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Fluctuating Asymmetry in the Context of Social Stratification: A Bronze Age Population

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And that may be the problem, that fluctuating asymmetry is not measuring a generalized instability, but multiple opportunities for error.

(Jeff Mitton, in Leamy, 1994, p. 373)

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1 Introduction

Symmetry and asymmetry are both universal features characterizing biological systems. Deviations from symmetry take different forms, differentiating them into three main categories of between-sides variability that can, but do not have to occur in any combination: fluctuating asymmetry (FA), directional asymmetry (DA), and antisymmetry (AS). Of these bilateral asymmetries, fluctuating asymmetry is widely used as an indicator and measure of developmental (in)stability and stress (Palmer & Strobeck, 1992; Graham, Freeman, & Emlen, 1994; Graham, Emlen, Freeman, Leamy, & Kieser, 1998; Graham, Raz, Hel-Or, & Nevo, 2010; Barrett, 2005). Stress and skeletal manifestations related to it (e.g. body height, fluctuating asymmetry) are connected to the socio-economic position of an individual in a given society (Teschler-Nicola, 1989; Özener, 2010; Özener & Ertuğrul, 2010). In a Bronze Age population (as was the focus of this study) this socio-economic position manifests itself in funerary material culture, which differentiates individuals into population subgroups (there were three such “status groups” in the present study, Krenn-Leeb, forthcoming) for which stress-pressure is likely to differ. Comparing fluctuating asymmetry levels between such population subgroups can thus provide information as to the situation and functioning of society – whether stress experienced by the population was sufficiently large to manifest differentially within subgroups treated differently by society, and whether these groups were maintained through an individual's life-course.

1.1 Bilateral Asymmetries

Seen as a function of its mean and distribution type, fluctuating asymmetry is distinctively different from other asymmetries: It is minor deviations from perfect symmetry that are random in regard to side (non-directional) – i.e. right-left differences are normally distributed around a mean that is zero. The variance of this normal distribution represents the degree of fluctuating asymmetry. Directional asymmetry, on the other hand, is the tendency of a character to be of greater size on one side. Here, the between-sides differences are also normally distributed, but around a mean significantly greater or less than zero. Antisymmetry, as a third type of asymmetry, can occur when this trend of greater development of a character is directionally random, resulting in a platykurtic or bimodal distribution of differences around a mean of zero. (Van Valen, 1962; Palmer & Strobeck, 1986, 1992; Plochocki, 2004)

1.1.1 Fluctuating asymmetry

The appearance of fluctuating asymmetry is based on deviations from an ideal, predetermined developmental program (both referring to Waddington, 1957; Palmer & Strobeck, 1986; Sommer, 1996): For bilateral characters neither predisposed to be directionally asymmetrical nor antisymmetric, the morphological target phenotype, as product of the same genome and homologous cell lineage, would exhibit perfect symmetry – i.e. the identical development of a character on both sides (Palmer & Strobeck, 1992). This ideal state can of course never be attained (Graham et al., 1994). Yet, like in reduced body height, the amount of deviation from such an ideal phenotype is markedly influenced by stress-affected growth. Growth is defined by coordinated deposition and resorption of material. Stress[1], as a developmental force, reduces optimal levels of bone deposition and remodelling since perturbations due to malnutrition, high work load, pathogens, diseases, parasitic load, poor habitat quality or extreme physical conditions decimate both (raw) material and especially energy (Palmer & Strobeck, 1992; Møller & Swaddle, 1997; Graham et al., 2010). Thus, stress and its compensation disrupt physiological processes (Goodman & Armelagos, 1989), including maintaining precise development according to the ideal developmental program. Compensative mechanisms that adhere development to such a program are altered and ultimately exhausted after certain levels of stress (Emlen, Freeman, & Graham, 1994; Graham et al., 1994; DeLeon, 2007). As a consequence, growth including remodelling is reduced, sometimes even to a functional minimum, and developmental imprecision (i.e. FA) is created through the

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[1] i.e. general cumulative stress, not time-specific stress marked by dental or skeletal lesions (e.g. linear enamel hypoplasia) or disease-specific stress marked by disease-specific lesions (e.g. cribra orbitalia). These different measures of different levels and time horizons for stress complement each other in indicating living conditions and life events (Goodman & Armelagos, 1989; Goodman, 1993; Goodman & Martin, 2002; Barrett, 2005). One of the advantages of FA is its relative resistance to the effect of short-term stress, which is due to the organisation and high level canalisation of pathways into which FA is introduced. (Barrett, 2005)

stressors mentioned above[2] (Goodman & Armelagos, 1989; Leung, Forbes, & Houle, 2000; DeLeon, 2007).

The presence of fluctuating asymmetry thus reflects the stress-increased metabolic cost, indicating an exhausted buffering capacity of the organism towards environmental perturbations, and these perturbations taking morphological as well as histological effect on the organism. Consequently, two mechanisms should be noted as responsible for its occurrence: The "effects of small, random perturbations [...] exclusively environmental in origin" (developmental noise, Palmer & Strobeck, 1992, p. 58), and the capacity of the organism to correct for such accidents (developmental stability), which is based both on genetic as well as environmental influences (both referring to Waddington, 1957; Palmer & Strobeck, 1992; Møller & Swaddle, 1997). Developmentally induced deviations will differ between individuals, not only if differences in their exposure to developmental noise are significantly large, but also because their buffering capacity varies individually (Van Valen, 1962).[3]

Another important relationship aside that of fluctuating asymmetry and stress is that between socio-economic situation and stress parameters such as growth rate, terminal height and fluctuating asymmetry: A lower socio-economic position is usually accompanied by higher stress load through less nutritional income and higher work load, which is then reflected in the body: Özener (2010) and Özener and Ertuğrul (2010) showed that developmental stress, as indicated by the socio-economic status, causes the degree of fluctuating asymmetry present, and that body symmetry increases with better living standards. This connection of fluctuating asymmetry and socio-economic status can also be seen in the relation either has to growth rate/body height (Teschler-Nicola, 1989; Crooks, 1999; Goodman & Martin, 2002; Özener & Ertuğrul, 2011). DeLeon (2007, comparing Early and Late Christian cemetery remains) and Gawlikowska et al. (2007,

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[2] for an overview of (genetic and environmental) stressors as causes of developmental instability see Graham et al. (2010) and Møller and Swaddle (1997).

[3] for discussion on organism-wide bases of FA, DA, and AS, the covariation of characters and their buffering capacity see Van Valen (1962), and Leamy (1994), for an overview of trait-specific FA due to the functional importance of symmetry, e.g. locomotion traits (Palmer & Strobeck, 1986), or due to signalling and sexual selection (Møller & Pomiankowski, 1994) e.g. facial traits, see DeLeon (2007)(2007).

comparing mediaeval and modern skull radiographs) showed differences of craniofacial fluctuating asymmetry between groups subjected to different levels of developmental stress, and noted some traits to be more or less sensitive indicators. Kujanová et al. (2008) compared the bilateral symmetry of two (medieval and recent) skeletal populations and found differences indicating different levels of biomechanical as well as environmental stress.

These findings show that fluctuating asymmetry may be a strong bioindicator reflecting differences between living conditions within as well as between populations, its analysis additionally providing information about social stratification and fitness. The use of fluctuating asymmetry as a measure of stress is not uncontroversial (Lens, Van Dongen, Kark, & Matthysen, 2002), and there are a number of studies where the link between stress and fluctuating asymmetry has not been found. Barret (2005) compared levels of fluctuating asymmetry with linear enamel hypoplasia, and though the latter varied significantly between Late Archaic, Protohistoric and modern dental samples, fluctuating asymmetry did not. This might be attributed to the fact that linear enamel hypoplasia measures a different kind of stress and stress-response than does fluctuating asymmetry, yet it also shows the complexity of stress asymmetry analysis – not least because in this study many traits had to be excluded from fluctuating asymmetry analysis on the basis of their non-normal distribution – which raises the question whether the most severely stressed individuals might in some traits exhibit more complex asymmetry patterns due to their higher stress level.

