	2	0.0150	0.0071	0.0150	0.0100	0.0200
CMAH	43	0.0426	0.0399	0.0300	0.0000	0.1600	41	0.0400	0.0277	0.0400	0.0000	0.1000	2	0.0350	0.0071	0.0350	0.0300	0.0400
CMPL	31	0.0539	0.0551	0.0400	0.0000	0.2500	48	0.0713	0.0563	0.0550	0.0000	0.2000	1	0.0900	NA	0.0900	0.0900	0.0900
CMPB	32	0.0431	0.0341	0.0400	0.0000	0.1100	51	0.0627	0.0516	0.0500	0.0000	0.1900	1	0.0800	NA	0.0800	0.0800	0.0800
CMSAST	23	0.0439	0.0255	0.0500	0.0000	0.1100	37	0.0384	0.0402	0.0300	0.0000	0.1600	1	0.0500	NA	0.0500	0.0500	0.0500
COCL	44	0.0484	0.0442	0.0400	0.0000	0.2200	54	0.0504	0.0485	0.0400	0.0000	0.2400	1	0.0300	NA	0.0300	0.0300	0.0300
COPO	47	0.0309	0.0242	0.0300	0.0000	0.1100	52	0.0231	0.0233	0.0150	0.0000	0.1000	1	0.0200	NA	0.0200	0.0200	0.0200
CBAPO	49	0.0247	0.0215	0.0200	0.0000	0.0800	56	0.0257	0.0218	0.0200	0.0000	0.1100	2	0.0050	0.0071	0.0050	0.0000	0.0100
CECMIS	11	0.0300	0.0190	0.0300	0.0000	0.0600	17	0.0271	0.0257	0.0200	0.0000	0.0800	2	0.0250	0.0212	0.0250	0.0100	0.0400
CNMS	29	0.0200	0.0185	0.0200	0.0000	0.0800	36	0.0164	0.0138	0.0100	0.0000	0.0600	1	0.0100	NA	0.0100	0.0100	0.0100
CBZO	35	0.0129	0.0089	0.0100	0.0000	0.0300	39	0.0100	0.0103	0.0100	0.0000	0.0400	1	0.0000	NA	0.0000	0.0000	0.0000
CFMTB	41	0.0200	0.0141	0.0200	0.0000	0.0500	43	0.0153	0.0133	0.0100	0.0000	0.0600	2	0.0050	0.0071	0.0050	0.0000	0.0100
CBPO	49	0.0216	0.0171	0.0200	0.0000	0.0600	53	0.0177	0.0141	0.0200	0.0000	0.0600	2	0.0100	0.0000	0.0100	0.0100	0.0100
CBAST	40	0.0178	0.0156	0.0100	0.0000	0.0700	45	0.0149	0.0122	0.0100	0.0000	0.0600	1	0.0100	NA	0.0100	0.0100	0.0100
CLFMT	38	0.0084	0.0079	0.0100	0.0000	0.0200	39	0.0085	0.0071	0.0100	0.0000	0.0200	2	0.0050	0.0071	0.0050	0.0000	0.0100
CLAST	37	0.0241	0.0201	0.0200	0.0000	0.0900	43	0.0200	0.0189	0.0200	0.0000	0.0900	1	0.0400	NA	0.0400	0.0400	0.0400
MAL	30	0.0113	0.0082	0.0100	0.0000	0.0300	33	0.0164	0.0160	0.0100	0.0000	0.0500	3	0.0067	0.0058	0.0100	0.0000	0.0100
MRH	22	0.0341	0.0302	0.0250	0.0000	0.1000	29	0.0445	0.0344	0.0400	0.0000	0.1200	1	0.0100	NA	0.0100	0.0100	0.0100
MXRB	28	0.0321	0.0295	0.0300	0.0000	0.1400	36	0.0403	0.0258	0.0300	0.0000	0.0900	3	0.0267	0.0252	0.0300	0.0000	0.0500
MIRB	28	0.0357	0.0281	0.0300	0.0000	0.1100	38	0.0439	0.0274	0.0400	0.0000	0.1200	2	0.0450	0.0636	0.0450	0.0000	0.0900
HML	27	0.0133	0.0100	0.0100	0.0000	0.0400	22	0.0145	0.0074	0.0100	0.0000	0.0300	0	NA	NA	NA	NA	NA
HXMS	42	0.0448	0.0314	0.0400	0.0000	0.1700	42	0.0343	0.0301	0.0300	0.0000	0.1700	0	NA	NA	NA	NA	NA
HIMS	42	0.0310	0.0228	0.0300	0.0000	0.0900	42	0.0281	0.0251	0.0200	0.0000	0.1300	0	NA	NA	NA	NA	NA
HDT	41	0.0388	0.0293	0.0300	0.0000	0.1200	42	0.0274	0.0214	0.0200	0.0000	0.0700	0	NA	NA	NA	NA	NA
HSIH	32	0.0178	0.0160	0.0200	0.0000	0.0700	34	0.0188	0.0149	0.0200	0.0000	0.0500	0	NA	NA	NA	NA	NA
HEB	22	0.0164	0.0147	0.0100	0.0000	0.0500	18	0.0211	0.0225	0.0150	0.0000	0.0700	0	NA	NA	NA	NA	NA
RML	28	0.0104	0.0092	0.0100	0.0000	0.0300	27	0.0111	0.0075	0.0100	0.0000	0.0300	0	NA	NA	NA	NA	NA
RXMS	33	0.0345	0.0256	0.0300	0.0000	0.0900	34	0.0415	0.0372	0.0300	0.0000	0.1500	0	NA	NA	NA	NA	NA
RIMS	34	0.0250	0.0218	0.0200	0.0000	0.0900	34	0.0288	0.0245	0.0300	0.0000	0.0900	0	NA	NA	NA	NA	NA
RGH	18	0.0328	0.0267	0.0250	0.0000	0.0900	17	0.0212	0.0145	0.0200	0.0000	0.0400	0	NA	NA	NA	NA	NA

Table A3.6 continued

	Grote Kerk																	
	Male						Female						Indeterminate					
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
FML	31	0.0094	0.0089	0.0100	0.0000	0.0300	27	0.0067	0.0055	0.0100	0.0000	0.0200	0	NA	NA	NA	NA	NA
FPL	33	0.0091	0.0084	0.0100	0.0000	0.0300	27	0.0074	0.0059	0.0100	0.0000	0.0200	0	NA	NA	NA	NA	NA
FXMS	51	0.0316	0.0256	0.0300	0.0000	0.0800	51	0.0227	0.0206	0.0200	0.0000	0.1000	0	NA	NA	NA	NA	NA
FIMS	51	0.0224	0.0221	0.0200	0.0000	0.1100	50	0.0268	0.0211	0.0300	0.0000	0.1200	0	NA	NA	NA	NA	NA
FEB	26	0.0104	0.0104	0.0100	0.0000	0.0400	19	0.0058	0.0084	0.0000	0.0000	0.0300	0	NA	NA	NA	NA	NA
FSIH	36	0.0133	0.0120	0.0100	0.0000	0.0500	29	0.0166	0.0129	0.0100	0.0000	0.0400	0	NA	NA	NA	NA	NA
FMLP	27	0.0133	0.0127	0.0100	0.0000	0.0400	22	0.0182	0.0122	0.0150	0.0000	0.0400	0	NA	NA	NA	NA	NA
TML	37	0.0059	0.0069	0.0000	0.0000	0.0200	32	0.0069	0.0064	0.0100	0.0000	0.0200	0	NA	NA	NA	NA	NA
TXNF	42	0.0319	0.0286	0.0200	0.0000	0.1300	58	0.0272	0.0221	0.0200	0.0000	0.0900	0	NA	NA	NA	NA	NA
TINF	43	0.0356	0.0303	0.0300	0.0000	0.1300	58	0.0383	0.0324	0.0300	0.0000	0.1400	0	NA	NA	NA	NA	NA
TMLD	32	0.0153	0.0127	0.0100	0.0000	0.0500	29	0.0214	0.0168	0.0200	0.0000	0.0700	0	NA	NA	NA	NA	NA
TMLP	22	0.0082	0.0101	0.0100	0.0000	0.0400	16	0.0075	0.0093	0.0050	0.0000	0.0300	0	NA	NA	NA	NA	NA
i1l_bl	4	0.0125	0.0126	0.0100	0.0000	0.0300	15	0.0347	0.0290	0.0200	0.0000	0.1100	2	0.0350	0.0212	0.0350	0.0200	0.0500
i1l_md	3	0.0100	0.0173	0.0000	0.0000	0.0300	13	0.0208	0.0166	0.0200	0.0100	0.0700	1	0.0300	NA	0.0300	0.0300	0.0300
i2l_bl	9	0.0211	0.0136	0.0200	0.0100	0.0500	18	0.0261	0.0197	0.0200	0.0000	0.0600	1	0.0200	NA	0.0200	0.0200	0.0200
i2l_md	4	0.0275	0.0250	0.0250	0.0000	0.0600	18	0.0250	0.0115	0.0250	0.0100	0.0500	1	0.0200	NA	0.0200	0.0200	0.0200
c1l_bl	10	0.0240	0.0222	0.0200	0.0000	0.0500	19	0.0237	0.0180	0.0200	0.0000	0.0500	1	0.0300	NA	0.0300	0.0300	0.0300
c1l_md	9	0.0233	0.0187	0.0200	0.0000	0.0600	20	0.0240	0.0235	0.0150	0.0000	0.0900	1	0.0200	NA	0.0200	0.0200	0.0200
pm1l_bl	11	0.0318	0.0248	0.0300	0.0000	0.0900	27	0.0289	0.0165	0.0300	0.0000	0.0600	1	0.0100	NA	0.0100	0.0100	0.0100
pm1l_md	11	0.0491	0.0455	0.0300	0.0100	0.1500	28	0.0350	0.0348	0.0200	0.0000	0.1500	1	0.0100	NA	0.0100	0.0100	0.0100
pm2l_bl	11	0.0191	0.0202	0.0200	0.0000	0.0600	21	0.0314	0.0226	0.0300	0.0000	0.0900	1	0.0700	NA	0.0700	0.0700	0.0700
pm2l_md	11	0.0364	0.0388	0.0300	0.0000	0.1400	21	0.0314	0.0304	0.0300	0.0000	0.1100	1	0.0300	NA	0.0300	0.0300	0.0300
m1l_bl	6	0.0283	0.0172	0.0300	0.0000	0.0500	5	0.0180	0.0205	0.0100	0.0000	0.0400	0	NA	NA	NA	NA	NA
m1l_md	6	0.0233	0.0151	0.0200	0.0100	0.0400	5	0.0200	0.0200	0.0100	0.0000	0.0500	0	NA	NA	NA	NA	NA
m2l_bl	7	0.0343	0.0230	0.0400	0.0000	0.0600	13	0.0262	0.0233	0.0200	0.0000	0.0600	0	NA	NA	NA	NA	NA
m2l_md	11	0.0282	0.0279	0.0100	0.0000	0.0800	13	0.0231	0.0221	0.0200	0.0000	0.0600	0	NA	NA	NA	NA	NA
i1u_bl	7	0.0229	0.0160	0.0200	0.0000	0.0500	17	0.0171	0.0145	0.0200	0.0000	0.0500	2	0.0300	0.0000	0.0300	0.0300	0.0300
i1u_md	2	0.0350	0.0495	0.0350	0.0000	0.0700	12	0.0183	0.0180	0.0100	0.0000	0.0500	1	0.0100	NA	0.0100	0.0100	0.0100
i2u_bl	4	0.0075	0.0050	0.0100	0.0000	0.0100	14	0.0421	0.0219	0.0500	0.0100	0.0800	1	0.0000	NA	0.0000	0.0000	0.0000
i2u_md	0	NA	NA	NA	NA	NA	9	0.0389	0.0293	0.0300	0.0000	0.0900	1	0.0400	NA	0.0400	0.0400	0.0400
c1u_bl	7	0.0129	0.0111	0.0100	0.0000	0.0300	21	0.0271	0.0215	0.0200	0.0000	0.0700	1	0.0400	NA	0.0400	0.0400	0.0400
c1u_md	6	0.0183	0.0133	0.0100	0.0100	0.0400	22	0.0223	0.0237	0.0100	0.0000	0.0800	1	0.0100	NA	0.0100	0.0100	0.0100
pm1u_bl	6	0.0150	0.0187	0.0100	0.0000	0.0500	19	0.0174	0.0185	0.0100	0.0000	0.0700	1	0.0000	NA	0.0000	0.0000	0.0000
pm1u_md	5	0.0540	0.0251	0.0400	0.0300	0.0900	19	0.0242	0.0164	0.0200	0.0000	0.0600	1	0.0200	NA	0.0200	0.0200	0.0200

Table A3.6 continued

	Grote Kerk																	
	Male						Female						Indeterminate					
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
pm2u_md	8	0.0388	0.0247	0.0400	0.0100	0.0700	18	0.0439	0.0331	0.0450	0.0000	0.1400	1	0.1600	NA	0.1600	0.1600	0.1600
m1u_bl	3	0.0100	0.0100	0.0100	0.0000	0.0200	8	0.0138	0.0092	0.0100	0.0000	0.0300	1	0.0100	NA	0.0100	0.0100	0.0100
m1u_md	4	0.0300	0.0082	0.0300	0.0200	0.0400	8	0.0413	0.0217	0.0500	0.0100	0.0700	1	0.0300	NA	0.0300	0.0300	0.0300
m2u_bl	3	0.0333	0.0153	0.0300	0.0200	0.0500	11	0.0236	0.0180	0.0200	0.0000	0.0600	1	0.0200	NA	0.0200	0.0200	0.0200
m2u_md	4	0.0500	0.0216	0.0450	0.0300	0.0800	15	0.0513	0.0442	0.0500	0.0000	0.1400	1	0.0200	NA	0.0200	0.0200	0.0200
Individual	61	0.0240	0.0048	0.0233	0.0164	0.0380	84	0.0254	0.0077	0.0246	0.0000	0.0543	3	0.0216	0.0020	0.0209	0.0200	0.0238
Skeleton	61	0.0241	0.0065	0.0224	0.0161	0.0600	83	0.0249	0.0082	0.0242	0.0000	0.0543	3	0.0184	0.0020	0.0190	0.0162	0.0200
Dentition	24	0.0287	0.0145	0.0262	0.0100	0.0700	38	0.0289	0.0102	0.0269	0.0050	0.0540	2	0.0340	0.0085	0.0340	0.0279	0.0400
Dentition: mandible	20	0.0269	0.0133	0.0269	0.0100	0.0520	34	0.0289	0.0124	0.0258	0.0100	0.0733	2	0.0380	0.0170	0.0380	0.0260	0.0500
Dentition: maxilla	19	0.0286	0.0157	0.0250	0.0100	0.0700	32	0.0295	0.0117	0.0282	0.0050	0.0550	2	0.0296	0.0005	0.0296	0.0293	0.0300
Cranium	54	0.0233	0.0056	0.0230	0.0100	0.0407	65	0.0230	0.0084	0.0213	0.0100	0.0550	2	0.0166	0.0004	0.0166	0.0164	0.0169
Cranium: orbit	41	0.0185	0.0086	0.0200	0.0000	0.0400	41	0.0187	0.0121	0.0150	0.0000	0.0550	1	0.0250	NA	0.0250	0.0250	0.0250
Cranium: facial	48	0.0218	0.0106	0.0220	0.0025	0.0500	47	0.0206	0.0082	0.0200	0.0075	0.0400	2	0.0168	0.0011	0.0168	0.0160	0.0175
Cranium: temporal	32	0.0475	0.0234	0.0417	0.0200	0.1033	50	0.0587	0.0353	0.0517	0.0100	0.1733	1	0.0733	NA	0.0733	0.0733	0.0733
Cranium: base	50	0.0316	0.0176	0.0300	0.0000	0.1033	62	0.0288	0.0183	0.0258	0.0000	0.0875	2	0.0125	0.0035	0.0125	0.0100	0.0150
Cranium: vault	49	0.0177	0.0109	0.0175	0.0000	0.0500	58	0.0165	0.0123	0.0150	0.0000	0.0900	2	0.0125	0.0035	0.0125	0.0100	0.0150
Mandible	32	0.0270	0.0137	0.0250	0.0067	0.0600	42	0.0353	0.0168	0.0363	0.0000	0.0850	3	0.0208	0.0063	0.0200	0.0150	0.0275
Humerus	47	0.0297	0.0145	0.0267	0.0033	0.0625	50	0.0275	0.0224	0.0242	0.0000	0.1500	0	NA	NA	NA	NA	NA
Radius	40	0.0233	0.0128	0.0200	0.0000	0.0600	37	0.0273	0.0189	0.0220	0.0025	0.0900	0	NA	NA	NA	NA	NA
Femur	52	0.0197	0.0140	0.0163	0.0000	0.0700	56	0.0187	0.0137	0.0150	0.0000	0.0800	0	NA	NA	NA	NA	NA
Tibia	51	0.0241	0.0190	0.0200	0.0000	0.1050	60	0.0277	0.0163	0.0233	0.0033	0.0750	0	NA	NA	NA	NA	NA
Upper limb	52	0.0263	0.0104	0.0255	0.0000	0.0600	58	0.0284	0.0212	0.0255	0.0000	0.1500	0	NA	NA	NA	NA	NA
Lower Limb	55	0.0222	0.0131	0.0189	0.0067	0.0700	69	0.0228	0.0123	0.0200	0.0000	0.0725	0	NA	NA	NA	NA	NA
Midshafts	55	0.0320	0.0135	0.0300	0.0100	0.0700	70	0.0308	0.0146	0.0283	0.0050	0.0817	0	NA	NA	NA	NA	NA
Upper limb: midshafts	46	0.0338	0.0131	0.0325	0.0050	0.0650	50	0.0333	0.0227	0.0300	0.0000	0.1500	0	NA	NA	NA	NA	NA
Lower limb: midshafts	55	0.0302	0.0163	0.0275	0.0075	0.0800	68	0.0292	0.0156	0.0250	0.0050	0.0800	0	NA	NA	NA	NA	NA
Lengths	50	0.0103	0.0082	0.0100	0.0000	0.0400	49	0.0091	0.0063	0.0100	0.0000	0.0300	0	NA	NA	NA	NA	NA
Upper limb: lengths	37	0.0124	0.0093	0.0100	0.0000	0.0400	32	0.0130	0.0074	0.0100	0.0000	0.0300	0	NA	NA	NA	NA	NA
Lower limb: lengths	42	0.0076	0.0064	0.0100	0.0000	0.0200	39	0.0069	0.0051	0.0100	0.0000	0.0200	0	NA	NA	NA	NA	NA