It must also be understood that the relationship of growth to fluctuating asymmetry is more complex in sub-adult individuals: While the most stressed individuals are usually expected to show the highest fluctuating asymmetry values, they experience reduced (longitudinal) growth during growing periods. Thus they also exhibit reduced fluctuating asymmetry levels compared to less stressed individuals, who, due to their rapid growth, exhibit a higher momentary asymmetry (Wilson & Manning, 1996). That stepchildren, for example, show suboptimal growth yet also exhibit lower fluctuating asymmetry (Flinn, Leone, & Quinlan, 1999) might not be entirely unexpected in this light.

1.1.2 Directional Asymmetry and Antisymmetry

Directional asymmetry – the tendency of a character to be greater on a determined body side, and thus variation of side differences around a mean significantly greater or less than zero – has to all probability a genetic basis (Palmer & Strobeck, 1992). Whereas fluctuating asymmetry is generally said to only represent deviations from normal or ideal development, directional asymmetry as well as antisymmetry are said to represent a target phenotype by their deviation (Graham et al., 1998): The distribution of right and left differences as the bias which side will develop to which degree is predictable, and the asymmetries reflect an adaptive or functional basis rather than developmental instability (Møller & Swaddle, 1997) This, however, does not mean that directional asymmetry and antisymmetry are not environmentally influenced – it has been shown that though genetic determinants exist for both, either may be produced in their absence, and that a character with a naturally antisymmetrical distribution can be environmentally influenced to express directional asymmetry (Graham et al., 1994). Thus, directional asymmetry can as such be connected to stress (for a discussion of asymmetries reflecting developmental instability see Graham et al., 1994; and Møller & Swaddle, 1997).

Directional asymmetry co-occurring with fluctuating asymmetry is a common pattern found in studies of bilateral symmetry. On the premise that fluctuating asymmetry reflects small, random deviations inherent to development, which in a natural environment must be deviating from a set ideal, it must be noted that if directional asymmetry occurs, the variation around the mean will be caused both by genetic factors producing the directional asymmetry as well as by largely environmental factors producing fluctuating asymmetry. This means that fluctuating asymmetry might in its ideal state occur individually (i.e. in absence of directional asymmetry or antisymmetry), but either of the other types of asymmetry will very probably not.

Apart from a pre-determined, genetic tendency of greater character expression on one side, and stress as the depletion of energy, other factors seem to effect the pattern of bilateral differences observed: According to Plato, Wood and Norris (1980), metacarpal bilateral differences including length measurements reflect both the general inclination of greater development on the right side and differential mechanical stress according to hand dominance. Roy, Ruff and Plato (1994) furthermore showed functional hand dominance to be the basis for bilaterally differentiated cortex expansion (i.e. bone strength increase) in second metacarpal midshafts. Likewise, Mays (2002) found varying directional asymmetry levels of second moment of area (i.e. bone strength) in metacarpals between different occupation categories in an 18th–19th century population. Manual workers, even in occupations favouring bilateral hand use, generally showed higher directional asymmetry levels than non-manual workers. Özener (2010) compared directional asymmetry levels between groups of different physical activity levels, which related to an increase of both the amount of directional asymmetry in traits and number of traits exhibiting directional asymmetry (e.g. whole upper limbs versus hand measurements only in lower physical activity groups). The directional asymmetries furthermore increased with the time span individuals spent under heavy working conditions. These studies indicate that differential mechanical loading plays an important role in the formation of directional asymmetries which thus may reflect activity patterns in populations (Mays, 1999).

Indications of correlation of fluctuating asymmetry with joint morphology especially in plane joints like intermetacarpal articulations (Nagar & Rak, 2001) and the small numbers of studies investigating asymmetries in 3D (studies usually use radiographs, which reduces examination to the mediolateral plane) or at locations other than the metacarpal mid-shaft (Palmer & Strobeck, 1986; Barker, Schultz, Krishnan, & Hearn, 2005) show the unexplored potential in assessing fluctuating asymmetry through metacarpal measurements.

1.2 Socio-economic status, and the social implications of burial sites

Socioeconomic status can be approached in different ways, depending largely on the population at hand. While socio-economic status can be examined by a multitude of measures in recent populations (e.g. income, educational level), it is not so easy in past populations where such information is not directly available. While for some communities information can be gained from tomb inscriptions, coffin plates or parish registers that include biographical information (e.g. profession, life events), the collection of data of this kind can be less straightforward in other groups: often the only information available is the interment itself.

Interments do, however, reflect certain concepts in their placement as well as their form, and exceed the notion of merely disposing of a dead body. Some of these concepts concern notions of spirituality, like the relationship and perception of death and the dead by the living (Pearson, 1993). Others refer to the deceased person, their persona, their social connections as well as their social roles – reflecting as well as constructing their social identity or social character that persists beyond death (see the following).
This social identity thus includes several basic components that have a bearing on funerary mode: physiological, chronological and social age, sex, gender, relative social standing within a social unit, social affiliation in society, the ability to actively participate within society, and the cause/location of death (Binford, 1971; Bello & Andrews, 2006; Gowland, 2006; Weiss-Krejci, 2011). Mortuary practices are thus events of multiple social dimensions in which social standing, the place in a status system, is one (Saxe, 1971), and where distinctions are made according to the relative rank and social position in society (Binford, 1971; Krenn-Leeb, 2011).

Funerary tradition can be seen as a direct link to the operating and structuring of society: The spatial relationships between places for living and dead, their intra-site organisation, the distribution of artefacts and deposits in each context all reflect the society in which they are employed (Pearson, 1993). Examples for this are differences or consistencies between sub-adult and adult burials that result from societal status being achievement-based or heritable (Gilman et al., 1981); and the concept of participant-ship that can also be addressed through burial comparison: Those who cannot participate in society to the same extent or in the same mode as others (e.g. sub-adult and old individuals versus adults, or individuals of different occupation) are represented differently. This can also bias a sample – social personality components determine funerary deposition, which influences preservation. Funerary structures as well as practices, and thus preservation, might vary for separate portions of a population, resulting in the preservation of a nonrepresentative sample. This conceptually interacts with taphonomic processes that likewise affect bone material differentially according to its structure (e.g. size, volume, mineral density), which is linked to individual characteristics like age or sex. (Bello & Andrews, 2006; Jackes, 2011)

A more complex society usually exhibits stronger variation in funerary practice: for one, because more distinctions are made based on the presence of differently perceived groups within society, for another, because more strongly structured groups tend to have a greater population density, which also leaves room for greater social inequalities. This insofar connects to subsistence and mode of living as (plough) agriculture usually leads to higher population densities as well as a stronger stratification. (Binford, 1971; Gilman et al., 1981). While hunters and gatherers base their funerary practice more strongly on characteristics like age and sex/gender, settled agriculturists additionally employ other and in total more distinctions, while they also show more incidences of stratification and sub-grouping. Differences in goods due to sex/gender as might be seen in sex/gender-differentiated clothing or tools (indicating division in labour according to sex/gender), usually pertain only to the form of goods, and not necessarily to their quantity or value, while differences due to social position pertain to either form, quantity or both, but might often include differentiation by location. (Binford, 1971). In the absence of spatial differentiations, interments might be classified by their content (amount as well as type and value), dimensions (length, breadth, depth), as well as amount of looting (e.g. Teschler-Nicola, 1989; Krenn-Leeb, 2011).