Table A3.6 continued

Meerenberg																		
	Male						Female						Indeterminate					
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
COBB	12	0.0217	0.0127	0.0200	0.0000	0.0400	23	0.0122	0.0104	0.0100	0.0000	0.0300	3	0.0100	0.0100	0.0100	0.0000	0.0200
COBH	11	0.0218	0.0204	0.0200	0.0000	0.0700	22	0.0214	0.0108	0.0200	0.0000	0.0400	3	0.0233	0.0231	0.0100	0.0100	0.0500
CNOR	11	0.0200	0.0126	0.0300	0.0000	0.0300	21	0.0157	0.0150	0.0100	0.0000	0.0500	3	0.0233	0.0208	0.0300	0.0000	0.0400
CFMTN	11	0.0145	0.0113	0.0200	0.0000	0.0300	23	0.0139	0.0123	0.0100	0.0000	0.0400	4	0.0175	0.0050	0.0200	0.0100	0.0200
CFMTNS	9	0.0100	0.0150	0.0000	0.0000	0.0400	20	0.0155	0.0115	0.0100	0.0000	0.0400	4	0.0175	0.0096	0.0150	0.0100	0.0300
CMAH	12	0.0433	0.0436	0.0350	0.0000	0.1600	22	0.0482	0.0491	0.0350	0.0000	0.2300	3	0.0633	0.0681	0.0400	0.0100	0.1400
CMPL	13	0.0600	0.0422	0.0500	0.0000	0.1400	21	0.0790	0.0605	0.0700	0.0000	0.2300	2	0.0300	0.0424	0.0300	0.0000	0.0600
CMPB	15	0.0573	0.0479	0.0500	0.0000	0.2000	23	0.0717	0.0600	0.0600	0.0000	0.1900	4	0.0475	0.0450	0.0400	0.0100	0.1000
CMSAST	9	0.0411	0.0215	0.0400	0.0100	0.0800	17	0.0324	0.0261	0.0300	0.0000	0.0900	1	0.0800	NA	0.0800	0.0800	0.0800
COCL	11	0.0482	0.0312	0.0600	0.0100	0.1000	19	0.0468	0.0275	0.0500	0.0000	0.1100	5	0.0400	0.0324	0.0200	0.0100	0.0800
COPO	15	0.0340	0.0232	0.0300	0.0000	0.0700	25	0.0228	0.0237	0.0100	0.0000	0.0800	3	0.0200	0.0100	0.0200	0.0100	0.0300
CBAPO	15	0.0207	0.0225	0.0100	0.0000	0.0700	27	0.0230	0.0200	0.0200	0.0000	0.1000	3	0.0233	0.0231	0.0100	0.0100	0.0500
CECMIS	6	0.0333	0.0242	0.0300	0.0100	0.0700	11	0.0345	0.0336	0.0300	0.0000	0.1000	1	0.0100	NA	0.0100	0.0100	0.0100
CNMS	11	0.0155	0.0144	0.0200	0.0000	0.0500	18	0.0172	0.0132	0.0200	0.0000	0.0400	1	0.0200	NA	0.0200	0.0200	0.0200
CBZO	6	0.0117	0.0133	0.0100	0.0000	0.0300	14	0.0129	0.0083	0.0150	0.0000	0.0200	0	NA	NA	NA	NA	NA
CFMTB	8	0.0138	0.0160	0.0100	0.0000	0.0400	14	0.0200	0.0130	0.0200	0.0000	0.0400	0	NA	NA	NA	NA	NA
CBPO	8	0.0100	0.0076	0.0100	0.0000	0.0200	15	0.0140	0.0150	0.0100	0.0000	0.0400	1	0.0100	NA	0.0100	0.0100	0.0100
CBAST	6	0.0267	0.0082	0.0250	0.0200	0.0400	14	0.0157	0.0122	0.0100	0.0000	0.0400	1	0.0000	NA	0.0000	0.0000	0.0000
CLFMT	5	0.0120	0.0110	0.0100	0.0000	0.0300	16	0.0138	0.0081	0.0100	0.0000	0.0300	1	0.0200	NA	0.0200	0.0200	0.0200
CLAST	4	0.0500	0.0424	0.0400	0.0100	0.1100	14	0.0321	0.0281	0.0200	0.0000	0.0800	1	0.0000	NA	0.0000	0.0000	0.0000
MAL	4	0.0150	0.0129	0.0150	0.0000	0.0300	15	0.0140	0.0124	0.0100	0.0000	0.0400	9	0.0144	0.0142	0.0100	0.0000	0.0400
MRH	5	0.0440	0.0336	0.0500	0.0000	0.0800	15	0.0160	0.0213	0.0100	0.0000	0.0800	7	0.0200	0.0141	0.0200	0.0000	0.0400
MXRB	4	0.0350	0.0129	0.0350	0.0200	0.0500	17	0.0282	0.0204	0.0200	0.0000	0.0700	7	0.0243	0.0190	0.0200	0.0000	0.0600
MIRB	11	0.0364	0.0225	0.0300	0.0100	0.0800	21	0.0381	0.0275	0.0300	0.0000	0.1100	8	0.0238	0.0245	0.0200	0.0000	0.0800
HML	16	0.0113	0.0109	0.0100	0.0000	0.0400	25	0.0128	0.0110	0.0100	0.0000	0.0300	0	NA	NA	NA	NA	NA
HXMS	17	0.0288	0.0209	0.0300	0.0000	0.0800	30	0.0350	0.0271	0.0350	0.0000	0.0900	0	NA	NA	NA	NA	NA
HIMS	17	0.0376	0.0282	0.0300	0.0000	0.1000	31	0.0355	0.0305	0.0200	0.0000	0.1300	0	NA	NA	NA	NA	NA
HDT	16	0.0288	0.0182	0.0250	0.0100	0.0700	30	0.0360	0.0291	0.0250	0.0100	0.1100	0	NA	NA	NA	NA	NA
HSIH	16	0.0144	0.0109	0.0200	0.0000	0.0300	28	0.0189	0.0150	0.0100	0.0000	0.0500	1	0.0000	NA	0.0000	0.0000	0.0000
HEB	6	0.0133	0.0052	0.0100	0.0100	0.0200	14	0.0179	0.0131	0.0150	0.0000	0.0400	1	0.0100	NA	0.0100	0.0100	0.0100
RML	6	0.0050	0.0055	0.0050	0.0000	0.0100	18	0.0083	0.0079	0.0100	0.0000	0.0300	3	0.0033	0.0058	0.0000	0.0000	0.0100
RXMS	14	0.0543	0.0448	0.0400	0.0000	0.1400	29	0.0507	0.0359	0.0500	0.0000	0.1200	3	0.0600	0.0693	0.0200	0.0200	0.1400
RIMS	14	0.0343	0.0238	0.0300	0.0100	0.1000	30	0.0310	0.0359	0.0200	0.0000	0.1200	2	0.0250	0.0212	0.0250	0.0100	0.0400
RGH	5	0.0160	0.0152	0.0200	0.0000	0.0300	13	0.0231	0.0165	0.0200	0.0000	0.0600	0	NA	NA	NA	NA	NA

Table A3.6 continued

Meerenberg																		
	Male						Female						Indeterminate					
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
RMLD	8	0.0300	0.0160	0.0200	0.0200	0.0600	25	0.0164	0.0135	0.0200	0.0000	0.0500	2	0.0650	0.0212	0.0650	0.0500	0.0800
FML	9	0.0033	0.0050	0.0000	0.0000	0.0100	23	0.0087	0.0076	0.0100	0.0000	0.0200	0	NA	NA	NA	NA	NA
FPL	9	0.0044	0.0053	0.0000	0.0000	0.0100	24	0.0058	0.0072	0.0000	0.0000	0.0200	0	NA	NA	NA	NA	NA
FXMS	13	0.0262	0.0189	0.0200	0.0000	0.0700	37	0.0300	0.0217	0.0300	0.0000	0.1000	0	NA	NA	NA	NA	NA
FIMS	13	0.0246	0.0151	0.0300	0.0100	0.0600	37	0.0249	0.0217	0.0200	0.0000	0.0800	0	NA	NA	NA	NA	NA
FEB	10	0.0140	0.0084	0.0100	0.0000	0.0300	12	0.0158	0.0100	0.0100	0.0000	0.0300	0	NA	NA	NA	NA	NA
FSIH	14	0.0136	0.0108	0.0100	0.0000	0.0400	29	0.0138	0.0124	0.0100	0.0000	0.0400	0	NA	NA	NA	NA	NA
FMLP	9	0.0178	0.0083	0.0200	0.0100	0.0300	17	0.0200	0.0150	0.0100	0.0000	0.0500	0	NA	NA	NA	NA	NA
TML	10	0.0080	0.0063	0.0100	0.0000	0.0200	23	0.0048	0.0051	0.0000	0.0000	0.0100	0	NA	NA	NA	NA	NA
TXNF	16	0.0369	0.0233	0.0300	0.0100	0.0800	39	0.0356	0.0363	0.0300	0.0000	0.1500	0	NA	NA	NA	NA	NA
TINF	15	0.0373	0.0215	0.0400	0.0100	0.0900	41	0.0315	0.0297	0.0300	0.0000	0.1300	0	NA	NA	NA	NA	NA
TMLD	6	0.0200	0.0141	0.0200	0.0000	0.0400	13	0.0115	0.0152	0.0000	0.0000	0.0500	0	NA	NA	NA	NA	NA
TMLP	7	0.0100	0.0115	0.0100	0.0000	0.0300	9	0.0144	0.0124	0.0100	0.0000	0.0300	0	NA	NA	NA	NA	NA
i1l_bl	4	0.0250	0.0058	0.0250	0.0200	0.0300	9	0.0111	0.0093	0.0100	0.0000	0.0300	3	0.0200	0.0265	0.0100	0.0000	0.0500
i1l_md	4	0.0125	0.0126	0.0100	0.0000	0.0300	10	0.0180	0.0140	0.0200	0.0000	0.0400	3	0.0133	0.0058	0.0100	0.0100	0.0200
i2l_bl	5	0.0140	0.0055	0.0100	0.0100	0.0200	8	0.0100	0.0076	0.0100	0.0000	0.0200	3	0.0167	0.0058	0.0200	0.0100	0.0200
i2l_md	4	0.0150	0.0173	0.0100	0.0000	0.0400	11	0.0227	0.0174	0.0200	0.0000	0.0500	3	0.0233	0.0153	0.0200	0.0100	0.0400
c1l_bl	7	0.0229	0.0236	0.0200	0.0000	0.0700	16	0.0225	0.0246	0.0200	0.0000	0.1000	5	0.0420	0.0377	0.0400	0.0000	0.1000
c1l_md	5	0.0200	0.0158	0.0200	0.0000	0.0400	18	0.0239	0.0158	0.0200	0.0000	0.0600	5	0.0160	0.0089	0.0100	0.0100	0.0300
pm1l_bl	9	0.0189	0.0078	0.0200	0.0100	0.0300	15	0.0300	0.0224	0.0300	0.0000	0.0800	6	0.0450	0.0251	0.0300	0.0300	0.0900
pm1l_md	11	0.0309	0.0187	0.0300	0.0100	0.0800	15	0.0300	0.0342	0.0200	0.0000	0.1100	5	0.0380	0.0192	0.0300	0.0200	0.0700
pm2l_bl	6	0.0350	0.0187	0.0350	0.0100	0.0600	10	0.0340	0.0241	0.0350	0.0000	0.0800	4	0.0500	0.0455	0.0450	0.0000	0.1100
pm2l_md	8	0.0450	0.0321	0.0400	0.0100	0.1000	11	0.0382	0.0354	0.0300	0.0000	0.0900	4	0.0550	0.0100	0.0500	0.0500	0.0700
m1l_bl	5	0.0180	0.0130	0.0200	0.0000	0.0300	2	0.0100	0.0000	0.0100	0.0100	0.0100	2	0.0100	0.0000	0.0100	0.0100	0.0100
m1l_md	4	0.0275	0.0150	0.0300	0.0100	0.0400	3	0.0167	0.0058	0.0200	0.0100	0.0200	3	0.0400	0.0346	0.0200	0.0200	0.0800
m2l_bl	4	0.0075	0.0050	0.0100	0.0000	0.0100	5	0.0120	0.0045	0.0100	0.0100	0.0200	3	0.0200	0.0100	0.0200	0.0100	0.0300
m2l_md	4	0.0325	0.0206	0.0300	0.0100	0.0600	7	0.0343	0.0270	0.0200	0.0100	0.0800	4	0.0325	0.0096	0.0350	0.0200	0.0400
i1u_bl	7	0.0314	0.0291	0.0300	0.0000	0.0900	9	0.0244	0.0151	0.0300	0.0100	0.0500	2	0.0200	0.0141	0.0200	0.0100	0.0300
i1u_md	3	0.0100	0.0100	0.0100	0.0000	0.0200	6	0.0217	0.0194	0.0150	0.0000	0.0500	0	NA	NA	NA	NA	NA
i2u_bl	5	0.0240	0.0270	0.0200	0.0000	0.0700	11	0.0364	0.0242	0.0300	0.0100	0.0700	1	0.0200	NA	0.0200	0.0200	0.0200
i2u_md	1	0.0800	NA	0.0800	0.0800	0.0800	11	0.0418	0.0469	0.0300	0.0100	0.1600	0	NA	NA	NA	NA	NA
c1u_bl	10	0.0260	0.0212	0.0250	0.0000	0.0700	15	0.0213	0.0200	0.0100	0.0000	0.0700	1	0.0000	NA	0.0000	0.0000	0.0000
c1u_md	7	0.0143	0.0127	0.0100	0.0000	0.0300	17	0.0176	0.0130	0.0200	0.0000	0.0400	1	0.0100	NA	0.0100	0.0100	0.0100
pm1u_bl	5	0.0140	0.0114	0.0100	0.0000	0.0300	8	0.0100	0.0076	0.0100	0.0000	0.0200	2	0.0150	0.0071	0.0150	0.0100	0.0200

Table A3.6 continued

Meerenberg																		
	Male						Female						Indeterminate					
Trait	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**	**N**	**Mean**	**SD**	**Median**	**Min**	**Max**
pm1u_md	5	0.0540	0.0365	0.0400	0.0200	0.1100	10	0.0370	0.0241	0.0400	0.0000	0.0700	2	0.0700	0.0707	0.0700	0.0200	0.1200
pm2u_bl	7	0.0186	0.0146	0.0100	0.0100	0.0500	11	0.0191	0.0217	0.0100	0.0000	0.0600	1	0.0000	NA	0.0000	0.0000	0.0000
pm2u_md	5	0.0300	0.0158	0.0300	0.0100	0.0500	11	0.0355	0.0305	0.0300	0.0000	0.1100	1	0.0300	NA	0.0300	0.0300	0.0300
m1u_bl	5	0.0100	0.0173	0.0000	0.0000	0.0400	9	0.0089	0.0093	0.0100	0.0000	0.0200	1	0.0000	NA	0.0000	0.0000	0.0000
m1u_md	5	0.0220	0.0179	0.0100	0.0100	0.0500	10	0.0550	0.0450	0.0650	0.0000	0.1400	1	0.0400	NA	0.0400	0.0400	0.0400
m2u_bl	7	0.0343	0.0270	0.0400	0.0000	0.0800	11	0.0300	0.0261	0.0200	0.0000	0.0700	1	0.0100	NA	0.0100	0.0100	0.0100
m2u_md	7	0.0357	0.0251	0.0400	0.0000	0.0700	11	0.0455	0.0378	0.0300	0.0100	0.1300	1	0.0600	NA	0.0600	0.0600	0.0600
Individual	29	0.0259	0.0060	0.0255	0.0133	0.0400	56	0.0253	0.0104	0.0230	0.0067	0.0625	18	0.0262	0.0149	0.0233	0.0050	0.0733
Skeleton	29	0.0268	0.0093	0.0257	0.0133	0.0600	56	0.0244	0.0106	0.0222	0.0067	0.0625	17	0.0252	0.0149	0.0207	0.0050	0.0733
Dentition	16	0.0261	0.0082	0.0237	0.0175	0.0500	27	0.0258	0.0099	0.0267	0.0115	0.0500	8	0.0339	0.0161	0.0304	0.0182	0.0650
Dentition: mandible	14	0.0271	0.0113	0.0219	0.0150	0.0500	23	0.0256	0.0141	0.0217	0.0100	0.0700	6	0.0308	0.0116	0.0304	0.0150	0.0467
Dentition: maxilla	13	0.0246	0.0092	0.0250	0.0050	0.0450	24	0.0265	0.0120	0.0238	0.0029	0.0514	3	0.0361	0.0253	0.0250	0.0182	0.0650
Cranium	16	0.0262	0.0109	0.0257	0.0100	0.0600	30	0.0222	0.0067	0.0208	0.0100	0.0389	5	0.0233	0.0082	0.0236	0.0100	0.0322
Cranium: orbit	10	0.0195	0.0093	0.0175	0.0050	0.0350	23	0.0185	0.0085	0.0200	0.0000	0.0350	3	0.0233	0.0176	0.0250	0.0050	0.0400
Cranium: facial	12	0.0203	0.0099	0.0167	0.0120	0.0440	25	0.0244	0.0206	0.0200	0.0000	0.1150	4	0.0296	0.0188	0.0242	0.0133	0.0567
Cranium: temporal	15	0.0523	0.0275	0.0433	0.0000	0.0950	24	0.0665	0.0439	0.0650	0.0000	0.1900	4	0.0438	0.0269	0.0475	0.0100	0.0700
Cranium: base	16	0.0282	0.0164	0.0271	0.0050	0.0600	27	0.0259	0.0157	0.0225	0.0050	0.0733	5	0.0257	0.0116	0.0250	0.0100	0.0400
Cranium: vault	8	0.0184	0.0130	0.0175	0.0000	0.0425	18	0.0176	0.0088	0.0175	0.0000	0.0350	1	0.0075	NA	0.0075	0.0075	0.0075
Mandible	11	0.0401	0.0181	0.0400	0.0200	0.0800	25	0.0268	0.0145	0.0250	0.0050	0.0700	10	0.0218	0.0091	0.0200	0.0100	0.0400
Humerus	18	0.0242	0.0133	0.0217	0.0000	0.0525	32	0.0293	0.0127	0.0275	0.0050	0.0700	1	0.0050	NA	0.0050	0.0050	0.0050
Radius	14	0.0390	0.0249	0.0265	0.0160	0.0900	36	0.0293	0.0225	0.0225	0.0000	0.1150	3	0.0389	0.0299	0.0233	0.0200	0.0733
Femur	15	0.0150	0.0067	0.0133	0.0050	0.0271	38	0.0194	0.0105	0.0176	0.0025	0.0550	0	NA	NA	NA	NA	NA
Tibia	16	0.0308	0.0130	0.0333	0.0100	0.0550	41	0.0276	0.0238	0.0233	0.0000	0.1050	0	NA	NA	NA	NA	NA
Upper limb	19	0.0299	0.0110	0.0300	0.0156	0.0480	41	0.0287	0.0144	0.0250	0.0000	0.0729	4	0.0304	0.0297	0.0217	0.0050	0.0733
Lower Limb	17	0.0216	0.0068	0.0220	0.0111	0.0350	45	0.0222	0.0123	0.0200	0.0050	0.0675	0	NA	NA	NA	NA	NA
Midshafts	21	0.0349	0.0129	0.0317	0.0150	0.0600	50	0.0323	0.0150	0.0306	0.0050	0.0814	3	0.0617	0.0683	0.0300	0.0150	0.1400
Upper limb: midshafts	19	0.0374	0.0169	0.0350	0.0150	0.0700	38	0.0378	0.0202	0.0350	0.0050	0.1200	3	0.0617	0.0683	0.0300	0.0150	0.1400
Lower limb: midshafts	17	0.0319	0.0112	0.0350	0.0100	0.0475	45	0.0293	0.0147	0.0275	0.0050	0.0675	0	NA	NA	NA	NA	NA
Lengths	18	0.0098	0.0101	0.0075	0.0000	0.0400	41	0.0089	0.0071	0.0100	0.0000	0.0300	3	0.0033	0.0058	0.0000	0.0000	0.0100
Upper limb: lengths	16	0.0106	0.0106	0.0100	0.0000	0.0400	30	0.0110	0.0096	0.0100	0.0000	0.0300	3	0.0033	0.0058	0.0000	0.0000	0.0100
Lower limb: lengths	11	0.0059	0.0063	0.0050	0.0000	0.0200	29	0.0064	0.0055	0.0050	0.0000	0.0200	0	NA	NA	NA	NA	NA

Appendix 4: Normality and skewness

Table A4.1. Normality, kurtosis and skew results for raw (left - right) asymmetry values for each trait for the entire sample

	Kolmogorov-Smirnov			Kurtosis		Skew	
Trait	**N**	**D**	**P**	**Kurtosis**	**P**	**Skewness**	**P**
COBB	119	0.0903	0.2858	0.1162	0.6933	0.4641	0.0018
COBH	121	0.0664	0.6596	-0.4842	0.1011	0.1031	0.4844
CNOR	119	0.1693	0.0022	-0.7191	0.0152	0.1224	0.4064
CFMTN	132	0.1442	0.0083	-0.2066	0.4832	-0.0815	0.5804
CFMTNS	111	0.1089	0.1434	0.9214	0.0019	-0.0857	0.5611
CMAH	127	0.1017	0.1446	1.0108	<0.001	0.5311	<0.001**
CMPL	121	0.2648	<0.001**	0.2418	0.4120	0.0022	0.9882
CMPB	131	0.1854	<0.001**	0.2271	0.4411	0.1162	0.4304
CMSAST	89	0.3231	<0.001**	0.5710	0.0534	0.0790	0.5917
COCL	136	0.1343	0.0148	1.3282	<0.001**	-0.0436	0.7675
COPO	143	0.1970	<0.001**	0.3684	0.2118	-0.2297	0.1197
CBAPO	152	0.1973	<0.001**	0.5070	0.0861	0.2067	0.1613
CECMIS	53	0.0755	0.9229	-0.4082	0.1666	0.1899	0.1980
CNMS	96	0.3106	<0.001**	1.8231	<0.001**	0.0569	0.6993
CBZO	95	0.3150	<0.001**	0.0209	0.9433	-0.1601	0.2776
CFMTB	108	0.3506	<0.001**	-0.3058	0.2997	-0.0597	0.6851
CBPO	128	0.2507	<0.001**	0.3290	0.2646	-0.1543	0.2953
CBAST	107	0.2763	<0.001**	0.4865	0.0995	0.3717	0.0121
CLFMT	101	0.2446	<0.001**	-0.5515	0.0620	0.3314	0.0251
CLAST	100	0.2464	<0.001**	1.1714	<0.001**	0.2880	0.0514
MAL	99	0.1920	0.0014	0.5352	0.0701	0.2948	0.0461
MRH	84	0.2273	<0.001**	0.2047	0.4875	0.0376	0.7984
MXRB	100	0.2554	<0.001**	0.3406	0.2482	0.1526	0.3008
MIRB	119	0.1105	0.1095	-0.3478	0.2384	0.0518	0.7250
HML	98	0.6169	<0.001**	-0.2059	0.4848	0.3440	0.0201
HXMS	144	0.2648	<0.001**	1.6942	<0.001**	0.2547	0.0847
HIMS	145	0.1671	<0.001**	0.0971	0.7417	-0.0614	0.6768
HDT	136	0.2343	<0.001**	0.0295	0.9201	0.3495	0.0182
HSIH	113	0.1142	0.1047	0.1012	0.7312	-0.0409	0.7813
HEB	61	0.2324	0.0027	-0.1126	0.7024	0.5457	<0.001**
HSMLD	8	0.3707	0.1709	-0.4599	0.1194	0.9349	<0.001**
HSMLP	9	0.1314	0.9916	-1.5512	<0.001**	0.1639	0.2663
RML	89	0.4725	<0.001**	0.1110	0.7064	0.2388	0.1058
RXMS	126	0.1864	<0.001**	0.1918	0.5151	0.1121	0.4470
RIMS	127	0.2743	<0.001**	0.8309	0.0051	0.6871	<0.001**
RGH	53	0.1730	0.0837	0.5379	0.0687	-0.1583	0.2830
RSMLD	10	0.2974	0.2795	-0.7908	0.0077	0.1191	0.4192
RMLD	95	0.2088	<0.001**	0.4362	0.1395	-0.0716	0.6270
FML	99	0.3207	<0.001**	-0.1375	0.6407	0.0804	0.5855
FPL	98	0.3548	<0.001**	-0.0999	0.7347	0.2634	0.0746
FXMS	165	0.0600	0.5923	0.0668	0.8207	-0.1409	0.3392
FIMS	164	0.1239	0.0130	1.5128	<0.001**	-0.5885	<0.001**
FEB	69	0.3696	<0.001**	-0.1950	0.5082	-0.0058	0.9686
FSMLD	9	0.3255	0.2959	1.4426	<0.001**	1.6348	<0.001**
FSIH	111	0.1465	0.0170	-0.0181	0.9510	0.1233	0.4027
FMLP	82	0.1759	0.0125	-0.5103	0.0841	-0.1951	0.1859
TML	112	0.2878	<0.001**	0.7782	0.0087	-0.0971	0.5101
TXNF	169	0.0622	0.5294	1.3328	<0.001**	0.3833	0.0097
TINF	170	0.1525	<0.001**	0.9661	0.0012	0.0323	0.8265
TSMLD	11	0.2463	0.4458	2.2195	<0.001**	1.7031	<0.001**
TMLD	81	0.2407	<0.001**	-0.4503	0.1272	-0.1175	0.4254
TSMLP	4	0.7157	0.0133	-2.0276	<0.001**	0.3452	0.0197

Table A4.1 continued

	Kolmogorov-Smirnov			Kurtosis		Skew	
Trait	**N**	**D**	**P**	**Kurtosis**	**P**	**Skewness**	**P**
TMLP	56	0.3393	<0.001**	-0.0106	0.9714	-0.2979	0.0439
di1l_bl	4	0.4801	0.2239	-1.8913	0.0602	0.1334	0.7835
di1l_md	3	0.5160	0.2971	-2.3333	0.0227	-0.3381	0.4880
di2l_bl	5	0.4052	0.2954	-1.4340	0.1481	-0.5120	0.2967
di2l_md	3	0.4404	0.4841	-2.3333	0.0227	0.0840	0.8626
dc1l_bl	4	0.4364	0.3288	-2.1195	0.0368	-0.2835	0.5603
dc1l_md	5	0.4801	0.1409	-1.7863	0.0748	0.4509	0.3569
dm1l_bl	4	0.5080	0.1748	-2.2164	0.0296	0.0162	0.9733
dm1l_md	6	0.4602	0.1104	-1.7865	0.0748	-0.1624	0.7382
dm2l_bl	2	0.5557	0.3949	-2.7500	0.0084	0.0000	1.0000
dm2l_md	2	0.6950	0.1861	-2.7500	0.0084	0.0000	1.0000
di1u_bl	5	0.4602	0.1747	-1.9305	0.0554	-0.1515	0.7550
di1u_md	4	0.4641	0.2585	-2.4274	0.0182	-0.0053	0.9914
di2u_bl	3	0.5753	0.1819	-2.3333	0.0227	0.2078	0.6690
di2u_md	3	0.5239	0.3825	-2.3333	0.0227	0.3849	0.4305
dc1u_bl	6	0.4602	0.1104	-1.1393	0.2468	0.6829	0.1675
dc1u_md	6	0.4090	0.2679	-0.8377	0.3916	-0.7680	0.1224
dm1u_bl	7	0.4681	0.0632	-1.9523	0.0529	-0.0277	0.9544
dm1u_md	4	0.5319	0.1402	-1.7331	0.0833	-0.6762	0.1716
dm2u_bl	5	0.4522	0.2581	-1.2012	0.2228	0.7836	0.1154
dm2u_md	4	0.4880	0.2084	-1.6933	0.0902	0.7409	0.1356
i1l_bl	42	0.3936	<0.001**	0.3543	0.2297	-0.5780	<0.001**
i1l_md	40	0.4168	<0.001**	0.3162	0.2837	-0.6603	<0.001**
i2l_bl	46	0.3834	<0.001**	0.1199	0.6840	-0.2105	0.1537
i2l_md	43	0.3897	<0.001**	-0.7800	0.0085	-0.1717	0.2443
c1l_bl	60	0.3374	<0.001**	0.8194	0.0057	-0.1727	0.2416
c1l_md	61	0.3733	<0.001**	0.6091	0.0394	-0.7901	<0.001**
pm1l_bl	73	0.3334	<0.001**	-0.5121	0.0830	-0.0885	0.5483
pm1l_md	75	0.3040	<0.001**	1.2873	<0.001**	-0.2570	0.0818
pm2l_bl	54	0.3187	<0.001**	-0.3179	0.2811	0.1475	0.3170
pm2l_md	57	0.2985	<0.001**	-0.0423	0.8859	0.3646	0.0138
m1l_bl	27	0.3483	0.0029	-1.0882	<0.001**	-0.0304	0.8365
m1l_md	28	0.2981	0.0138	-0.0605	0.8373	-0.4190	0.0047
m2l_bl	33	0.3106	0.0034	-0.1412	0.6319	-0.0433	0.7690
m2l_md	40	0.2906	0.0023	-0.6768	0.0222	0.0758	0.6072
i1u_bl	50	0.3520	<0.001**	0.1165	0.6925	-0.2790	0.0590
i1u_md	30	0.3286	0.0031	0.4059	0.1690	-0.2314	0.1170
i2u_bl	40	0.3270	<0.001**	-0.7484	0.0115	-0.1091	0.4590
i2u_md	26	0.3474	0.0038	-0.2800	0.3424	-0.4700	0.0016
c1u_bl	56	0.3156	<0.001**	-0.3992	0.1762	0.0990	0.5015
c1u_md	55	0.3831	<0.001**	0.9350	0.0017	0.8064	<0.001**
pm1u_bl	46	0.4147	<0.001**	0.9953	<0.001	1.0959	<0.001**
pm1u_md	47	0.2946	<0.001**	0.1213	0.6806	-0.3322	0.0248
pm2u_bl	50	0.3097	<0.001**	0.2947	0.3176	0.5945	<0.001**
pm2u_md	47	0.2983	<0.001**	0.8260	0.0054	0.3245	0.0283
m1u_bl	34	0.3502	<0.001**	0.1971	0.5036	0.2844	0.0544
m1u_md	36	0.2798	0.0071	0.6648	0.0247	0.1460	0.3222
m2u_bl	35	0.3104	0.0024	-0.4834	0.1017	-0.0005	0.9972
m2u_md	40	0.2733	0.0051	-0.3010	0.3074	-0.0128	0.9309

**significant after a Holm's adjustment, p-value < 0.05; D = test statistic for the Kolmogorov-Smirnov test

Table A4.2. Normality, kurtosis and skew results for raw (left - right) asymmetry values for each trait per population, ages pooled