Mortuary deposits can either consist of a more or less highly selected sample of objects taken from their domestic context (i.e. that are available to and used by the living), or of objects only used as funerary deposits or other parts of the funerary ritual, which in some cultures indicates a separation within material culture, and thus, a marginalisation of death (Pearson, 1993). Mortuary deposits can be used to construct, legitimise, reinforce, transform or subvert social, cultural and political norms (Pearson, 1993; Gowland, 2006).
It must be noted that this analysis of mortuary deposits is limited to materials that are preserved while materials that are not are lost to the record despite their possible value.

1.3 The Necropolis of Hainburg-Teichtal

The site of Hainburg-Teichtal has been known to be populated since the Early Neolithic in the 6th century BC. The Early Bronze Age necropolis situated there belongs to the Wieselburg or Gata group, which is documented by more than 750 graves distributed across south-eastern Lower Austria (east of the Wienerwald and south of the Danube), the northern part of Burgenland, the region around Bratislava in Slovakia, and the region west of Győr in Hungary. (Krenn-Leeb, 2011; Umgeher-Mayer, Aczél, & Krenn-Leeb, 2011)

In this cultural complex, Hainburg-Teichtal represents the largest known burial ground with skeletal remains of 304 individuals. This is uncommonly large compared with other Wieselburg settlements, which yielded burial areas of 10–30 individuals, but not compared to contemporaneous communities (cf. Reiter, 2008). Burial grounds of the Wieselburg culture were usually located apart from the settlement, containing flat graves partly equipped with tree trunk coffins, wooden floorboards, or stone settings. The deceased was interred in a flexed to contracted position (partly so contracted that some kind of binding device would have to have been used), with the hands in front of the face. Graves were mainly SW-NO oriented with a prevalent but not entirely strict gender/sex specific siding (the orientation of the face O/SO for females, W/NW for males). (Krenn-Leeb, 2011)

Situated at the Hainburger Gate (Devín Gate, Germ. Hainburger Pforte) – a passage created by the Danube passing through the Lesser Carpathians – Hainburg-Teichtal is encompassed by mountains belonging to that mountain range (Fig. 1): the Hundsheimer Berge (also called Hainburger Berge) to the south, the Braunsberg to the north-east, and the Schlossberg to the north-west. This is a crucial point for multiple reasons: For one, the area is sheltered by mountain ranges and it has access to a large stream network as well as quite fertile soil. Climatically it is similar to the Carpathian basin into which it provides access. For another it is located at a significant position amidst other Early Bronze Age cultural groups (for an overview of material differentiation see Pellegrini, 2009), as well as at one of the pathways for the European Amber Road. It is thus situated at both a concourse of cultural complexes and major transport routes, thus lending itself to inter-

Fig. 1. Hainburg-Teichtal was situated between today's Vienna and Bratislava. The location of the settlement is unique due to its geographical and cultural positioning: The surrounding mountains broken by the Danube made it an ideal settlement site, set in a region of three adjoining cultural core areas.

regional contact and long-distance trading that is reflected by the corpus of finds. Cultural complexes adjoining the Wieselburg culture (Fig. 2) were the Unterwölbling culture to the west, the Únětice culture (Germ. Aunjetitz-Kultur) to the north and north-east, and communities of the Carpathians and the Carpathian Basin to the east and south-east. (Pellegrini, 2009; Krenn-Leeb, 2011; Spannagl-Steiner, Novotny, & Teschler-Nicola, 2011)

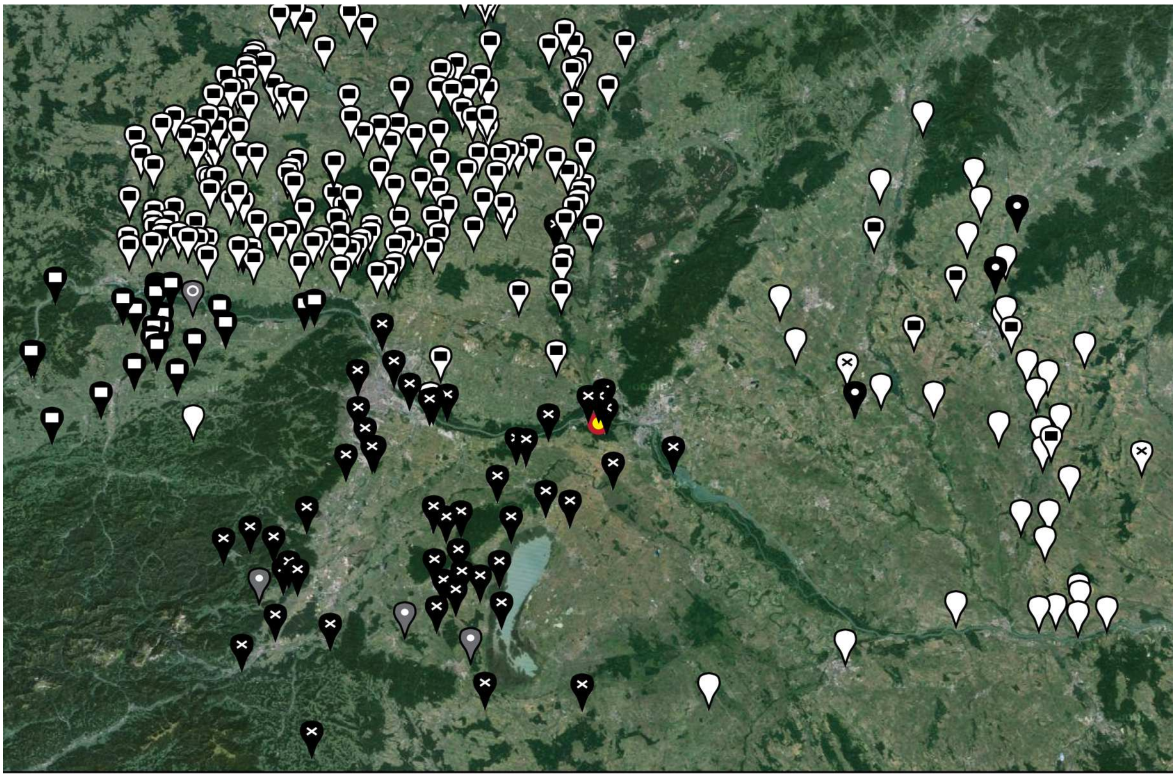

Fig. 2. Distribution of Early Bronze Age cultural groups (modified from Stadler, 2013)

1.3.1 Health and Mortality

Spannagl-Steiner et al. (2011) showed that of the 304 found skeletal remains 43% were sub-adult at the time of death, 29% adult females, 19% adult males, and 8% adults which could not be assigned to either sex. Both a mortality peak between the age of 20 and 40 (42,1%, i.e. 74,2% of the adult female and 69,5% of the adult male individuals) and a life expectancy of 22,8 years at birth, and of 31 and 32 years for females and males respectively are comparable to contemporaneous communities. Analysis of the skeletal remains (ibid.) did not find many indications of physical/nutritional stress, suggesting nutrition to have been more or less adequate, though a deficiency of vitamin C and – in some cases – of iron has been noted, as well as indications of meningitis and perisinusitis in a few cases. Caries had developed in 26% of both male and female individuals, indicating similar diet with regard to carbohydrates.

Due to the scarcity of settlement structures found, there is little definite knowledge about subsistence modes. Both agriculture and animal husbandry comparable to that of adjoining cultural complexes were quite likely employed in Hainburg-Teichtal due to the fertility of the soil, the lay of the land, and its climate. Fishing was also a possibility because of the stream network of that area, as was hunting because of floodplains and areas covered by reed (Krenn-Leeb, 2011).

1.3.2 Material culture and mortuary deposits

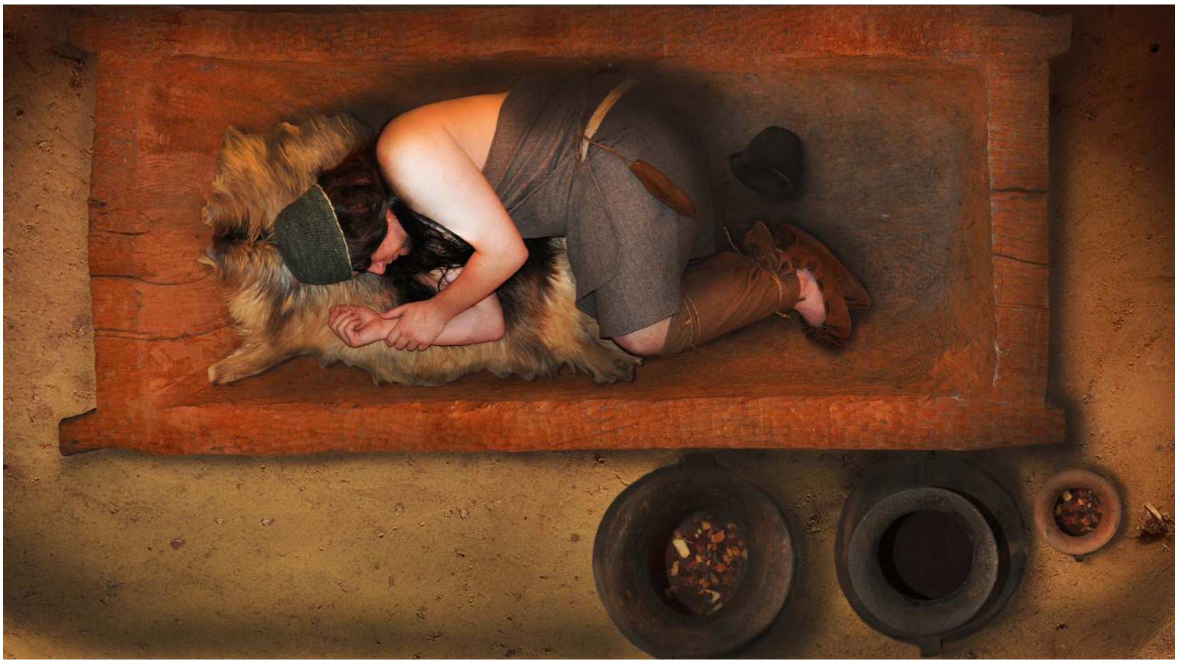

Fig. 3. Reconstruction of an interment: a 30-40 year old male, buried in flexed position on his right side. Grave furniture included a tree trunk coffin and four vessels.
(Source: A.Krenn-Leeb, IUF Wien & K. Kalser & G. Peyerl, ASINOE)

In Hainburg-Teichtal, mortuary deposits (e.g. Fig. 3) consisted of an individual's attire as well as grave goods such as tools, weapons, and vessels. They thus included earrings (bronze, silver or gold), hair decorations (e.g. bronze rings), and in many cases items worn around the neck, like solid neck rings or (complex) necklaces including animal teeth, shells, spiral, bronze, glass-faience and/or amber beads (which, originating from the Baltic sea, indicate long-distance trade). Other items were spiral bracelets, finger-rings, and (one or two) dress pins on the upper torso. Tools included small riveted daggers of everyday use, stone blades, bronze awls, bone points; weapons larger daggers and axes, which can be counted as prestigious goods even if made of stone or antler, while of greater material value when made of metal. Interred vessels sometimes formed whole ensembles (Fig. 4), and sometimes held animal remains. The foreign workmanship of some items indicate contact and trade with the Únětice culture and south-eastern Pannonian cultures, which is also indicated by some individuals' being buried according to customs of the Únětice culture. Deposits generally contained less bronze than in adjoining communities, thus less gender differentiation can be seen. (Krenn-Leeb, 2011)

Fig. 4. Example of an assemblage of vessels buried with an individual.
(Source: G. Gattinger, N. Fank & K. Klein/IUF Wien)

The absence or presence of deposits and their composition indicate the position of the individual in society, and thus allowed differentiation into three groups: Furnished graves that included prestigious items (status group 1), graves that were furnished but did not include such items (status group 2), and unfurnished graves (status group 3) (Krenn-Leeb, forthcoming).

Connecting this classification with fluctuating asymmetry, the aim of the present study was to elucidate whether fluctuating asymmetry levels are homogeneous in this population through low general stress pressure, or, if they are heterogeneous, whether they are in line with social rank scores or point to significant social rank change after growth had stopped.

2 Material

Material was provided by the Museum of Natural History in Vienna. The sample consisted of specimens of the Hainburg-Teichtal excavations that have a sufficient preservation of second and third metacarpal bones without evidence of trauma or physiologic pathology. Unpaired and fundamentally damaged metacarpal bones as well as unfused (sub-adult) specimens were omitted. Slightly damaged bones were included, but for measurements in which the damaged parts would be essential.

Since the first metacarpal is not available for most studies using hand radiographs (dissimilar orientation), there is little comparative data; additionally, it differs fundamentally in situation and range of movement from other metacarpal bones. The index usually exhibits strong directional asymmetry and is thus chosen for a number of studies that additionally involve directional asymmetry. It is a standard for human metacarpal studies, which recommends its inclusion despite possibly higher directional asymmetry values. The third metacarpal is present more often than other metacarpal bones in this sample, though preservation is slightly worse for length measurements, but better for whole joint surfaces compared to second metacarpals. Third and fourth metacarpal bones have an advantage in assessing fluctuating asymmetry by being less exposed to differential loading, i.e. directional asymmetry, than the second and fifth. This, in case of the latter, is due to its role in power grip tool stabilization (Nagar & Rak, 2001) The low numbers of well preserved first, forth and fifth metacarpals did not warrant their inclusion into this study.

Population parameters (Krenn-Leeb, forthcoming) received after data-collection as follow:

The sample size (Table 1) for maximal length measurements was 30 individuals in second metacarpals (of these, 14 of status group 1 and eight each of status groups 2 and 3; 11 individuals were male, 16 female, and three indifferent), and 23 individuals in third metacarpals (nine each of status groups 1 and 2, five of status group 3; 10 individuals were male, 11 female, and 2 indifferent). The mean age was 31.4 years in second metacarpals. It ranged from 17 to 55 years, with a maximal age range of 15–60 (it should be noted that the lowest value – 15 – is quite low since the metacarpal bones are fully fused without any traces of fusion). In third metacarpals the mean age was 31.3 years and ranged from 19–55 years, with a maximal age range of 18–60.

The proximal joint structure was present in 18 individuals, seven each of status groups 1 and 2, and four of status group 3; ten of these individuals were male and eight female. The mean age was 30.3 years, with a mean age range of 20–55, and a maximal age range of 18–60. These numbers pertain to 3D analysis of the proximal joint structure. Since 2D analysis was conducted (addressing mostly methodological considerations), four more specimens could be procured, scanned, and segmented, yet two of these, and two others had to be discarded for 3D analysis on closer inspection of the material for the 3D suitability of their ridge-curves.