	Grote Kerk							Meerenberg						
	Kolmogorov-Smirnov			Kurtosis		Skew		Kolmogorov-Smirnov			Kurtosis		Skew	
Trait	**N**	**D**	**P**	**Kurtosis**	**P**	**Skewness**	**P**	**N**	**D**	**P**	**Kurtosis**	**P**	**Skewness**	**P**
COBB	81	0.0674	0.8549	0.0533	0.8871	0.5644	0.0030	38	0.1904	0.1273	-0.6338	0.1858	0.2863	0.2316
COBH	85	0.0578	0.9386	-0.4040	0.2824	0.2532	0.1783	36	0.1743	0.2242	-0.4653	0.3304	-0.2153	0.3677
CNOR	84	0.2150	<0.001	-0.2862	0.4459	0.0213	0.9097	35	0.2066	0.0868	-1.3053	0.0072	0.3797	0.1135
CFMTN	94	0.1806	0.0044	-0.1321	0.7248	-0.1171	0.5327	38	0.1282	0.5188	-0.9149	0.0572	-0.0994	0.6768
CFMTNS	78	0.1470	0.0688	0.9336	0.0137	-0.2057	0.2737	33	0.1425	0.5141	0.3022	0.5267	0.1443	0.5455
CMAH	90	0.1006	0.3217	0.5402	0.1512	0.7001	<0.001**	37	0.1481	0.3917	1.0851	0.0246	0.2464	0.3027
CMPL	83	0.2232	<0.001	0.4654	0.2158	-0.1334	0.4772	38	0.4177	<0.001**	-0.1169	0.8065	0.1027	0.6669
CMPB	87	0.1462	0.0484	0.3914	0.2976	0.0248	0.8947	44	0.2985	<0.001	-0.3708	0.4375	0.2413	0.3128
CMSAST	62	0.3316	<0.001**	0.8702	0.0214	0.1196	0.5241	27	0.3205	0.0078	-0.8986	0.0617	-0.1222	0.6085
COCL	100	0.1570	0.0145	1.6293	<0.001**	0.1356	0.4701	36	0.2440	0.0226	-0.6085	0.2038	-0.5245	0.0297
COPO	100	0.2282	<0.001**	0.5482	0.1453	-0.1798	0.3385	43	0.2604	0.0059	-0.2017	0.6726	-0.2970	0.2147
CBAPO	107	0.2103	<0.001**	0.3675	0.3280	0.3485	0.0646	45	0.2083	0.0403	0.6973	0.1458	-0.2768	0.2472
CECMIS	35	0.0908	0.9350	-0.5346	0.1554	0.0090	0.9617	18	0.1455	0.7896	-0.7096	0.1389	0.3856	0.1081
CNMS	66	0.3110	<0.001**	2.3072	<0.001**	0.0739	0.6937	30	0.3772	<0.001	-0.3233	0.4983	0.0284	0.9051
CBZO	75	0.2680	<0.001**	0.1675	0.6554	-0.0802	0.6691	20	0.4913	<0.001**	-1.0035	0.0373	-0.2429	0.3097
CFMTB	86	0.3530	<0.001**	-0.2142	0.5683	-0.0028	0.9882	22	0.4332	<0.001	-1.1803	0.0147	-0.2181	0.3614
CBPO	104	0.2849	<0.001**	0.1905	0.6117	-0.1259	0.5026	24	0.2163	0.2113	0.0714	0.8810	-0.0183	0.9389
CBAST	86	0.2716	<0.001**	0.6353	0.0917	0.3522	0.0618	21	0.4058	0.0020	-0.6104	0.2024	0.3734	0.1195
CLFMT	79	0.2051	0.0026	-0.3633	0.3335	0.4140	0.0284	22	0.4777	<0.001**	-0.9594	0.0463	-0.1630	0.4947
CLAST	81	0.2555	<0.001**	0.8777	0.0203	-0.0542	0.7728	19	0.2553	0.1404	-0.2580	0.5888	0.4019	0.0941
MAL	71	0.1728	0.0289	0.9275	0.0143	0.4949	0.0090	28	0.2607	0.0362	-0.6554	0.1714	-0.1636	0.4931
MRH	57	0.2467	0.0019	-0.1749	0.6413	-0.0210	0.9107	27	0.2301	0.0972	0.9910	0.0397	0.1445	0.5450
MXRB	72	0.2187	0.0020	0.2363	0.5290	0.0742	0.6925	28	0.3683	0.0010	-0.4195	0.3800	0.2542	0.2877
MIRB	79	0.0922	0.5126	-0.3217	0.3918	0.0182	0.9229	40	0.1631	0.2374	-0.5228	0.2744	0.1092	0.6473
HML	55	0.6863	<0.001**	0.0056	0.9881	0.1998	0.2877	43	0.5623	<0.001**	-0.4444	0.3525	0.5205	0.0309
HXMS	94	0.2992	<0.001**	2.3768	<0.001**	0.3642	0.0535	50	0.2001	0.0365	-0.5712	0.2327	-0.0980	0.6812
HIMS	94	0.1998	0.0011	0.0125	0.9735	0.0333	0.8592	51	0.1471	0.2198	-0.1833	0.7008	-0.1178	0.6215
HDT	87	0.2265	<0.001**	0.1270	0.7350	0.4336	0.0218	49	0.2499	0.0044	-0.4065	0.3948	0.1556	0.5144
HSIH	67	0.1398	0.1459	0.4277	0.2552	-0.0492	0.7930	46	0.1094	0.6023	-0.7245	0.1309	-0.0500	0.8339
HEB	40	0.3415	<0.001**	-0.3392	0.3665	0.6329	<0.001	21	0.1109	0.9336	-0.8385	0.0810	0.2752	0.2499
HSMLD	5	0.3859	0.3485	-1.4520	<0.001**	0.6654	<0.001	3	0.3707	0.6760	-2.3333	<0.001**	0.1868	0.4340
HSMLP	7	0.1799	0.9479	-1.2497	0.0010	0.3367	0.0740	2	0.3686	0.8874	-2.7500	<0.001**	0.0000	1.0000
RML	61	0.5234	<0.001**	0.1557	0.6782	0.1353	0.4710	28	0.3701	<0.001	-0.6908	0.1495	0.3224	0.1783

Table A4.2 continued

	Grote Kerk							Meerenberg						
	Kolmogorov-Smirnov			Kurtosis		Skew		Kolmogorov-Smirnov			Kurtosis		Skew	
Trait	**N**	**D**	**P**	**Kurtosis**	**P**	**Skewness**	**P**	**N**	**D**	**P**	**Kurtosis**	**P**	**Skewness**	**P**
RXMS	77	0.2228	0.0010	-0.6238	0.0978	0.5033	0.0079	49	0.1611	0.1570	-0.1586	0.7396	-0.0996	0.6765
RIMS	78	0.2719	<0.001**	0.3790	0.3132	0.0530	0.7777	49	0.3168	<0.001**	0.4699	0.3257	1.0795	<0.001**
RGH	35	0.1735	0.2430	0.3838	0.3070	-0.2386	0.2045	18	0.1949	0.5011	-1.0055	0.0370	0.0964	0.6861
RSMLD	9	0.2863	0.3788	-0.9205	0.0150	-0.0258	0.8905	1	NA	NA	NA	NA	NA	NA
RMLD	59	0.2370	0.0026	0.6397	0.0895	-0.3837	0.0421	36	0.1864	0.1640	-0.0086	0.9857	0.2767	0.2474
FML	67	0.3072	<0.001**	0.0826	0.8258	0.2229	0.2357	32	0.3835	<0.001**	-1.1486	0.0175	-0.3305	0.1677
FPL	65	0.3640	<0.001**	-0.0286	0.9392	0.3740	0.0474	33	0.3712	<0.001**	-0.9298	0.0533	-0.1396	0.5585
FXMS	113	0.0770	0.5149	0.2188	0.5600	-0.1303	0.4876	52	0.1168	0.4777	-0.4511	0.3453	-0.1929	0.4194
FIMS	112	0.1252	0.0597	1.9813	<0.001**	-0.8445	<0.001**	52	0.1521	0.1802	-0.2857	0.5496	0.0321	0.8928
FEB	46	0.3913	<0.001**	-0.2291	0.5416	0.5929	0.0018	23	0.4306	<0.001	-0.1952	0.6825	-0.7683	0.0017
FSMLD	9	0.3255	0.2959	1.4426	<0.001**	1.6348	<0.001**	0	NA	NA	NA	NA	NA	NA
FSIH	68	0.1517	0.0875	0.0469	0.9005	0.0911	0.6275	43	0.1448	0.3280	-0.4457	0.3511	0.1744	0.4651
FMLP	55	0.2049	0.0197	-0.6081	0.1064	-0.1693	0.3673	27	0.3403	0.0027	-0.3514	0.4619	-0.4138	0.0849
TML	78	0.2901	<0.001**	0.9046	0.0168	-0.1857	0.3230	34	0.3302	0.0012	-0.3363	0.4813	0.2849	0.2338
TXNF	111	0.0494	0.9490	1.2541	0.0010	0.0801	0.6694	58	0.1508	0.1430	0.7318	0.1271	0.5559	0.0214
TINF	111	0.1698	0.0033	1.0667	0.0050	-0.0266	0.8873	59	0.1206	0.3578	-0.0933	0.8449	0.1394	0.5592
TSMLD	10	0.3372	0.1621	2.1062	<0.001**	1.7907	<0.001**	1	NA	NA	NA	NA	NA	NA
TMLD	62	0.2284	0.0031	-0.4609	0.2203	-0.2063	0.2724	19	0.2895	0.0828	-0.9395	0.0510	0.3319	0.1659
TSMLP	4	0.7157	0.0133	-2.0276	<0.001**	0.3452	0.0671	0	NA	NA	NA	NA	NA	NA
TMLP	39	0.3974	<0.001**	-0.5806	0.1231	0.1460	0.4368	17	0.2059	0.4670	-0.9543	0.0475	-0.1776	0.4571
i1l_bl	26	0.4052	<0.001	-0.5310	0.1582	-0.4349	0.0214	16	0.4247	0.0062	-0.0571	0.9047	0.7024	0.0039
i1l_md	22	0.4247	<0.001	-0.0484	0.8974	-0.4664	0.0137	18	0.4168	0.0024	0.1489	0.7550	-0.6911	0.0045
i2l_bl	29	0.3707	<0.001	-0.3127	0.4050	-0.4339	0.0217	17	0.4483	0.0022	-1.3957	0.0041	0.0586	0.8060
i2l_md	24	0.4286	<0.001**	-1.1608	0.0023	-0.0967	0.6064	19	0.4090	0.0035	-0.7014	0.1434	-0.0942	0.6930
c1l_bl	31	0.3483	0.0011	-0.9180	0.0153	-0.0859	0.6471	29	0.3400	0.0024	0.9596	0.0463	-0.1667	0.4850
c1l_md	31	0.3594	<0.001	0.5074	0.1774	-0.7848	<0.001**	30	0.3897	<0.001**	-0.7962	0.0972	-0.4905	0.0417
pm1l_bl	41	0.3501	<0.001**	-0.8554	0.0236	-0.2932	0.1194	32	0.3170	0.0032	-0.3790	0.4276	0.1522	0.5236
pm1l_md	42	0.2993	0.0011	0.8474	0.0250	-0.4877	0.0100	33	0.3368	0.0011	1.4002	0.0040	0.3830	0.1105
pm2l_bl	34	0.3338	0.0010	0.1620	0.6661	-0.3023	0.1084	20	0.3156	0.0372	-0.9034	0.0604	0.5555	0.0215
pm2l_md	34	0.3300	0.0012	0.6554	0.0820	0.2404	0.2010	23	0.2901	0.0416	-0.7639	0.1114	0.5454	0.0239
m1l_bl	16	0.3483	0.0308	-1.4730	<0.001**	0.0774	0.6800	11	0.3859	0.0552	-1.3074	0.0071	0.0669	0.7791
m1l_md	16	0.3818	0.0188	-0.1128	0.7637	-0.4243	0.0248	12	0.3336	0.1383	-0.4350	0.3627	-0.0747	0.7541
m2l_bl	20	0.2909	0.0678	-1.0693	0.0049	0.0731	0.6967	13	0.4364	0.0141	-1.4261	0.0034	-0.1343	0.5737
m2l_md	24	0.3094	0.0202	-0.1302	0.7287	-0.0336	0.8580	16	0.3300	0.0471	-1.5370	0.0017	0.1885	0.4300

Table A4.2 continued

	Grote Kerk							Meerenberg						
	Kolmogorov-Smirnov			Kurtosis		Skew		Kolmogorov-Smirnov			Kurtosis		Skew	
Trait	**N**	**D**	**P**	**Kurtosis**	**P**	**Skewness**	**P**	**N**	**D**	**P**	**Kurtosis**	**P**	**Skewness**	**P**
i1u_bl	30	0.3718	<0.001	-0.5581	0.1381	0.0266	0.8874	20	0.3821	0.0058	-0.1813	0.7039	-0.3005	0.2094
i1u_md	19	0.3470	0.0206	0.0361	0.9234	-0.1910	0.3093	11	0.4286	0.0352	-0.8786	0.0676	0.4354	0.0701
i2u_bl	21	0.3632	0.0079	-1.2814	<0.001	0.0714	0.7034	19	0.3681	0.0116	-0.9099	0.0586	-0.2939	0.2195
i2u_md	12	0.3859	0.0406	-1.2244	0.0013	-0.3261	0.0835	14	0.3145	0.1254	-0.4371	0.3604	-0.5105	0.0342
c1u_bl	29	0.3557	0.0013	-1.0257	0.0068	0.2362	0.2090	27	0.3527	0.0024	-0.0976	0.8378	-0.2011	0.4000
c1u_md	29	0.3863	<0.001**	0.5492	0.1445	0.9249	<0.001**	26	0.4013	<0.001	-1.0504	0.0294	-0.0221	0.9260
pm1u_bl	29	0.4364	<0.001**	0.0911	0.8083	0.8928	<0.001**	17	0.4364	0.0031	-1.1911	0.0138	0.3152	0.1882
pm1u_md	28	0.4129	<0.001**	-0.8166	0.0307	0.4816	0.0110	19	0.3256	0.0356	-0.8012	0.0952	-0.1744	0.4653
pm2u_bl	30	0.3231	0.0038	-0.3523	0.3484	0.4417	0.0195	20	0.3864	0.0051	0.4987	0.2970	0.2317	0.3324
pm2u_md	29	0.2991	0.0112	0.2927	0.4357	0.1958	0.2974	18	0.4207	0.0034	-0.3207	0.5018	-0.5603	0.0204
m1u_bl	17	0.3520	0.0296	-0.6711	0.0750	0.3065	0.1036	17	0.3658	0.0211	0.8589	0.0739	0.0082	0.9724
m1u_md	18	0.3535	0.0223	-0.7163	0.0576	-0.4835	0.0107	18	0.2521	0.1705	-0.1272	0.7897	0.3089	0.1970
m2u_bl	16	0.3082	0.0957	-0.5255	0.1625	0.3159	0.0935	19	0.3194	0.0414	-0.9534	0.0477	0.0758	0.7508
m2u_md	21	0.2098	0.2734	-0.6184	0.1007	0.0446	0.8121	19	0.3483	0.0145	-0.9219	0.0554	0.2154	0.3674

**significant after a Holm's adjustment, p-value < 0.05; D = test statistic for the Kolmogorov-Smirnov test

Table A4.3. Normality, kurtosis and skew results for adult raw (left - right) asymmetry values for each trait per population