Table 1. Sample size and mean age for different sets of data.

maximal length measurements						
second metacarpals	n	30	status group 1	14	indifferent	3
	mean age	31.35	status group 2	8	male	11
	mean age range	17-55				
	maximal age range	15–60	status group 3	8	female	16
third metacarpals	n	23	status group 1	9	indifferent	2
	mean age	31.30	status group 2	9	male	10
	mean age range	19-55				
	maximal age range	18-60	status group 3	5	female	11
proximal joint analysis						
	n	18	status group 1	7		
	mean age	30.31	status group 2	7	male	10
	mean age range	20–55				
	maximal age range	18–60	status group 3	4	female	8

Health parameters of the sub-sample used indicate subtle differences in pathology markers (Table 2): The absence of pathologies was noted more often for individuals of status group 1 (35%, n=20) than for individuals of groups 2 (27%, n=15) and 3 (20%, n=10). Definite pathology markers like indicators of nutritional deficiency (e.g. cribra orbitalia, linear enamel hypoplasia) or inflammatory processes (e.g. stomatitis, periostitis, sinusitis) were recorded in 50% of status group 1, 47% of status group 2, and 70% of status group 3. Contrasting cases of pathology, 15% of group 1, 20% of group 2 and 30% of group 3 showed more than one pathological alteration, while 35%, 27%, and 40% showed only one. Indications of inflammatory processes are somewhat more frequent in status group 3 (50%) than in groups 1 (15%) and 2 (20%), as is linear enamel hypoplasia (25%–33%–40% in groups 1–3). Differentiating according to sex (17 males, 24 females), inflammatory processes are similarly frequent (29% in males, 21% in females), while linear enamel hypoplasia is a little more common in males (41% versus 29%) as well as more strongly formed in 24% of males. No instances of strong linear enamel hypoplasia could be seen in females. In general, 12% of males and 38% of females did not exhibit any pathologies, while 59% and 54% evidenced definite pathological alterations. The low number of males without signs of pathology might be explained by the fact that more males exhibited alterations of unclear origin (i.e. skeletal changes that could be related either to age itself, epigenetic factors, pathology or trauma, 29% versus 8%), which might be connected to a slightly higher rate of definite traumata in males (27% versus 19%). Trauma is most frequent in status group 1 (32%), followed by status group 3 (20%) and status group 2 (9%). (Percentages derived from analysis in Krenn-Leeb, forthcoming)

These numbers should be used with caution due to the small and unequal sample sizes – yet they indicate both differences in stress-pressure as well as different levels or modes of activity between status groups and sexes.

Table 2. Health parameters of population subgroups used in the present study.

	n	no visible alterations	alterations of unclear origin[1]	pathological alterations[2]	inflammatory processes	linear enamel hypoplasia[3]	trauma
status group 1	20	35%	15%	50% (35%–15%)	15%	25% (10%)	32%
status group 2	15	27%	27%	47% (27%–20%)	20%	33% (7%)	9%
status group 3	10	20%	10%	70% (40%–30%)	50%	40% (10%)	20%
males[4]	17	12%	29%	59% (29%–29%)	29%	41% (24%)	27%
females[4]	24	38%	8%	54% (37%–17%)	21%	29% (0%)	19%

[1] Skeletal changes that could reflect age appropriate changes, epigenetic factors, pathology, or trauma, but cannot be specified to be due to any of them (differentiation by the author according to analyses provided in Krenn-Leeb, forthcoming).

[2] Numbers in brackets differentiating cases of pathologies into percentage of individuals that exhibited only one kind of pathological alteration versus percentage of individuals exhibiting more than one.

[3] Numbers in brackets stating percentage of individuals with strongly formed linear enamel hypoplasia.

[4] Review of pathologies in groups excluded indifferent individuals due to low number.

3 Methods

Examining µCT scans of Hainburg-Teichtal metacarpals, I focused both on total length measurements in second and third metacarpals as well as on a ridge structure of the proximal surface of third metacarpals. An approach to capture the whole joint surface by (semi-) landmarks proved to be unsuitable due to imperfect preservation of the more fragile ulnar joint rim. I thus chose to investigate the interarticular ridge which separates the carpometacarpal and the radial intermetacarpal joint surface and reflects proximal joint structuring in third metacarpals.

Surveying proximal joint faces has shown that only very few true landmarks can be found, and that their topology varies greatly. An overall shape approach would be most satisfactory, yet archaeological material does not always allow it due to preservation issues.

Additionally to the 3D advantage, CT investigation is necessary with this sample due to partly massive coverings by sinter which can be removed in Amira® with sufficient precision (segmentation-threshold and visible boundary) but make the sample unavailable for traditional measurements. This deposition of sinter on the bones is caused by the highly calciferous sediment.

The material was imaged using a µCT-scanner with a precision of 50µm: Paired bones were always scanned together, as well as were cases of several metacarpal pairs from one individual. Export (producing image stacks) was done one bone pair at a time, which, for the sake of file size, were separated in Amira® as a next step. During segmentation (also done in Amira®), visual boundaries were repeatedly compared to image histograms and scanning artefacts as well as sinter were removed if they affected measurement points.

3.1 Maximal length measurements

In order to procure length measurements, the segmentation procedure was followed by surface generation (constrained smoothing), and lengths were measured directly in Amira®. For third metacarpals the maximal length spanned the most proximal portion of the dorso-proximal stylus to the most distal portion of the head (Fig. 5), for second metacarpals the most proximal portion of the ulnar, more proximally protruding portion of the base to the most distal portion of the head. All measurements were taken by the author, on separate days, and without reference to each other. All specimens were measured twice, and segmentation and surface generation repeated for nine second metacarpal pairs and seven third metacarpal pairs randomly selected from the total of respectively 30 and 23 pairs to estimate error introduced by this procedure (also on separate days to the first segmentation and without reference to it). This sub-sample was consequently measured a third time. Further processing was conducted using SPSS®.

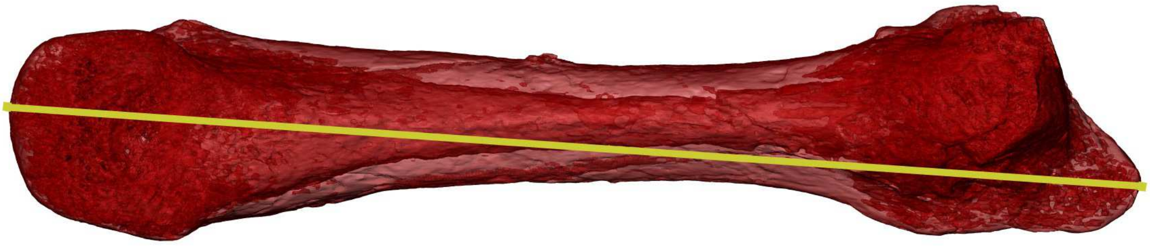

Fig. 5. Maximal length measurement of a third metacarpal

Since due to re-measurement and re-segmentation, two levels of error can be tested, individuals with values for all three instances (16 pairs) were subjected to a correlation test (Pearson) to see whether there were differences between a simple remeasuring and additional re-segmentation of specimens. Additionally, paired T-Tests of first and second measurement as well as first/second and re-segmented measurement were conducted. Since re-segmented measurements were taken solely for the purpose of identifying variance introduced by surface generating processes, which was addressed by this step, and did not comprise all individuals, they were not used further.

Further analysis of data followed the guidelines provided by Palmer (1994) and Palmer and Strobeck (1986, 2003).

Scatter-plots were visually inspected for outliers: Since a scatter plot of replicate measurements for both traits (second and third metacarpals) only showed a small number of cases (10 pairs for measurements 1 and 2), a scatter plot of replicate measurements

($m_1 - m_2$) for right and left side was conducted additionally for each trait. Like a differential scatter plots of two traits, a differential scatter plot of left and right replicates identifies anomalous values due to measurement imprecision as well as individual difficulty of measuring. This was followed by testing for extreme values (histogram, box plot and comparing original and trimmed mean), with subsequent application of Grubbs' test (Grubbs, 1969; using the R package "outliers", see Komsta, 2011). Scatter plots of lengths (mean of repeated measurements for each individual) for right and left side were conducted for each trait to identify aberrant individuals in trait size and asymmetry. After this I tested these lengths, as well as right-left-differentials for extreme values, and subjected extreme values to Grubbs' test.

A Side x Individual ANOVA for second and third metacarpals (MC2 and MC3) and each status group was conducted both for estimation of measurement error, directional asymmetry, and fluctuating asymmetry. Differences in measurement error between sexes, status groups, traits or interaction of those were addressed by reinspecting scatter plots of replicate measurements, Side x Individual ANOVA and measurement error indices derived from it, and a Levene's test for heterogeneity of variance (Trait x Sex x Status ANOVA excluding indifferent individuals due to the small number of such individuals).

Asymmetry dependence on trait size was investigated by scatter plots and correlation tests (Spearman, Kendall). For the latter, since group sizes for separate trait-sex-status groups were between one and five individuals but for second metacarpals of status group 1 females (n=9), analyses were conducted pooled for sex <u>or</u> status.

In order to test for departures from ideal fluctuating asymmetry, I inspected frequency distributions of right-left differentials, and conducted tests for kurtosis, skew, and directional asymmetry for either trait and each status-group or each sex respectively. Kurtosis was measured with Eq.7 (Palmer & Strobeck, 2003). Directional asymmetry was addressed by the Side x Individual ANOVA and additional T-tests. ANOVA analyses of trait asymmetry $|R-L|$ were conducted to test for differences of trait asymmetry between status-groups as well as sexes.

3.2 Articulation facets

Addressing proximal surface measurement, the volumes were cropped after segmentation to include only the proximal third of the bone.

3.2.1 2D curves

The surface of 18 bone pairs for which a fitting of 2D curves was possible were reconstructed and aligned using principal axes (Amira®). The resulting 2D images were processed using programs of the TPS suite (Rohlf, 2012). 25 landmarks were placed onto the curves, 23 of them being semi-landmarks representing the curve (Fig. 6). Semi-

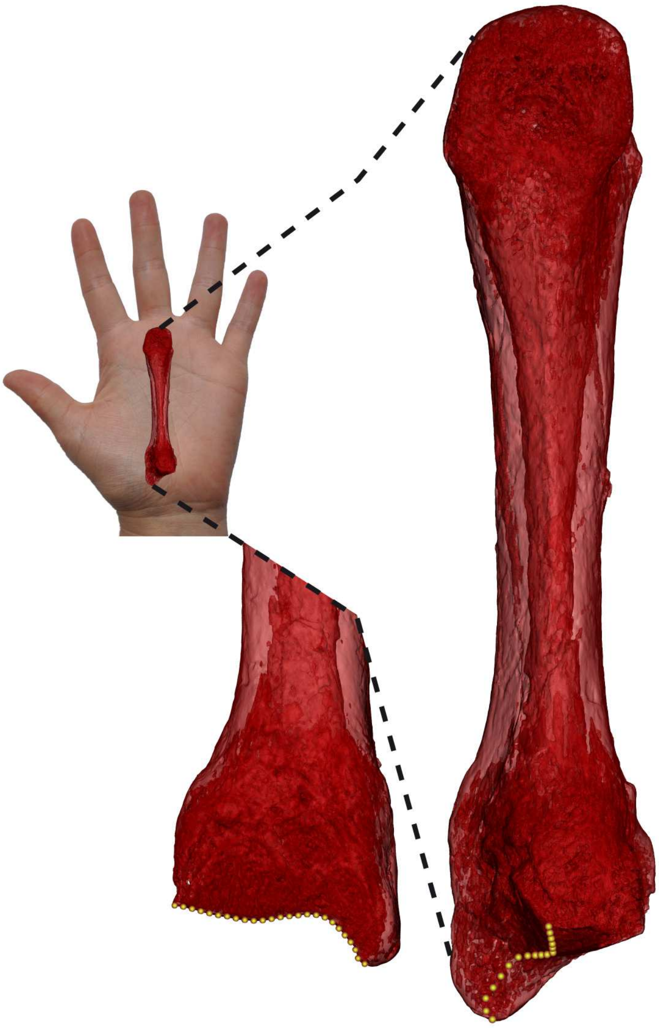

Fig. 6. Third metacarpal in approximate anatomical position (left), radial 2D ridge in aligned position (middle), and position of 3D ridge (right).

landmarks were slid according to minimal Procrustes distance during Procrustes superimposition, which was chosen over sliding by minimal bending energy since the latter may retain some tangential variation thus yielding biologically non-interpretable data (Perez, Bernal, & Gonzalez, 2006). This was followed by a Procrustes fit and Procrustes ANOVA using MorphoJ (Klingenberg, 2011).

3.2.2 3D curves

For 3D surfaces, the file size had to be reduced since processing surfaces is computationally intensive. Thus inner bone cavities were eliminated so that only one outer surface remained. This surface was fitted with two curves of approximately 30 landmarks (on separate days and without reference to each other) using Templand of the EVAN Toolbox. These two preliminary curves (Fig. 7) were then compared (to see whether fitting the curve on the ridge was sufficiently precise), and in case of overall concordance averaged and fitted with about 115 to 140 points to produce a close-fitting curve on which landmarks could be placed (landmarks distributed along the curve, right of Fig. 6). If two curves were significantly divergent as was the case with two specimens, another set of preliminary curves was produced on separate days, by which in each case one of the curves in question could be identified as misplaced due to an erroneous lighting setting.

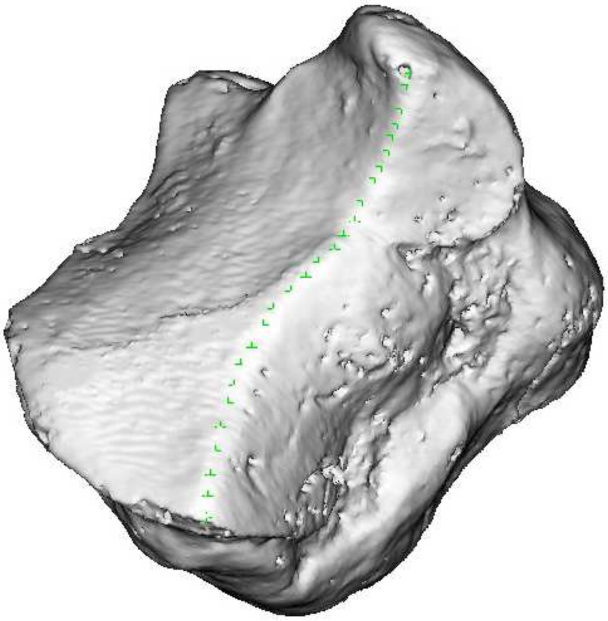

Fig. 7. Placing a pre-ridge on the articular ridge.