	Grote Kerk							Meerenberg						
	Kolmogorov-Smirnov			Kurtosis		Skew		Kolmogorov-Smirnov			Kurtosis		Skew	
Trait	**N**	**D**	**P**	**Kurtosis**	**P**	**Skewness**	**P**	**N**	**D**	**P**	**Kurtosis**	**P**	**Skewness**	**P**
COBB	81	0.0674	0.8549	0.0533	0.8949	0.5644	0.0057	38	0.1904	0.1273	-0.6338	0.1922	0.2863	0.2383
COBH	85	0.0578	0.9386	-0.4040	0.3174	0.2532	0.2106	36	0.1743	0.2242	-0.4653	0.3374	-0.2153	0.3746
CNOR	84	0.2150	<0.001	-0.2862	0.4783	0.0213	0.9160	35	0.2066	0.0868	-1.3053	0.0080	0.3797	0.1188
CFMTN	89	0.1942	0.0024	-0.0994	0.8054	-0.1524	0.4505	38	0.1282	0.5188	-0.9149	0.0609	-0.0994	0.6812
CFMTNS	78	0.1470	0.0688	0.9336	0.0218	-0.2057	0.3087	33	0.1425	0.5141	0.3022	0.5327	0.1443	0.5513
CMAH	86	0.1014	0.3393	0.4534	0.2620	0.7091	<0.001	37	0.1481	0.3917	1.0851	0.0267	0.2464	0.3096
CMPL	80	0.2235	<0.001**	0.4488	0.2669	-0.1682	0.4048	36	0.4455	<0.001**	-0.1572	0.7453	0.1767	0.4657
CMPB	84	0.1540	0.0371	0.3011	0.4558	0.0235	0.9073	42	0.2974	<0.001	-0.2899	0.5494	0.2546	0.2939
CMSAST	61	0.3388	<0.001**	0.8070	0.0469	0.1123	0.5780	27	0.3205	0.0078	-0.8986	0.0656	-0.1222	0.6137
COCL	99	0.1598	0.0127	1.6448	<0.001**	0.1552	0.4420	35	0.2305	0.0406	-0.6599	0.1746	-0.4799	0.0495
COPO	100	0.2282	<0.001**	0.5482	0.1755	-0.1798	0.3733	43	0.2604	0.0059	-0.2017	0.6770	-0.2970	0.2213
CBAPO	107	0.2103	<0.001**	0.3675	0.3630	0.3485	0.0856	45	0.2083	0.0403	0.6973	0.1517	-0.2768	0.2540
CECMIS	30	0.1286	0.7042	-0.7471	0.0656	0.2585	0.2013	18	0.1455	0.7896	-0.7096	0.1446	0.3856	0.1132
CNMS	66	0.3110	<0.001**	2.3072	<0.001**	0.0739	0.7142	30	0.3772	<0.001**	-0.3233	0.5045	0.0284	0.9065
CBZO	75	0.2680	<0.001**	0.1675	0.6781	-0.0802	0.6909	20	0.4913	<0.001**	-1.0035	0.0401	-0.2429	0.3166
CFMTB	86	0.3530	<0.001**	-0.2142	0.5956	-0.0028	0.9891	22	0.4332	<0.001**	-1.1803	0.0162	-0.2181	0.3683
CBPO	104	0.2849	<0.001**	0.1905	0.6368	-0.1259	0.5329	24	0.2163	0.2113	0.0714	0.8827	-0.0183	0.9397
CBAST	86	0.2716	<0.001**	0.6353	0.1168	0.3522	0.0823	21	0.4058	0.0020	-0.6104	0.2089	0.3734	0.1249
CLFMT	79	0.2051	0.0026	-0.3633	0.3684	0.4140	0.0415	22	0.4777	<0.001**	-0.9594	0.0495	-0.1630	0.5009
CLAST	81	0.2555	<0.001**	0.8777	0.0309	-0.0542	0.7883	19	0.2553	0.1404	-0.2580	0.5942	0.4019	0.0989
MAL	66	0.1920	0.0154	0.6945	0.0867	0.4662	0.0220	28	0.2607	0.0362	-0.6554	0.1776	-0.1636	0.4993
MRH	52	0.2754	<0.001	-0.3745	0.3539	0.0269	0.8937	27	0.2301	0.0972	0.9910	0.0426	0.1445	0.5508
MXRB	67	0.2294	0.0017	0.0681	0.8659	0.0520	0.7967	28	0.3683	0.0010	-0.4195	0.3869	0.2542	0.2947
MIRB	68	0.1231	0.2544	-0.4738	0.2412	0.0866	0.6677	40	0.1631	0.2374	-0.5228	0.2814	0.1092	0.6520
HML	49	0.7732	<0.001**	0.2585	0.5219	0.0097	0.9615	41	0.5974	<0.001**	-0.4552	0.3479	0.4730	0.0528
HXMS	84	0.3594	<0.001**	2.2854	<0.001**	0.1964	0.3310	47	0.2128	0.0283	-0.5502	0.2570	-0.1587	0.5122
HIMS	84	0.1860	0.0060	-0.2135	0.5968	-0.0607	0.7636	48	0.1618	0.1620	-0.1542	0.7500	-0.1805	0.4564
HDT	83	0.2456	<0.001**	0.1617	0.6886	0.3941	0.0522	46	0.2650	0.0031	-0.4265	0.3790	0.1394	0.5647
HSIH	66	0.1361	0.1733	0.3759	0.3521	-0.0439	0.8275	45	0.1202	0.4968	-0.7370	0.1299	-0.0848	0.7260
HEB	40	0.3415	<0.001**	-0.3392	0.4010	0.6329	0.0020	21	0.1109	0.9336	-0.8385	0.0854	0.2752	0.2568
RML	55	0.5514	<0.001**	-0.0340	0.9329	0.0206	0.9185	27	0.3847	<0.001**	-0.6995	0.1504	0.2620	0.2802
RXMS	67	0.2152	0.0040	-0.8687	0.0326	0.3869	0.0566	46	0.1647	0.1649	-0.3020	0.5329	-0.0513	0.8322
RIMS	68	0.2715	<0.001**	0.1693	0.6748	0.0153	0.9395	46	0.3155	<0.001**	0.3552	0.4635	1.0785	<0.001**

Table A4.3 continued

	Grote Kerk							Meerenberg						
	Kolmogorov-Smirnov			Kurtosis		Skew		Kolmogorov-Smirnov			Kurtosis		Skew	
Trait	**N**	**D**	**P**	**Kurtosis**	**P**	**Skewness**	**P**	**N**	**D**	**P**	**Kurtosis**	**P**	**Skewness**	**P**
RGH	35	0.1735	0.2430	0.3838	0.3421	-0.2386	0.2380	18	0.1949	0.5011	-1.0055	0.0397	0.0964	0.6904
RMLD	59	0.2370	0.0026	0.6397	0.1143	-0.3837	0.0587	35	0.2070	0.0996	0.0073	0.9880	0.2288	0.3454
FML	58	0.3566	<0.001**	-0.3135	0.4375	0.2349	0.2452	32	0.3835	<0.001**	-1.1486	0.0192	-0.3305	0.1739
FPL	60	0.3832	<0.001**	-0.2196	0.5863	0.3836	0.0587	33	0.3712	<0.001**	-0.9298	0.0569	-0.1396	0.5641
FXMS	102	0.0821	0.4977	-0.0565	0.8885	-0.1309	0.5168	50	0.1398	0.2823	-0.4536	0.3496	-0.1517	0.5312
FIMS	101	0.1194	0.1124	1.5719	<0.001**	-0.7952	<0.001**	50	0.1483	0.2218	-0.3272	0.4995	0.0692	0.7749
FEB	45	0.4111	<0.001**	-0.2178	0.5894	0.5773	0.0048	22	0.4187	<0.001	-0.3386	0.4846	-0.7077	0.0042
FSIH	65	0.1623	0.0651	0.0728	0.8568	0.1050	0.6030	43	0.1448	0.3280	-0.4457	0.3580	0.1744	0.4715
FMLP	49	0.2135	0.0194	-0.7530	0.0635	-0.1462	0.4691	26	0.3597	0.0016	-0.4568	0.3462	-0.4055	0.0960
TML	69	0.2761	<0.001**	0.6768	0.0950	-0.1149	0.5692	33	0.3409	<0.001	-0.2677	0.5805	0.3498	0.1503
TXNF	100	0.0711	0.6921	0.9845	0.0157	0.0454	0.8221	55	0.1658	0.0971	0.5630	0.2462	0.5394	0.0276
TINF	101	0.1790	0.0031	0.8256	0.0421	-0.1008	0.6175	56	0.1266	0.3306	-0.1403	0.7719	0.1270	0.5999
TMLD	61	0.2348	0.0024	-0.4948	0.2212	-0.1867	0.3552	19	0.2895	0.0828	-0.9395	0.0544	0.3319	0.1721
TMLP	38	0.3947	<0.001**	-0.6270	0.1216	0.1687	0.4034	16	0.1875	0.6272	-0.9008	0.0649	-0.0792	0.7436

**significant after a Holm's adjustment, p-value < 0.05; D = test statistic for the Kolmogorov-Smirnov test

Table A4.4. Normality, kurtosis and skew results for adult raw (left - right) asymmetry values for each trait per adult age category, populations pooled

	YA							MDA						
	Kolmogorov-Smirnov			Kurtosis		Skew		Kolmogorov-Smirnov			Kurtosis		Skew	
Trait	N	D	P	Kurtosis	P	Skewness	P	N	D	P	Kurtosis	P	Skewness	P
COBB	4	0.6915	0.0192	-1.7518	0.2874	-0.6264	0.4396	62	0.1507	0.2704	-0.2299	0.7000	-0.0301	0.9196
COBH	4	0.3410	0.6361	-1.9093	0.2490	-0.4905	0.5423	66	0.0993	0.8020	-0.5628	0.3469	0.3343	0.2644
CNOR	2	0.5040	0.4921	-2.7500	0.1096	0.0000	1.0000	67	0.2582	0.0085	-0.4825	0.4196	-0.1196	0.6884
CFMTN	2	0.8340	0.0551	-2.7500	0.1096	0.0000	1.0000	70	0.1857	0.0839	0.8748	0.1456	-0.2914	0.3301
CFMTNS	3	0.4056	0.5792	-2.3333	0.1663	-0.1673	0.8338	55	0.1345	0.3898	0.5560	0.3527	-0.5323	0.0776
CMAH	4	0.7291	0.0108	-1.9692	0.2355	-0.2910	0.7159	65	0.1078	0.6720	1.2757	0.0354	0.2974	0.3204
CMPL	1	NA	NA	NA	NA	NA	NA	70	0.2782	0.0041	-0.7860	0.1903	0.2869	0.3376
CMPB	0	NA	NA	NA	NA	NA	NA	76	0.2362	0.0184	-0.0250	0.9666	0.0691	0.8169
CMSAST	1	NA	NA	NA	NA	NA	NA	49	0.3247	<0.001	0.0821	0.8905	0.5721	0.0583
COCL	2	0.7123	0.1656	-2.7500	0.1096	0.0000	1.0000	78	0.1969	0.0659	0.8818	0.1424	0.6849	0.0242
COPO	4	0.3897	0.4705	-1.7226	0.2950	-0.7034	0.3875	85	0.2104	0.0373	1.4363	0.0184	-0.6621	0.0292
CBAPO	4	0.3749	0.5198	-2.2910	0.1733	-0.0763	0.9237	88	0.2006	0.0330	0.0822	0.8904	-0.1671	0.5756
CECMIS	2	0.5239	0.4533	-2.7500	0.1096	0.0000	1.0000	17	0.1031	0.9605	-0.6736	0.2609	0.4863	0.1063
CNMS	0	NA	NA	NA	NA	NA	NA	59	0.3413	<0.001	-0.1420	0.8118	-0.2079	0.4863
CBZO	4	0.2500	0.9063	-1.9001	0.2511	0.1637	0.8373	51	0.4203	<0.001**	0.7929	0.1865	-0.3590	0.2311
CFMTB	4	0.2500	0.9063	-1.9073	0.2495	0.1843	0.8173	60	0.5318	<0.001**	0.9795	0.1039	-0.8018	0.0088
CBPO	4	0.3413	0.6347	-1.8750	0.2570	0.3527	0.6596	74	0.2997	<0.001**	0.2065	0.7293	-0.3349	0.2636
CBAST	4	0.2500	0.9639	-1.7427	0.2897	0.6450	0.4266	57	0.2732	0.0028	1.5927	0.0092	0.7761	0.0111
CLFMT	4	0.5000	0.2700	-2.2801	0.1752	-0.1389	0.8617	53	0.3187	<0.001	-1.2719	0.0359	0.1251	0.6750
CLAST	4	0.5789	0.0860	-1.7303	0.2930	-0.6724	0.4079	51	0.3059	<0.001	0.3495	0.5583	0.4638	0.1232
MAL	2	0.3264	0.9534	-2.7500	0.1096	0.0000	1.0000	47	0.2469	0.0333	0.2045	0.7317	0.1214	0.6841
MRH	1	NA	NA	NA	NA	NA	NA	43	0.2231	0.1283	0.1450	0.8079	-0.1618	0.5877
MXRB	2	0.8264	0.0603	-2.7500	0.1096	0.0000	1.0000	46	0.3009	0.0022	0.8170	0.1737	-0.2079	0.4863
MIRB	2	0.5080	0.4842	-2.7500	0.1096	0.0000	1.0000	55	0.1616	0.2740	-0.6794	0.2569	0.3342	0.2645
HML	5	0.6000	0.0301	-1.9611	0.2373	0.0905	0.9096	37	0.6908	<0.001**	-0.6538	0.2750	0.0796	0.7896
HXMS	6	0.2202	0.8778	-1.9062	0.2497	-0.2398	0.7639	63	0.2622	0.0062	2.1951	<0.001	1.1941	<0.001**
HIMS	6	0.3134	0.4992	-1.1557	0.4747	0.3638	0.6497	63	0.2369	0.0160	-0.1352	0.8207	0.0471	0.8744
HDT	5	0.3517	0.4634	-2.0140	0.2259	-0.0109	0.9891	63	0.2788	0.0034	-0.5728	0.3384	0.0839	0.7784
HSIH	4	0.3577	0.5786	-2.1517	0.1983	-0.2177	0.7850	49	0.1783	0.1675	-0.5979	0.3179	-0.1619	0.5875
HEB	2	0.3632	0.8975	-2.7500	0.1096	0.0000	1.0000	28	0.2774	0.0875	-0.5178	0.3865	0.1462	0.6241
RML	3	0.6439	0.0923	-2.3333	0.1663	-0.3351	0.6755	42	0.5080	<0.001**	0.1450	0.8079	0.0335	0.9106
RXMS	5	0.2810	0.8248	-2.1844	0.1921	-0.0063	0.9937	55	0.2628	0.0159	0.7047	0.2397	-0.3621	0.2271

Table A4.4 Continued

	YA							MDA						
	Kolmogorov-Smirnov			Kurtosis		Skew		Kolmogorov-Smirnov			Kurtosis		Skew	
Trait	**N**	**D**	**P**	**Kurtosis**	**P**	**Skewness**	**P**	**N**	**D**	**P**	**Kurtosis**	**P**	**Skewness**	**P**
RIMS	5	0.3707	0.3968	-1.1411	0.4801	0.8451	0.3036	57	0.3338	0.0010	0.0961	0.8720	0.6310	0.0373
RGH	1	NA	NA	NA	NA	NA	NA	27	0.1983	0.4114	-0.2480	0.6777	0.5569	0.0652
RMLD	2	0.7054	0.1736	-2.7500	0.1096	0.0000	1.0000	43	0.1569	0.3728	0.4384	0.4631	-0.4600	0.1262
FML	2	0.9332	0.0089	-2.7500	0.1096	0.0000	1.0000	48	0.4611	<0.001**	-1.0373	0.0854	-0.1286	0.6664
FPL	2	0.9772	0.0010	-2.7500	0.1096	0.0000	1.0000	49	0.4934	<0.001**	-1.1152	0.0649	0.0962	0.7470
FXMS	4	0.2517	0.9023	-2.1689	0.1950	-0.1871	0.8145	81	0.0997	0.7381	-0.4512	0.4502	-0.0975	0.7439
FIMS	4	0.4920	0.2011	-2.0673	0.2148	0.1556	0.8453	80	0.0904	0.8369	-0.0680	0.9092	-0.5279	0.0801
FEB	1	NA	NA	NA	NA	NA	NA	41	0.4412	0.0027	-0.0070	0.9907	-0.3717	0.2152
FSIH	3	0.3594	0.7071	-2.3333	0.1663	-0.0799	0.9201	57	0.0992	0.8708	-0.4402	0.4613	-0.1653	0.5796
FMLP	3	0.6736	0.0695	-2.3333	0.1663	-0.0511	0.9488	36	0.3914	<0.001**	-0.9350	0.1202	-0.0944	0.7517
TML	2	0.9772	0.0010	-2.7500	0.1096	0.0000	1.0000	53	0.3106	0.0019	-1.1097	0.0661	0.0637	0.8308
TXNF	7	0.3322	0.3444	-1.3752	0.3978	0.5759	0.4761	76	0.1223	0.4431	0.8766	0.1448	0.7125	0.0193
TINF	7	0.2109	0.8568	-1.3554	0.4044	-0.4047	0.6139	78	0.1663	0.1332	0.1594	0.7892	0.3711	0.2159
TMLD	3	0.5000	0.3333	-2.3333	0.1663	0.2656	0.7396	39	0.2413	0.0607	-0.6679	0.2649	-0.0766	0.7973
TMLP	0	NA	NA	NA	NA	NA	NA	29	0.3000	0.0546	-0.5120	0.3919	-0.3072	0.3048

	MA						
	Kolmogorov-Smirnov			Kurtosis		Skew	
Trait	**N**	**D**	**P**	**Kurtosis**	**P**	**Skewness**	**P**
COBB	44	0.0880	0.7226	-0.0991	0.8264	0.6150	0.0074
COBH	42	0.0999	0.5252	-0.5402	0.2334	-0.0409	0.8565
CNOR	41	0.1505	0.0959	-0.8167	0.0727	0.2327	0.3043
CFMTN	46	0.1454	0.1038	-0.9310	0.0412	0.1584	0.4837
CFMTNS	45	0.1207	0.3992	1.0304	0.0241	0.3941	0.0831
CMAH	45	0.1288	0.2313	0.4691	0.3004	0.8486	<0.001**
CMPL	40	0.2716	<0.001**	0.3057	0.4992	-0.6052	0.0083
CMPB	42	0.1688	0.0263	0.2005	0.6574	0.0676	0.7647
CMSAST	35	0.3673	<0.001**	1.0082	0.0273	-0.5541	0.0155
COCL	44	0.1462	0.0712	1.5669	<0.001	-0.5956	0.0094
COPO	45	0.2135	<0.001	-0.3682	0.4159	-0.2334	0.3028
CBAPO	51	0.1898	0.0035	-0.0381	0.9329	0.3143	0.1660
CECMIS	24	0.1597	0.7212	-1.0662	0.0197	0.0861	0.7033
CNMS	34	0.2993	<0.001**	2.4459	<0.001**	0.2078	0.3587
CBZO	38	0.2531	0.0029	-0.3323	0.4627	0.0038	0.9865