To better estimate error introduced by fitting the curves, the whole process of placing two preliminary curves and by then creating the close-fitting curve was repeated for a third of all specimens, chosen randomly from the set. The close-fitting curve was then imported into Morpheus et al., 32 points were equally distributed along it, and a Generalized Procrustes Analysis (GPA, references see “gpagen” in Adams & Otarola-Castillo, 2013b) performed sliding the 30 semi-landmarks (according to minimal Procrustes distance) using the R-package geomorph (Adams & Otarola-Castillo, 2013a) for each of the following batches of data: Since not all curves had been repeated, I created a sub-sample including only specimens with repeat curves, for testing of error (Palmer & Strobeck, 2003). For this, a Side x Individual Procrustes ANOVA was performed. All specimens, excluding repeat curves, were subsequently used as another sub-sample for all other analyses. After Generalized Procrustes Analysis, a Sex x Status ANOVA was performed on the aligned coordinates, with 5000 random permutations (suitable for 0,01 significance level, see Manly, 1997; in Anderson, 2001), to elucidate a possible relationship of shape rather than shape asymmetry, and status. This was followed by Principal Component Analysis and visual inspection of status-related shapes.

To compare shape asymmetry levels between status groups, shape coordinates (as computed by GPA) were used to obtain the Procrustes distance between left and right sides as a “measure of overall shape asymmetry” (Klingenberg & McIntyre, 1998, p. 1375; FA 18 in Palmer & Strobeck, 2003), which was followed by a Sex x Status ANOVA.

3.2.3 Ridge lengths

The Generalized Procrustes Analysis coordinates were also used to obtain ridge lengths. Even though they are length measurements, they do not include trait size information due to GPA. They do however exhibit shape information – a more intense structuring of articular facets leading to longer lengths. Lengths were calculated as the sum of lengths between the 32 (semi-) landmarks (i.e. the sum of $\surd\sum(xyz_i-xyz_{i+1})^2$ for i=1 to k, the total number of (semi-)landmarks per specimen). These lengths were further processed using SPSS®, according to a similar protocol as for maximum length measurements. After looking at scatter plots of replicate measurements, I checked for extreme values of replicate measurement differentials by descriptive statistics mentioned above. Scatter plots of left versus right side were conducted to test for aberrant individuals, right-left differentials investigated for extreme values, and extreme specimens subjected to Grubbs' test. Next, a Side x Individual ANOVA was performed for the subgroup with replicate measurements. This however could not be performed for each status group separately due to the small number of cases, but pooled. Following this, the homogeneity of variances of measurement error (as the absolute replicate measurement differential) of status groups was tested. In order to discern departures from ideal fluctuating asymmetry frequency distributions of right-left differentials, tests for kurtosis, skew, and directional asymmetry were administered for each status group. A single two-way Sex x Status ANOVA of right-left differentials was conducted for detecting directional asymmetry, a one-way Sex/Status ANOVA of trait asymmetry ($|R-L|$) for fluctuating asymmetry.

3.3 Error levels

Both length measurements as well as working with curves implement a number of error levels. For both exporting data from µCT scans (using a gray-value threshold) as well as creating the surface (segmentation) are potential sources for error. For length measurements measuring itself is another, while for curves both placing the 3D pre-curves as well as the actual curve can introduce variation into the signal. While I strove to correct for the latter, I did not for the initial data export from the µCT nor for the CT procedure itself.

4 Results

4.1 Maximal length measurements

Regarding the levels of error due to re-measurement versus re-segmentation of the specimens, Pearson Correlations revealed reliability coefficients ranged from 0.999991 in the re-measurement to 0.999987/0.999990 in the re-segmentation condition (correlated to measurement 1 and 2 respectively; all significant at 0.01). Re-measurement included all 104 individuals, and re-segmentation 30. Paired T-Tests of measurement 1 (mean=69.431, SD=4.707) and re-segmented measurement (mean=69.434, SD=4.706) as well as measurement 2 (mean=69.431, SD=4.709) and re-segmented measurement (s.a.) showed that there was no significant difference between measurements (t=–0.607; df=29; p=0.549 and t=–0.775; df=29; p=0.445 respectively).

Inspection of scatter plots of replicate measurements in both traits (Fig. 8, n=20) as well as right versus left replicate measurements of either metacarpal (Fig. 9) yielded four out-

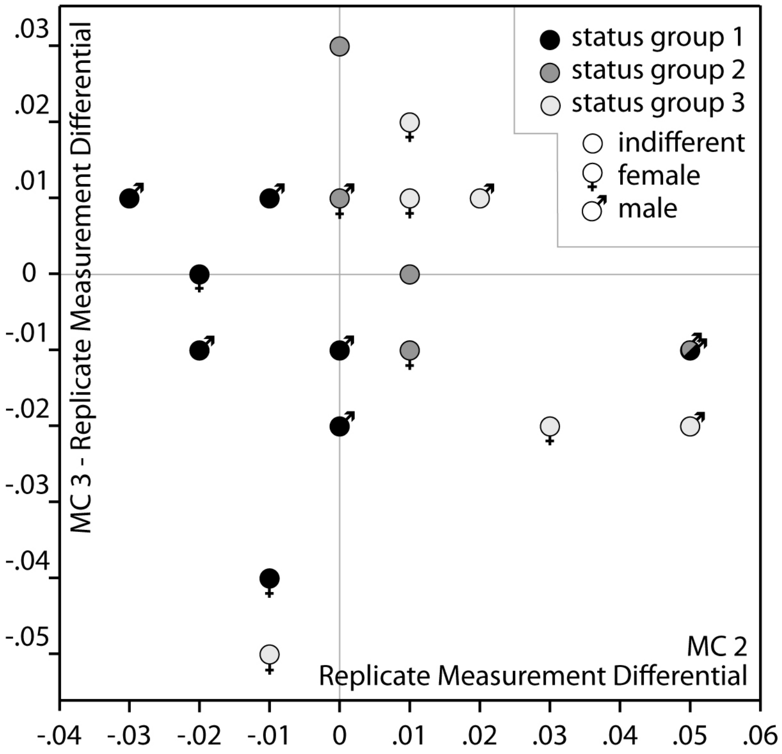

Fig. 8. Scatterplot of replicate measurements (m1-m2) in individuals with both traits.

most measurements, but did not suggest a value to be an outlier. Testing for extreme values confirmed these differentials to be furthest apart from the rest.