Table A4.4 Continued

	MA						
	Kolmogorov-Smirnov			Kurtosis		Skew	
Trait	**N**	**D**	**P**	**Kurtosis**	**P**	**Skewness**	**P**
CFMTB	42	0.2439	0.0016	-0.1086	0.8101	0.4372	0.0549
CBPO	48	0.3016	<0.001**	0.3685	0.4156	-0.0330	0.8839
CBAST	44	0.3106	<0.001**	-0.5399	0.2337	-0.0011	0.9961
CLFMT	41	0.2351	0.0057	-0.2616	0.5630	0.4249	0.0620
CLAST	42	0.2515	0.0025	1.7611	<0.001**	0.2186	0.3343
MAL	32	0.2238	0.0180	0.4937	0.2759	0.4811	0.0350
MRH	26	0.3596	<0.001**	-0.2108	0.6411	0.3171	0.1623
MXRB	36	0.2181	0.0252	-0.5977	0.1877	0.2034	0.3689
MIRB	38	0.1995	0.0250	-0.4061	0.3697	0.1626	0.4723
HML	33	0.7340	<0.001**	0.1437	0.7506	0.1318	0.5600
HXMS	42	0.3489	<0.001**	1.2308	0.0073	-0.5369	0.0189
HIMS	43	0.2030	0.0111	-0.4241	0.3490	-0.1800	0.4262
HDT	41	0.2851	<0.001**	0.2478	0.5838	0.4440	0.0513
HSIH	39	0.1190	0.4914	0.7053	0.1206	0.0309	0.8914
HEB	19	0.2986	0.0104	-0.3854	0.3945	0.6387	0.0054
RML	27	0.5284	<0.001**	-0.3860	0.3938	0.1421	0.5298
RXMS	35	0.2025	0.0220	-0.3266	0.4704	0.6784	0.0032
RIMS	34	0.2375	0.0032	0.4142	0.3602	0.2970	0.1903
RGH	20	0.1719	0.4025	0.0932	0.8366	-0.4535	0.0466
RMLD	34	0.2776	0.0026	-0.2935	0.5164	0.0520	0.8181
FML	31	0.3830	<0.001**	-0.4719	0.2975	0.0174	0.9385
FPL	31	0.3209	<0.001**	-0.7736	0.0889	-0.0261	0.9080
FXMS	47	0.0803	0.6731	0.1194	0.7917	-0.1155	0.6096
FIMS	47	0.1413	0.0820	1.9686	<0.001**	-0.6153	0.0073
FEB	17	0.3537	<0.001**	-0.5398	0.2338	0.1612	0.4760
FSIH	36	0.2052	0.0164	-0.0516	0.9091	0.1673	0.4597
FMLP	27	0.2186	0.0545	-0.9829	0.0313	0.1789	0.4293
TML	36	0.3130	<0.001**	0.7562	0.0963	-0.1982	0.3813
TXNF	50	0.1033	0.3925	0.6793	0.1347	-0.0721	0.7499
TINF	49	0.1812	0.0119	0.7691	0.0908	-0.1735	0.4431
TMLD	30	0.2436	0.0195	-0.4308	0.3414	-0.1266	0.5756
TMLP	20	0.4310	<0.001**	0.2492	0.5816	-0.0152	0.9465

**significant after a Holm's adjustment, p-value < 0.05; D = test statistic for the Kolmogorov-Smirnov test

Appendix 5: Measurement error

Table A5.1. Interobserver technical error of measurement (TEM) values

Trait	N	TEM	Mean	%TEM	Trait	N	TEM	Mean	%TEM
COBB	22	0.47	39.54	1.20	FIMS	20	0.39	25.21	1.55
COBH	22	0.52	33.88	1.53	FEB	22	0.77	81.38	0.94
CNOR	22	0.95	54.26	1.75	FSIH	22	0.34	46.09	0.74
CFMTN	22	1.62	57.78	2.81	FMLP	22	0.63	93.50	0.68
CFMTNS	22	1.56	77.20	2.03	TML	20	2.10	403.09	0.52
CMAH	11	1.44	22.97	6.26	TXNF	20	0.91	36.57	2.49
CMPL	22	2.68	29.24	9.15	TINF	20	0.51	26.05	1.96
CMPB	22	2.68	26.63	10.06	TMLD	20	2.85	49.58	5.75
CMSAST	22	0.47	49.83	0.94	TMLP	20	1.46	77.45	1.88
COCL	22	1.03	24.19	4.27	i1l_bl	16	0.15	6.03	2.54
COPO	22	1.69	72.33	2.34	i1l_md	16	0.14	5.55	2.54
CBAPO	22	1.39	59.90	2.33	i2l_bl	21	0.09	6.42	1.38
CECMIS	22	0.69	32.52	2.13	i2l_md	19	0.15	6.17	2.44
CNMS	22	1.36	126.84	1.07	c1l_bl	18	0.23	8.20	2.75
CBZO	22	0.97	133.17	0.73	c1l_md	22	0.29	7.29	3.94
CFMTB	22	1.75	113.67	1.54	pm1l_bl	20	0.24	8.29	2.89
CBPO	22	1.16	125.42	0.93	pm1l_md	22	0.28	7.53	3.74
CBAST	20	1.18	134.40	0.88	pm2l_bl	20	0.23	8.57	2.70
CLFMT	22	3.38	167.41	2.02	pm2l_md	22	0.37	7.38	5.05
CLAST	22	1.20	85.26	1.41	m1l_bl	16	0.22	10.78	2.04
MAL	22	1.44	127.29	1.13	m1l_md	18	0.56	11.51	4.87
MRH	20	3.11	60.99	5.10	m2l_bl	20	0.32	10.72	2.95
MXRB	22	1.02	46.33	2.20	m2l_md	19	0.46	11.22	4.14
MIRB	22	0.19	37.29	0.51	i1u_bl	24	0.35	7.37	4.75
HML	21	1.64	327.02	0.50	i1u_md	20	0.23	8.97	2.58
HXMS	22	0.46	22.39	2.05	i2u_bl	20	0.14	6.75	2.03
HIMS	22	0.24	18.07	1.31	i2u_md	20	0.37	7.11	5.21
HDT	22	1.19	23.19	5.12	c1u_bl	22	0.20	8.81	2.30
HSIH	21	0.48	44.69	1.08	c1u_md	22	0.34	7.99	4.22
HEB	20	0.85	62.17	1.37	pm1u_bl	22	0.21	9.59	2.22
RML	22	0.38	264.66	0.15	pm1u_md	22	0.24	7.24	3.37
RXMS	22	0.10	15.45	0.67	pm2u_bl	20	0.11	9.67	1.17
RIMS	20	0.16	11.90	1.35	pm2u_md	20	0.26	6.92	3.74
RGH	22	0.25	23.18	1.08	m1u_bl	20	0.18	11.23	1.65
RMLD	20	0.65	32.98	1.98	m1u_md	20	0.42	10.88	3.87
FML	22	1.43	463.70	0.31	m2u_bl	20	0.15	11.74	1.30
FPL	21	1.35	460.83	0.29	m2u_md	20	0.61	10.62	5.77
FXMS	20	0.98	31.04	3.16					

Table A5.2. Interobserver measurement error results for asymmetry values from a two-way side by individual ANOVA and subsequent indices

	Sides x Individuals				Error			
Trait	**df**	**MS_{int}**	**F**	**P**	**df**	**MS_m**	**ME3 (%)**	**ME5**
COBB	10	0.3831	1.6979	0.1444	22	0.2256	58.8978	0.2587
COBH	10	1.2008	4.4942	0.0016*	22	0.2672	22.2507	0.6360
CNOR	10	0.4972	0.5502	0.8356	22	0.9037	181.7564	-0.2902
CFMTN	10	0.6824	0.2586	0.9844	22	2.6386	386.6592	-0.5890
CFMTNS	10	2.4887	1.0181	0.4599	22	2.4445	98.2228	0.0090
CMAH	4	0.1188	0.0575	0.9930	11	2.0668	1739.1238	-0.8913
CMPL	10	6.2949	0.8791	0.5655	22	7.1604	113.7489	-0.0643
CMPB	10	2.5578	0.3564	0.9529	22	7.1777	280.6215	-0.4745
CMSAST	10	6.4651	29.2386	<0.001**	22	0.2211	3.4201	0.9339
COCL	10	2.8414	2.6664	0.0265*	22	1.0656	37.5034	0.4545
COPO	10	0.9727	0.3403	0.9595	22	2.8584	293.8659	-0.4922
CBAPO	10	0.7916	0.4073	0.9285	22	1.9434	245.5019	-0.4211
CECMIS	10	0.8791	1.8255	0.1151	22	0.4816	54.7805	0.2922
CNMS	10	1.7182	0.9333	0.5228	22	1.8409	107.1429	-0.0345
CBZO	10	1.0670	1.1382	0.3798	22	0.9375	87.8594	0.0646
CFMTB	10	2.9784	0.9689	0.4958	22	3.0739	103.2049	-0.0158
CBPO	10	2.8420	2.1105	0.0694	22	1.3466	47.3810	0.3570
CBAST	9	3.0111	2.1508	0.0738	20	1.4000	46.4945	0.3652
CLFMT	10	2.0136	0.1765	0.9964	22	11.4091	566.5914	-0.7000
CLAST	10	5.6501	3.9046	0.0037*	22	1.4470	25.6105	0.5922
MAL	10	1.9175	0.9217	0.5318	22	2.0804	108.4961	-0.0407
MRH	8	5.5924	0.5787	0.7834	20	9.6636	172.8004	-0.2669
MXRB	10	0.9128	0.8811	0.5639	22	1.0360	113.4881	-0.0632
MIRB	10	0.7320	20.1639	<0.001**	22	0.0363	4.9594	0.9055
HML	9	10.9227	4.0404	0.004*	21	2.7033	24.7498	0.6032
HXMS	10	0.2875	1.3591	0.2619	22	0.2115	73.5776	0.1522
HIMS	10	0.1062	1.8984	0.1010	22	0.0559	52.6755	0.3100
HDT	10	0.9516	0.6756	0.7351	22	1.4086	148.0240	-0.1936
HSIH	9	0.8894	3.8425	0.0053*	21	0.2315	26.0245	0.5870
HEB	9	1.6729	2.3197	0.0562	20	0.7212	43.1090	0.3975
RML	10	5.7136	38.6769	<0.001**	22	0.1477	2.5855	0.9496
RXMS	10	0.3766	34.9542	<0.001**	22	0.0108	2.8609	0.9444
RIMS	9	0.1579	6.1169	<0.001**	20	0.0258	16.3481	0.7190
RGH	10	0.3846	6.1665	<0.001**	22	0.0624	16.2167	0.7209
RMLD	9	0.5827	1.3720	0.2645	20	0.4247	72.8857	0.1568
FML	10	19.9477	9.8067	<0.001**	22	2.0341	10.1971	0.8149
FPL	9	24.1361	13.3384	<0.001**	21	1.8095	7.4972	0.8605
FXMS	9	1.7019	1.7695	0.1379	20	0.9618	56.5127	0.2779
FIMS	9	0.1127	0.7384	0.6705	20	0.1526	135.4238	-0.1505
FEB	10	0.6727	1.1495	0.3729	22	0.5852	86.9932	0.0696
FSIH	10	0.7219	6.1314	<0.001**	22	0.1177	16.3094	0.7196
FMLP	10	1.8298	4.5584	0.0014*	22	0.4014	21.9376	0.6402
TML	9	12.3618	2.8055	0.0262*	20	4.4063	35.6441	0.4744
TXNF	9	1.1457	1.3864	0.2584	20	0.8264	72.1292	0.1619
TINF	9	0.5643	2.1578	0.0730	20	0.2615	46.3431	0.3667
TMLD	9	0.7264	0.0895	0.9996	20	8.1178	1117.5915	-0.8357
TMLP	9	1.4972	0.7046	0.6981	20	2.1250	141.9295	-0.1733
i1l_bl	7	0.0122	0.5191	0.8074	16	0.0234	192.6463	-0.3166
i1l_md	8	0.0494	2.4937	0.0570	16	0.0198	40.1018	0.4275
i2l_bl	10	0.0213	2.7111	0.0260*	21	0.0078	36.8852	0.4611

Table A5.2 continued

	Sides x Individuals				Error			
Trait	**df**	**MS_{int}**	**F**	**P**	**df**	**MS_m**	**ME3 (%)**	**ME5**
i2l_md	8	0.0423	1.8681	0.1257	19	0.0226	53.5294	0.3027
c1l_bl	8	0.0637	1.2557	0.3248	18	0.0507	79.6364	0.1134
c1l_md	10	0.1437	1.7436	0.1331	22	0.0824	57.3535	0.2710
pm1l_bl	10	0.1195	2.0869	0.0775	20	0.0573	47.9180	0.3521
pm1l_md	11	0.1037	1.3058	0.2849	22	0.0794	76.5806	0.1326
pm2l_bl	10	0.0917	1.7142	0.1463	20	0.0535	58.3362	0.2631
pm2l_md	11	0.1950	1.4042	0.2391	22	0.1389	71.2156	0.1681
m1l_bl	8	0.0638	1.3207	0.3017	16	0.0483	75.7191	0.1382
m1l_md	9	0.1151	0.3666	0.9365	18	0.3140	272.7694	-0.4635
m2l_bl	9	0.0403	0.4044	0.9180	20	0.0997	247.3061	-0.4241
m2l_md	9	0.0301	0.1399	0.9976	19	0.2152	714.5721	-0.7545
i1u_bl	11	0.0071	0.0579	1.0000	24	0.1230	1725.9230	-0.8905
i1u_md	9	0.1456	2.7136	0.0302*	20	0.0536	36.8514	0.4614
i2u_bl	9	0.0540	2.8898	0.0231*	20	0.0187	34.6047	0.4858
i2u_md	9	0.8105	5.9153	<0.001**	20	0.1370	16.9053	0.7108
c1u_bl	10	0.0240	0.5815	0.8116	22	0.0412	171.9613	-0.2646
c1u_md	10	0.0687	0.6044	0.7935	22	0.1137	165.4634	-0.2466
pm1u_bl	11	0.1501	3.3012	0.0082*	22	0.0455	30.2920	0.5350
pm1u_md	11	0.0528	0.8862	0.5665	22	0.0596	112.8389	-0.0603
pm2u_bl	9	0.0548	4.2939	0.0032*	20	0.0128	23.2886	0.6222
pm2u_md	9	0.1148	1.7145	0.1510	20	0.0670	58.3257	0.2632
m1u_bl	9	0.0462	1.3535	0.2725	20	0.0342	73.8841	0.1502
m1u_md	9	0.1918	1.0821	0.4170	20	0.1773	92.4106	0.0394
m2u_bl	9	0.0687	2.9468	0.0211*	20	0.0233	33.9353	0.4933
m2u_md	9	0.1349	0.3589	0.9416	20	0.3758	278.6424	-0.4718

*p < 0.05; **significant after a Holm's adjustment, p < 0.05; df = degrees of freedom; MS_{int} = $MS_{interaction,}$ sides by individual expected mean squares; F = test statistic of two-way ANOVA; MS_m = measurement error or residual

Appendix 6: Effect of DA on FA

Table A6.1. Results of adults for the evaluation of the effect of directional asymmetry on the interpretation of fluctuating asymmetry by means of one sample student t-tests and a comparison of mean (right - left) and FA4a

Trait	N	t-value	p-value	Mean (R-L)	FA4a
COBB	113	1.4202	0.1582	0.1463	0.7173
COBH	121	0.8803	0.3804	0.0740	0.6944
CNOR	119	4.6157	<0.001**	0.4183	0.8143
CFMTN	127	3.4114	<0.001	0.3144	0.8835
CFMTNS	112	0.7815	0.4362	0.1001	1.3490
CMAH	123	1.9097	0.0585	0.2177	0.9681
CMPL	116	-1.9222	0.0571	-0.3873	1.8991
CMPB	126	1.7949	0.0751	0.2766	1.5251
CMSAST	88	2.1363	0.0355	0.5606	1.9172
COCL	134	-0.1877	0.8514	-0.0391	1.2563
COPO	143	-0.0235	0.9813	0.0233	1.9357
CBAPO	152	1.9404	0.0542	0.3052	1.4447
CECMIS	48	1.0804	0.2855	0.1598	0.8636
CNMS	96	1.3338	0.1855	0.3750	2.1615
CBZO	95	2.7640	0.0069	0.5368	1.4495
CFMTB	108	2.2988	0.0235	0.5093	1.9309
CBPO	128	-0.7461	0.4570	-0.1523	2.2629
CBAST	107	-0.2256	0.8220	-0.0701	2.2266
CLFMT	101	1.9610	0.0527	0.4505	1.4795
CLAST	100	-0.6016	0.5488	-0.1374	2.3880
MAL	94	-0.4385	0.6620	-0.0810	1.7494
MRH	79	-0.9635	0.3383	-0.3751	2.1249
MXRB	96	-1.9775	0.0509	-0.3405	1.3606
MIRB	108	-0.3455	0.7304	-0.0444	1.0369
HML	90	9.8228	<0.001**	3.5667•	2.8867
HXMS	131	7.4067	<0.001**	0.5565	0.6978
HIMS	132	2.5420	0.0122	0.1679	0.5367
HDT	129	6.4309	<0.001**	0.4923	0.6819
HSIH	111	1.7924	0.0758	0.1945	0.7997
HEB	62	4.0329	<0.001**	0.7242	1.1080
RML	83	5.1441	<0.001**	1.5410	2.0797
RXMS	114	3.7242	<0.001**	0.2931	0.6969
RIMS	115	1.9316	0.0559	0.0785	0.3530
RGH	53	1.2441	0.2191	0.1213	0.5811
RMLD	94	4.0067	<0.001**	0.3114	0.6413
FML	90	-1.1792	0.2414	-0.2000	3.5465
FPL	93	-1.4220	0.1584	-0.4978	3.3493
FXMS	152	-0.7697	0.4427	-0.0757	0.8441
FIMS	152	0.3098	0.7572	0.0130	0.6440
FEB	67	5.0075	<0.001**	0.5896	0.7856
FSIH	107	1.8169	0.0720	0.1572	0.6661
FMLP	75	0.5463	0.5865	0.0679	1.5533
TML	103	0.6378	0.5251	0.2767	2.3801
TXNF	155	1.1799	0.2398	0.1043	1.1013
TINF	157	2.8357	0.0052	0.2290	0.8081
TMLD	80	2.1028	0.0387	0.2518	0.8388
TMLP	55	2.2797	0.0266	0.3818	0.8445

**significant after a Holm's adjustment, $p < 0.05$; •mean (R-L) is larger than the deviation around the mean (FA4a)

Table A6.2. Results of subadults for the evaluation of the effect of directional asymmetry on the interpretation of fluctuating asymmetry by means of non-parametric sign tests and a comparison of mean (right - left) and FA4a

Trait	N	S	p-value	Mean (R-L)	FA4a
CFMTN	5	1.0000	1.0000	0.0360	0.8259
CMAH	4	2.0000	1.0000	0.3825	0.4174
CMPL	5	1.0000	0.3750	-0.7600	0.9696
CMPB	5	4.0000	0.3750	0.9540	1.4772
CECMIS	5	2.0000	1.0000	-0.7120	1.0848
CFMTB	0	NA	NA	NA	NA
CMSAST	1	1.0000	1.0000	0.3600	NA
COCL	2	2.0000	0.5000	1.2100•	0.0451
MAL	5	1.0000	1.0000	-0.2340	0.6449
MRH	5	3.0000	1.0000	0.2780	0.7418
MXRB	5	1.0000	0.3750	-0.4780	0.5765
MIRB	11	6.0000	0.5078	0.2373	0.6323
HML	8	2.0000	2.0000	-0.2975	0.7723
HXMS	13	6.0000	1.0000	-0.0500	0.2701
HIMS	13	5.0000	1.0000	-0.0938	0.2342
HDT	7	1.0000	0.2188	-0.3714	0.4075
HSIH	2	1.0000	1.0000	-0.0550	0.4458
HSMLD	8	3.0000	1.0000	0.2425	0.4825
HSMLP	9	4.0000	1.0000	0.0056	0.6735
RML	7	3.0000	0.6250	0.3229	0.7166
RXMS	13	8.0000	0.2266	0.1485	0.2908
RIMS	13	7.0000	0.7744	0.0092	0.1916
RGH	0	NA	NA	NA	NA
RSMLD	10	5.0000	1.0000	0.1070	0.3623
RMLD	1	0.0000	1.0000	-0.5200	NA
FML	9	1.0000	1.0000	0.1589	0.5982
FPL	5	1.0000	1.0000	0.0640	0.9985
FXMS	13	7.0000	0.7744	0.0677	0.3246
FIMS	13	8.0000	0.5811	0.1238	0.2564
FEB	2	1.0000	1.0000	0.2750	0.9649
FSMLD	9	2.0000	0.2891	0.1167	1.3021
FSIH	3	2.0000	1.0000	-0.0300	0.7636
FMLP	7	3.0000	1.0000	-0.4271	1.0697
TML	10	6.0000	0.2891	0.5460	1.7324
TXNF	14	5.0000	0.5811	-0.0800	0.4541
TINF	13	4.0000	1.0000	-0.0485	0.3210
TSMLD	10	4.0000	1.0000	0.1740	0.7390
TMLD	1	1.0000	1.0000	0.7000	NA
TSMLP	4	4.0000	0.1250	0.8225•	0.2271
TMLP	2	2.0000	0.5000	1.0300•	0.3611

**significant after a Holm's adjustment, $p < 0.05$; •mean (R-L) is larger than the deviation around the mean (FA4a);S = test statistic for the non-parametric sign tests

Appendix 7: FA comparisons

Table A7.1. Mann-Whitney U test results for differences in fluctuating asymmetry levels between the sexes, populations pooled

Trait	Male (n)	Female (n)	W	p-value
COBB	51	63	1457.50	0.384
COBH	52	64	1469.00	0.269
CNOR	54	60	1651.00	0.858
CFMTN	55	66	1976.00	0.388
CFMTNS	44	61	1390.50	0.748
CMAH	55	63	1837.50	0.570
CMSAST	32	54	652.00	0.057
COCL	55	73	2016.00	0.969
COPO	62	77	1817.50	0.014*
CBAPO	64	83	2780.00	0.624
CNMS	40	54	1036.00	0.731
CBZO	41	53	961.50	0.320
CFMTB	49	57	1263.00	0.387
CBPO	57	68	1797.50	0.478
CBAST	46	59	1160.50	0.190
CLFMT	43	55	1287.00	0.425
CLAST	41	57	1047.50	0.378
MAL	34	48	887.00	0.486
MRH	27	44	567.00	0.751
MXRB	32	53	943.50	0.384
MIRB	39	59	1311.00	0.242
HXMS	59	72	1871.50	0.240
HIMS	59	73	1982.50	0.430
HSIH	48	62	1603.50	0.476
HEB	28	32	488.00	0.544
RML	34	45	819.50	0.556
RXMS	47	63	1586.50	0.521
RIMS	48	64	1481.50	0.747
RGH	23	30	310.50	0.535
RMLD	39	53	929.50	0.404
FML	40	50	1009.00	0.940
FPL	42	51	986.50	0.479
FXMS	64	88	2548.50	0.313
FIMS	64	87	3070.00	0.272
FEB	36	31	493.00	0.391
FSIH	50	58	1554.50	0.503
FMLP	36	39	827.00	0.174
TML	47	55	1272.50	0.884
TXNF	58	97	2590.00	0.405
TINF	58	99	2738.00	0.627
individual	90	140	6578.50	0.572
skeleton	90	139	6058.00	0.688
dentition	40	65	1381.00	0.595
d_permanent	40	65	1381.00	0.595
d_mandible	34	57	981.00	0.925
d_maxilla	32	56	971.50	0.514
cranium	70	95	2866.50	0.131

Table A7.1 continued

Trait	Male (n)	Female (n)	W	p-value
c_orbit	51	64	1567.00	0.713
c_facial	60	72	2153.00	0.976
c_base	66	89	2558.50	0.171
c_vault	57	76	2043.00	0.575
mandible	43	67	1584.00	0.380
humerus	65	82	2608.00	0.825
radius	54	73	1950.50	0.922
femur	67	94	3300.00	0.605
tibia	67	101	3527.00	0.642
UL	71	99	3384.00	0.681
LL	72	114	4244.50	0.695
midshafts	76	120	4211.50	0.368
UL_midshafts	65	88	2783.00	0.777
LL_midshafts	72	113	3844.50	0.529
lengths	68	90	2956.00	0.712
UL_lengths	53	62	1708.00	0.711
LL_lengths	53	68	1747.00	0.766

*p-value < 0.05, **significant after a Holm's adjustment,
p < 0.05; W = test statistic for the Mann-Whitney U test

Table A7.2. Mann-Whitney U test results for differences in fluctuating asymmetry levels between the sexes for both the GRK and MeB populations

	Grote Kerk				Meerenberg			
Trait	Male (n)	Female (n)	W	p-value	Male (n)	Female (n)	W	p-value
COBB	39	40	812.00	0.751	12	23	78.50	0.033*
COBH	41	42	688.00	0.108	11	22	133.00	0.651
CNOR	43	39	933.00	0.366	11	21	91.00	0.328
CFMTN	44	43	1118.00	0.132	11	23	120.00	0.819
CFMTNS	35	41	695.50	0.818	9	20	124.00	0.095
CMAH	43	41	925.00	0.698	12	22	142.00	0.730
CMSAST	23	37	320.50	0.109	9	17	59.00	0.354
COCL	44	54	1193.50	0.971	11	19	102.00	0.930
COPO	47	52	953.00	0.056	15	25	130.50	0.110
CBAPO	49	56	1411.50	0.800	15	27	235.00	0.389
CNMS	29	36	468.00	0.466	11	18	109.50	0.642
CBZO	35	39	550.50	0.133	6	14	44.50	0.860
CFMTB	41	43	710.00	0.114	8	14	70.50	0.327
CBPO	49	53	1185.00	0.439	8	15	64.00	0.814
CBAST	40	45	826.00	0.502	6	14	19.00	0.055
CLFMT	38	39	750.00	0.926	5	16	47.00	0.564
CLAST	37	43	695.50	0.329	4	14	20.50	0.448
MAL	30	33	550.00	0.428	4	15	28.00	0.877
MRH	22	29	380.50	0.241	5	15	19.00	0.108
MXRB	28	36	613.50	0.136	4	17	24.00	0.387
MIRB	28	38	640.50	0.158	11	21	114.50	0.984
HXMS	42	42	672.50	0.059	17	30	283.50	0.532
HIMS	42	42	783.00	0.373	17	31	244.50	0.686
HSIH	32	34	577.50	0.663	16	28	250.50	0.515
HEB	22	18	210.00	0.747	6	14	49.00	0.570

Table A7.2 continued

	Grote Kerk				Meerenberg			
Trait	Male (n)	Female (n)	W	p-value	Male (n)	Female (n)	W	p-value
RML	28	27	412.50	0.531	6	18	66.00	0.388
RXMS	33	34	592.00	0.699	14	29	199.50	0.938
RIMS	34	34	618.00	0.622	14	30	158.50	0.193
RGH	18	17	121.00	0.292	5	13	39.50	0.509
RMLD	31	28	435.00	0.994	8	25	52.00	0.039*
FML	31	27	358.00	0.311	9	23	144.00	0.068
FPL	33	27	407.00	0.538	9	24	115.50	0.750
FXMS	51	51	1060.00	0.104	13	37	263.50	0.613
FIMS	51	50	1499.00	0.121	13	37	222.50	0.693
FEB	26	19	179.50	0.098	10	12	65.00	0.749
FSIH	36	29	600.50	0.279	14	29	198.50	0.914
FMLP	27	22	362.50	0.179	9	17	78.50	0.932
TML	37	32	644.50	0.489	10	23	84.00	0.173
TXNF	42	58	1134.00	0.554	16	39	267.00	0.406
TINF	43	58	1295.00	0.742	15	41	236.00	0.185
individual	61	84	2959.50	0.112	29	56	698.00	0.293
skeleton	61	83	2757.00	0.363	29	56	644.00	0.120
dentition	24	38	499.50	0.534	16	27	215.00	0.990
d_permanent	24	38	499.50	0.534	16	27	215.00	0.990
d_mandible	20	34	364.00	0.673	14	23	137.00	0.461
d_maxilla	19	32	337.50	0.520	13	24	157.50	0.974
cranium	54	65	1587.50	0.373	16	30	177.50	0.153
c_orbit	41	41	795.00	0.673	10	23	110.00	0.858
c_facial	48	47	1070.50	0.671	12	25	175.50	0.414
c_base	50	62	1356.50	0.258	16	27	193.50	0.580
c_vault	49	58	1298.00	0.441	8	18	73.50	0.955
mandible	32	42	905.00	0.011*	11	25	74.50	0.031*
humerus	47	50	1016.00	0.252	18	32	356.50	0.168
radius	40	37	800.00	0.543	14	36	176.50	0.104
femur	52	56	1424.50	0.849	15	38	350.50	0.199
tibia	51	60	1787.00	0.128	16	41	247.00	0.152
UL	52	58	1479.00	0.864	19	41	352.50	0.561
LL	55	69	2024.50	0.524	17	45	364.00	0.776
midshafts	55	70	1783.50	0.483	21	50	466.00	0.461
UL_midshafts	46	50	1058.50	0.503	19	38	362.00	0.993
LL_midshafts	55	68	1800.00	0.723	17	45	332.50	0.434
lengths	50	49	1176.50	0.733	18	41	382.00	0.834
UL_lengths	37	32	646.50	0.503	16	30	250.50	0.814
LL_lengths	42	39	780.00	0.703	11	29	172.00	0.704

*p-value < 0.05, **significant after a Holm's adjustment, p < 0.05; W = test statistic for the Mann-Whitney U test

Table A7.3. Kruskall-Wallis ANOVA results for differences in fluctuating asymmetry levels between the adult age categories: young adult (YA), middle adult (MDA) and mature adult (MA), populations pooled

Trait	YA (n)	MDA (n)	MA (n)	df	Chi2	p-value
COBB	4	62	44	2	0.885	0.642
COBH	4	66	42	2	1.076	0.584
CNOR	2	67	41	2	1.210	0.546
CFMTN	2	70	46	2	1.539	0.463
CFMTNS	3	55	45	2	0.395	0.821
CMAH	4	65	45	2	0.640	0.726
CMSAST	1	49	35	2	2.526	0.283
COCL	2	78	44	2	1.804	0.406
COPO	4	85	45	2	2.651	0.266
CBAPO	4	88	51	2	1.486	0.476
CNMS	0	59	34	1	0.003	0.954
CBZO	4	51	38	2	0.177	0.915
CFMTB	4	60	42	2	1.940	0.379
CBPO	4	74	48	2	0.453	0.797
CBAST	4	57	44	2	2.045	0.360
CLFMT	4	53	41	2	1.839	0.399
CLAST	4	51	42	2	0.113	0.945
MAL	2	47	32	2	1.214	0.545
MRH	1	43	26	2	3.199	0.202
MXRB	2	46	36	2	0.512	0.774
MIRB	2	55	38	2	5.040	0.080
HXMS	6	63	42	2	1.802	0.406
HIMS	6	63	43	2	0.311	0.856
HSIH	4	49	39	2	0.265	0.876
HEB	2	28	19	2	0.232	0.890
RML	3	42	27	2	1.499	0.473
RXMS	5	55	35	2	0.891	0.641
RIMS	5	57	34	2	0.785	0.675
RGH	1	27	20	2	6.532	0.038*
RMLD	2	43	34	2	0.809	0.667
FML	2	48	31	2	0.784	0.676
FPL	2	49	31	2	0.267	0.875
FXMS	4	81	47	2	0.625	0.731
FIMS	4	80	47	2	8.558	0.014*
FEB	1	41	17	2	1.175	0.556
FSIH	3	57	36	2	1.495	0.474
FMLP	3	36	27	2	1.055	0.590
TML	2	53	36	2	3.092	0.213
TXNF	7	76	50	2	0.789	0.674
TINF	7	78	49	2	0.866	0.649
individual	10	118	68	2	1.829	0.401
skeleton	9	118	68	2	0.240	0.887
dentition	7	41	46	2	0.871	0.647
d_permanent	7	41	46	2	0.871	0.647
d_mandible	7	35	39	2	1.764	0.414
d_maxilla	7	33	40	2	0.330	0.848
cranium	4	99	56	2	0.475	0.789
c_orbit	4	64	42	2	1.556	0.459
c_facial	4	76	49	2	0.648	0.723

Table A7.3 continued

Trait	YA (n)	MDA (n)	MA (n)	df	Chi2	p-value
c_base	4	94	53	2	2.482	0.289
c_vault	4	79	50	2	0.087	0.958
mandible	2	61	43	2	3.033	0.219
humerus	6	72	47	2	1.436	0.488
radius	5	64	41	2	0.383	0.826
femur	5	85	49	2	2.853	0.240
tibia	7	85	52	2	3.190	0.203
UL	6	85	53	2	2.906	0.234
LL	7	97	55	2	1.420	0.492
midshafts	7	97	57	2	2.121	0.346
UL_midshafts	6	75	47	2	1.312	0.519
LL_midshafts	7	96	55	2	2.182	0.336
lengths	5	78	49	2	3.942	0.139
UL_lengths	5	55	38	2	1.674	0.433
LL_lengths	2	63	40	2	1.624	0.444

*p-value < 0.05, **significant after a Holm's adjustment, p < 0.05; df = degrees of freedom; Chi^2 = test statistic for the Kruskall-Wallis ANOVA

Table A7.4. Kruskall-Wallis ANOVA results for differences in fluctuating asymmetry levels between the adult age categories: young adult (YA), middle adult (MDA) and mature adutl (MA) for both populations

	Grote Kerk						Meerenberg					
Trait	YA (n)	MDA (n)	MA (n)	df	Chi2	p-value	YA (n)	MDA (n)	MA (n)	df	Chi2	p-value
COBB	2	48	29	2	0.610	0.737	2	14	15	2	0.429	0.807
COBH	2	52	29	2	0.434	0.805	2	14	13	2	0.953	0.621
CNOR	2	53	27	2	3.119	0.210	0	14	14	1	0.681	0.409
CFMTN	2	55	30	2	1.387	0.500	0	15	16	1	1.619	0.203
CFMTNS	2	44	30	2	1.147	0.564	1	11	15	2	0.162	0.922
CMAH	2	51	31	2	0.386	0.824	2	14	14	2	0.248	0.883
CMSAST	0	36	24	1	0.056	0.814	1	13	11	2	3.732	0.155
COCL	1	65	31	2	3.174	0.205	1	13	13	2	0.813	0.666
COPO	2	66	30	2	4.669	0.097	2	19	15	2	0.276	0.871
CBAPO	2	69	34	2	3.867	0.145	2	19	17	2	1.279	0.527
CNMS	0	44	21	1	0.038	0.845	0	15	13	1	0.144	0.704
CBZO	2	45	26	2	3.426	0.180	2	6	12	2	2.642	0.267
CFMTB	2	53	29	2	5.719	0.057	2	7	13	2	4.384	0.112
CBPO	2	66	34	2	2.328	0.312	2	8	14	2	2.672	0.263
CBAST	2	51	31	2	4.716	0.095	2	6	13	2	1.704	0.427
CLFMT	2	46	29	2	1.349	0.509	2	7	12	2	0.397	0.820
CLAST	2	46	31	2	0.826	0.662	2	5	11	2	0.513	0.774
MAL	1	41	21	2	0.034	0.983	1	6	11	2	1.689	0.430
MRH	0	34	17	1	0.344	0.558	1	9	9	2	1.702	0.427
MXRB	1	40	24	2	1.798	0.407	1	6	12	2	4.204	0.122
MIRB	1	43	21	2	2.535	0.281	1	12	17	2	2.992	0.224
HXMS	2	55	23	2	0.238	0.888	4	8	19	2	1.958	0.376
HIMS	2	55	23	2	1.062	0.588	4	8	20	2	1.684	0.431
HSIH	1	40	21	2	0.525	0.769	3	9	18	2	1.779	0.411
HEB	0	26	11	1	0.076	0.783	2	2	8	2	0.353	0.838
RML	1	38	13	2	0.001	0.999	2	4	14	2	3.202	0.202
RXMS	1	46	18	2	1.217	0.544	4	9	17	2	1.774	0.412
RIMS	1	48	17	2	2.340	0.310	4	9	17	2	0.182	0.913
RGH	1	20	12	2	8.254	0.016*	0	7	8	1	0.032	0.859
RMLD	0	38	18	1	0.489	0.485	2	5	16	2	0.707	0.702
FML	1	39	13	2	2.712	0.258	1	9	18	2	1.463	0.481

Table A7.4 continued

	Grote Kerk						Meerenberg					
Trait	**YA (n)**	**MDA (n)**	**MA (n)**	**df**	**Chi2**	**p-value**	**YA (n)**	**MDA (n)**	**MA (n)**	**df**	**Chi2**	**p-value**
FPL	1	40	13	2	0.116	0.944	1	9	18	2	2.460	0.292
FXMS	1	67	28	2	0.402	0.818	3	14	19	2	1.626	0.444
FIMS	1	66	28	2	5.875	0.053	3	14	19	2	3.242	0.198
FEB	0	33	9	1	3.010	0.083	1	8	8	2	2.038	0.361
FSIH	0	44	19	1	0.006	0.938	3	13	17	2	1.672	0.434
FMLP	0	30	15	1	0.026	0.872	3	6	12	2	2.507	0.285
TML	1	45	19	2	3.257	0.196	1	8	17	2	0.684	0.710
TXNF	3	65	27	2	1.544	0.462	4	11	23	2	2.820	0.244
TINF	3	66	27	2	0.123	0.940	4	12	22	2	1.162	0.559
individual	6	95	39	2	4.739	0.094	4	23	29	2	2.599	0.273
skeleton	5	95	39	2	2.548	0.280	4	23	29	2	4.321	0.115
dentition	5	29	27	2	0.856	0.652	2	12	19	2	0.274	0.872
d_permanent	5	29	27	2	0.856	0.652	2	12	19	2	0.274	0.872
d_mandible	5	23	25	2	2.286	0.319	2	12	14	2	0.107	0.948
d_maxilla	5	22	25	2	0.598	0.742	2	11	15	2	0.177	0.915
cranium	2	80	37	2	3.310	0.191	2	19	19	2	1.265	0.531
c_orbit	2	50	29	2	2.389	0.303	2	14	13	2	1.383	0.501
c_facial	2	61	32	2	1.412	0.494	2	15	17	2	3.797	0.150
c_base	2	75	35	2	3.723	0.155	2	19	18	2	0.099	0.952
c_vault	2	69	36	2	0.392	0.822	2	10	14	2	0.126	0.939
mandible	1	48	25	2	2.129	0.345	1	13	18	2	4.089	0.129
humerus	2	63	27	2	0.255	0.880	4	9	20	2	3.349	0.187
radius	1	53	20	2	2.693	0.260	4	11	21	2	1.679	0.432
femur	1	71	29	2	1.486	0.476	4	14	20	2	2.169	0.338
tibia	3	73	29	2	0.519	0.771	4	12	23	2	5.585	0.061
UL	2	73	29	2	1.694	0.429	4	12	24	2	2.509	0.285
LL	3	82	32	2	0.197	0.906	4	15	23	2	3.635	0.162
midshafts	3	82	32	2	0.555	0.758	4	15	25	2	6.005	0.050
UL_midshafts	2	64	25	2	0.437	0.804	4	11	22	2	2.027	0.363
LL_midshafts	3	81	32	2	0.567	0.753	4	15	23	2	5.168	0.075
lengths	1	66	25	2	0.730	0.694	4	12	24	2	3.214	0.201
UL_lengths	1	45	19	2	0.632	0.729	4	10	19	2	2.732	0.255
LL_lengths	1	53	20	2	1.368	0.505	1	10	20	2	0.896	0.639

*p-value < 0.05, **significant after a Holm's adjustment, $p < 0.05$; df = degrees of freedom; Chi^2 = test statistic for the Kruskall-Wallis ANOVA

Table A7.5. Mann-Whitney U test results for differences in fluctuating asymmetry levels between adults and subadults, populations GRK and MeB pooled

Trait	Adult (n)	Subadult (n)	W	p-value
CFMTN	127	5	389.00	0.382
CMAH	123	4	331.00	0.240
CMSAST	88	1	72.50	0.272
COCL	134	2	112.00	0.696
MAL	94	5	321.00	0.151
MRH	79	5	194.50	0.962
MXRB	95	5	215.50	0.731
MIRB	108	11	640.00	0.674
HXMS	131	13	1113.00	0.066
HIMS	132	13	1026.00	0.241
HSIH	111	2	147.00	0.427
RML	82	7	356.00	0.250
RXMS	113	13	793.50	0.637
RIMS	114	13	575.00	0.182
RMLD	94	1	41.50	0.852
FML	90	9	610.50	0.007*
FPL	93	5	287.50	0.336
FXMS	152	13	1025.00	0.823
FIMS	151	13	857.00	0.441
FEB	67	2	44.00	0.395
FSIH	108	3	91.50	0.184
FMLP	75	7	330.50	0.247
TML	102	10	381.50	0.145
TXNF	155	14	932.50	0.381
TINF	157	13	1239.50	0.196
individual	251	26	3412.00	0.702
skeleton	249	24	3158.00	0.646
dentition	115	15	997.00	0.329
d_mandible	99	13	547.00	0.383
d_maxilla	93	15	940.00	0.031*
cranium	172	7	654.00	0.701
c_facial	138	6	532.00	0.239
c_base	162	2	33.00	0.054
mandible	123	11	710.00	0.789
humerus	148	13	1119.00	0.331
radius	130	14	638.00	0.067
femur	161	16	1207.00	0.680
tibia	168	15	1289.00	0.884
UL	174	17	1505.50	0.905
LL	186	19	1703.50	0.798
midshafts	199	23	2583.00	0.313
UL_midshafts	156	16	1551.00	0.110
LL_midshafts	185	18	1650.50	0.953
lengths	161	17	1729.50	0.069
UL_lengths	118	11	906.00	0.026*
LL_lengths	121	14	925.50	0.556

*p-value < 0.05, **significant after a Holm's adjustment, p < 0.05; W = test statistic for the Mann-Whitney U test

Table A7.6. Mann-Whitney U test results for differences in fluctuating asymmetry levels between the permanent and deciduous dentition, populations GRK and MeB pooled

Permanent (n)	Deciduous (n)	W	p-value
123	10	649	0.775

W = test statistic for the Mann-Whitney U test

Table A7.7. Mann-Whitney U test results for differences in fluctuating asymmetry levels between the population groups, ages pooled

Trait	GRK (n)	MeB (n)	W	p-value
COBB	81	38	1689.00	0.381
COBH	85	36	1479.50	0.772
CNOR	84	35	1369.00	0.546
CFMTN	94	38	2025.50	0.214
CFMTNS	78	33	1391.50	0.489
CMAH	90	37	1574.00	0.629
CMSAST	62	27	832.00	0.968
COCL	100	36	1683.00	0.563
COPO	100	43	2157.50	0.975
CBAPO	107	45	2596.50	0.439
CNMS	66	30	992.50	0.987
CBZO	75	20	675.00	0.476
CFMTB	86	22	915.50	0.814
CBPO	104	24	1577.00	0.040*
CBAST	86	21	795.50	0.384
CLFMT	79	22	579.50	0.011*
CLAST	81	19	626.50	0.204
MAL	71	28	927.00	0.587
MRH	57	27	1025.50	0.013*
MXRB	72	28	1160.00	0.239
MIRB	79	40	1754.00	0.325
HXMS	94	50	2556.50	0.383
HIMS	94	51	1996.50	0.094
HSIH	67	46	1602.50	0.714
HEB	40	21	410.50	0.887
RML	61	28	1028.50	0.090
RXMS	77	49	1449.50	0.028*
RIMS	78	49	1827.00	0.675
RGH	35	18	353.00	0.474
RMLD	59	36	938.00	0.334
FML	67	32	1061.00	0.932
FPL	65	33	1276.50	0.094
FXMS	113	52	2689.00	0.377
FIMS	112	52	2861.00	0.855
FEB	46	23	308.50	0.003*
FSIH	68	43	1541.50	0.618
FMLP	55	27	620.50	0.216
TML	78	34	1387.00	0.669

Table A7.7 continued

Trait	GRK (n)	MeB (n)	W	p-value
TXNF	111	58	2937.00	0.346
TINF	111	59	3366.00	0.764
individual	171	106	8953.00	0.866
skeleton	168	105	8758.00	0.923
dentition	77	53	2308.50	0.205
d_permanent	70	53	2093.00	0.225
d_mandible	67	45	1810.00	0.073
d_maxilla	66	42	1511.50	0.430
cranium	127	52	3093.50	0.509
c_orbit	83	36	1410.00	0.625
c_facial	103	41	2033.00	0.730
c_base	115	49	3068.50	0.368
c_vault	109	27	1363.00	0.554
mandible	88	46	2245.00	0.300
humerus	107	54	2865.00	0.933
radius	88	56	2071.00	0.107
femur	121	56	3203.50	0.561
tibia	123	60	3453.50	0.482
UL	124	67	3846.50	0.399
LL	140	65	4382.00	0.672
midshafts	145	77	4901.50	0.135
UL_midshafts	109	63	2853.50	0.065
LL_midshafts	138	65	4163.50	0.410
lengths	114	64	3913.50	0.414
UL_lengths	78	51	2300.50	0.124
LL_lengths	94	41	2059.00	0.510

*p-value < 0.05, **significant after a Holm's adjustment, p < 0.05;
W = test statistic for the Mann-Whitney U test

Table A7.8. Mann-Whitney U test results for differences in fluctuating asymmetry levels between the population groups, for adults

Trait	GRK (n)	MeB (n)	W	p-value
COBB	81	38	1689.00	0.381
COBH	85	36	1479.50	0.772
CNOR	84	35	1369.00	0.546
CFMTN	89	38	1942.50	0.172
CFMTNS	78	33	1391.50	0.489
CMAH	86	37	1526.50	0.722
CMSAST	61	27	827.00	0.978
COCL	99	35	1625.50	0.588
COPO	100	43	2157.50	0.975
CBAPO	107	45	2596.50	0.439
CNMS	66	30	992.50	0.987
CBZO	75	20	675.00	0.476
CFMTB	86	22	915.50	0.814
CBPO	104	24	1577.00	0.040*
CBAST	86	21	795.50	0.384
CLFMT	79	22	579.50	0.011*
CLAST	81	19	626.50	0.204
MAL	66	28	883.00	0.726
MRH	52	27	939.00	0.013*
MXRB	67	28	1073.00	0.267
MIRB	68	40	1529.00	0.280
HXMS	84	47	2197.50	0.281
HIMS	84	48	1778.00	0.256
HSIH	66	45	1541.50	0.730
HEB	40	21	410.50	0.887
RML	55	27	929.00	0.044*
RXMS	67	46	1211.00	0.053
RIMS	68	46	1492.00	0.675
RGH	35	18	353.00	0.474
RMLD	59	35	913.50	0.345
FML	58	32	984.50	0.609
FPL	60	33	1201.50	0.064
FXMS	102	50	2330.50	0.385
FIMS	101	50	2475.00	0.842
FEB	45	22	295.00	0.005*
FSIH	65	43	1447.00	0.748
FMLP	49	26	538.00	0.258
TML	69	33	1172.50	0.789
TXNF	100	55	2460.50	0.274
individual	148	103	7566.00	0.922
skeleton	147	102	7638.00	0.801
dentition	64	51	1822.00	0.286
d_permanent	70	53	1822.00	0.286
d_mandible	56	43	1357.50	0.280
d_maxilla	53	40	1199.00	0.281
cranium	121	51	2983.00	0.732
c_orbit	83	36	1410.00	0.625
c_facial	97	41	1946.00	0.845
c_base	114	48	3010.50	0.314

Table A7.8 continued

Trait	GRK (n)	MeB (n)	W	p-value
c_vault	109	27	1363.00	0.554
mandible	77	46	1979.00	0.277
humerus	97	51	2520.50	0.851
radius	77	53	1693.00	0.100
femur	108	53	2816.00	0.870
tibia	111	57	3002.50	0.590
UL	110	64	3300.00	0.493
LL	124	62	3742.50	0.770
midshafts	125	74	4173.50	0.250
UL_midshafts	96	60	2513.00	0.181
LL_midshafts	123	62	3524.00	0.400
lengths	99	62	3413.50	0.225
UL_lengths	69	49	2010.00	0.074
LL_lengths	81	40	1786.50	0.339

*p-value < 0.05, **significant after a Holm's adjustment, p < 0.05; W = test statistic for the Mann-Whitney U test

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Faculty of Health Sciences Research Ethics Committee

14/11/2014

Approval Certificate
New Application

Ethics Reference No.: 393/2014

Title: Assessment of skeletal and dental fluctuating asymmetry in two historic Dutch populations

Dear Mrs Alieske Anholts

The **New Application** as supported by documents specified in your cover letter for your research received on the 27/10/2014, was approved by the Faculty of Health Sciences Research Ethics Committee on the 14/11/2014.

Please note the following about your ethics approval:
- Ethics Approval is valid for 1 year.
- Please remember to use your protocol number (**393/2014**) on any documents or correspondence with the Research Ethics Committee regarding your research.
- Please note that the Research Ethics Committee may ask further questions, seek additional information, require further modification, or monitor the conduct of your research.

Ethics approval is subject to the following:
- The ethics approval is conditional on the receipt of 6 monthly written Progress Reports, and
- The ethics approval is conditional on the research being conducted as stipulated by the details of all documents submitted to the Committee. In the event that a further need arises to change who the investigators are, the methods or any other aspect, such changes must be submitted as an Amendment for approval by the Committee.

We wish you the best with your research.

Yours sincerely

Dr R Sommers; MBChB; MMed (Int); MPharMed.
Deputy Chairperson of the Faculty of Health Sciences Research Ethics Committee, University of Pretoria

The Faculty of Health Sciences Research Ethics Committee complies with the SA National Act 61 of 2003 as it pertains to health research and the United States Code of Federal Regulations Title 45 and 46. This committee abides by the ethical norms and principles for research, established by the Declaration of Helsinki, the South African Medical Research Council Guidelines as well as the Guidelines for Ethical Research: Principles Structures and Processes 2004 (Department of Health).

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