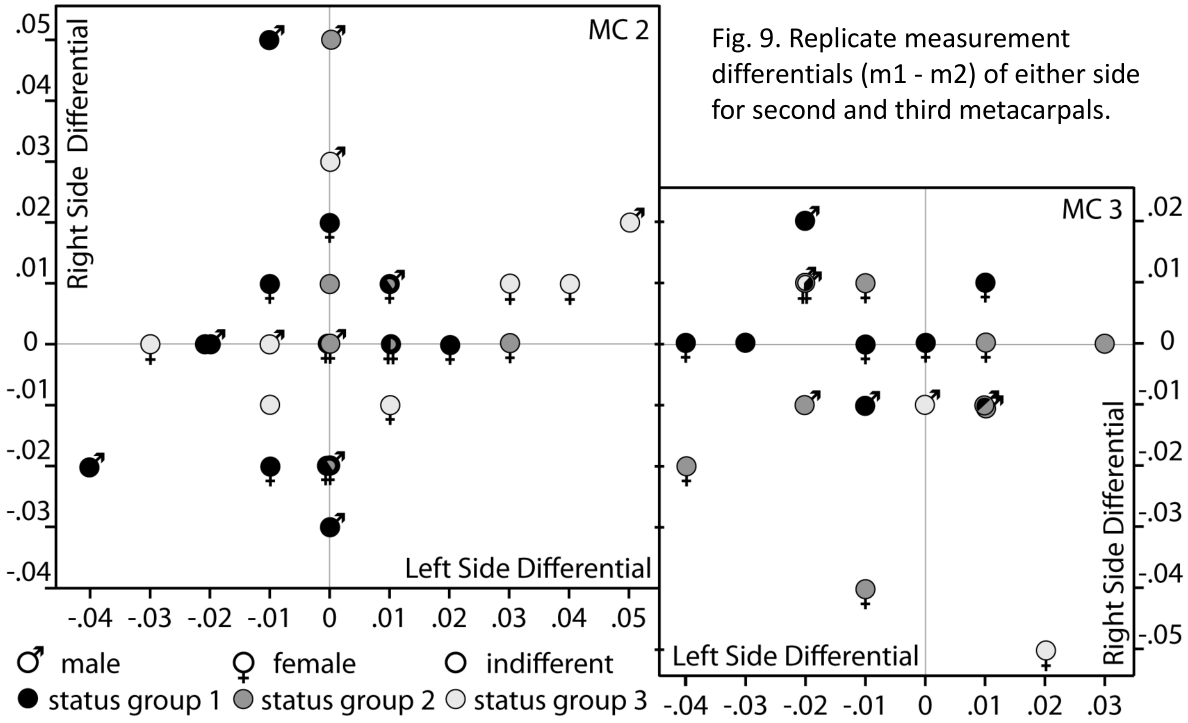

Fig. 9. Replicate measurement differentials (m1 - m2) of either side for second and third metacarpals.

However, applying Grubbs' test showed that though furthest from the rest, neither was a significant outlier (p=0.542 and 0.365 for m1-m2 in second and third metacarpals respectively). Scatter plots of right versus left side measurements (mean of replicate measurements 1 and 2, Fig. 10) showed neither extreme-sized individuals (largest and smallest values were subjected to Grubbs' test) nor anomalous asymmetry measurements for third metacarpals but one anomalous asymmetry measure for second metacarpals. Testing for extreme values in trait asymmetry (|R−L|) also yielded that same metacarpal pair. This most extreme value was subjected to Grubbs' test, and found a significant outlier (n=30, mean=0.753, SD=0.716, z=3.349, p=0.005, significant at 0.05 after sequential Bonferroni correction). Inspection of the material showed no visible indications of pathology, though the side difference is very marked. Though both bones are very similar in morphology and colouring there remains a possibility that they might have belonged to different individuals. They were therefore removed from the sample for all subsequent analyses.

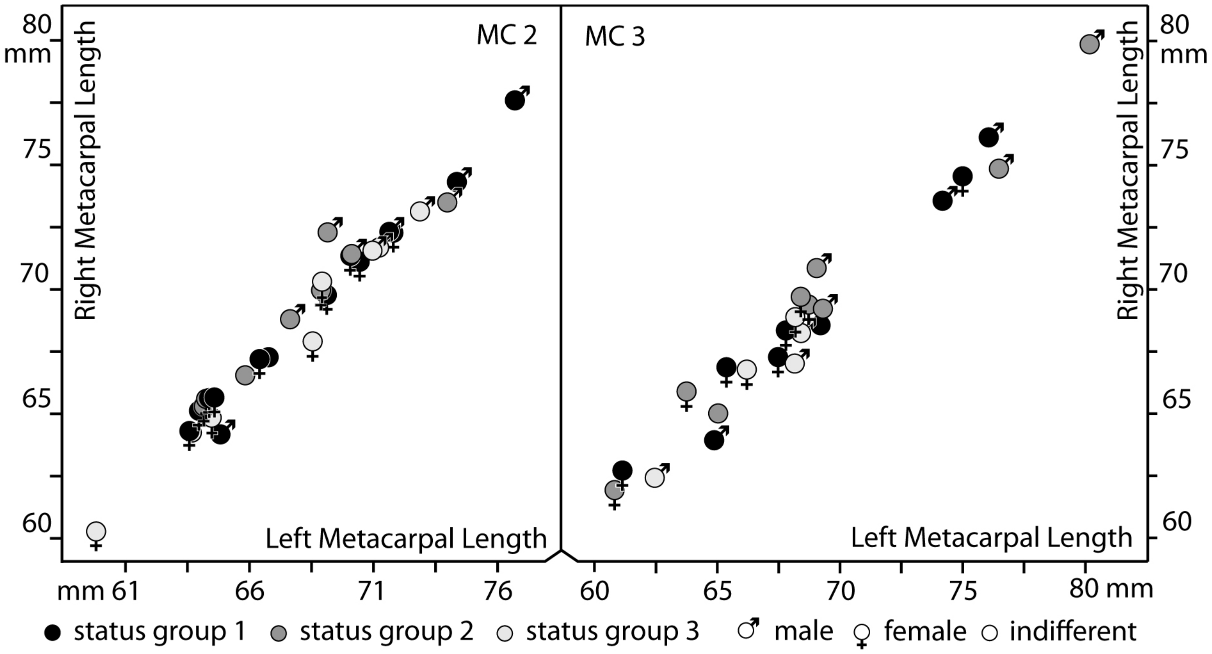

Fig. 10. Scatter-plots of mean replicate measurements of right and left sides for both traits.

The Side x Individual ANOVA separated by trait and status group (Table 3) revealed that the between-sides variation was greater than expected due to measurement error for both second and third metacarpals and across all groups: The error variance contributing to total between-sides variance (Table 4, ME3) ranged from 0.01% to 0.08%, the repeatability of measurements (ME5) being equally high for all groups. The average difference between replicate measurements (ME1 as % FA4a) ranged from 1.15% to 2.83%. The difference between FA10a and FA4a represents the contribution of measurement error to fluctuating asymmetry, which ranged from 0.00004 to 0.00018. Comparing fluctuating asymmetry between groups (FA10a and FA4) showed the asymmetry values of second metacarpals to be quite similar. Note that had the fluctuating asymmetry outlier remained, the fluctuating asymmetry of status group 2 would have been increased to be nearly twice as high as that of status groups 1 and 3 (0.794 to 0.434 and 0.443). In third metacarpals, values were overall higher, with status group 3 having the lowest value and status group 2 the highest.

Table 3. Side x Individual ANOVA for both traits separated by status groups: (1) Furnished burial with prestigious goods, (2) Furnished burial without prestigious goods, and (3) Unfurnished burial.

Source of Variation		MC 2			MC 3		
		Status group 1	Status group 2	Status group 3	Status group 1	Status group 2	Status group 3
Side	MS_S	7.0361	4.9982	1.6245	0.0455	2.5493	0.0048
	df	1	1	1	1	1	1
	F	23.7370	13.2742	5.2672	0.0543	1.8500	0.0088
	P	0.0003**	0.0108+	0.0554	0.8215	0.2109	0.9297
Individual	MS_I	69.4163	43.5683	80.7579	95.6130	128.8952	25.0721
	df	13	6	7	8	8	4
	F	234.1824	115.7090	261.8460	114.1633	93.5357	46.0688
	P	<0.0001***	<0.0001***	<0.0001***	<0.0001***	<0.0001***	0.0013**
Side x Individual	MS_{SI}	0.2964	0.3765	0.3084	0.8375	1.3780	0.5442
	df	13	6	7	8	8	4
	F	1865.1141	6201.7255	1249.2857	7178.6667	7516.5379	2654.7805
	P	<0.0001***	<0.0001***	<0.0001***	<0.0001***	<0.0001***	<0.0001***
error	MS_{Err}	0.0002	0.0001	0.0002	0.0001	0.0002	0.0002
	df	28	14	16	18	18	10

Significances at 0.1 (+), 0.05 (*), 0.01 (**), and 0.001 (***) after sequential Bonferroni correction.

Table 4. Indices derived from the Side x Individual ANOVA.

	MC 2			MC 3		
	Status group 1	Status group 2	Status group 3	Status group 1	Status group 2	Status group 3
FA1	0.8075	0.9821	0.6106	0.7167	0.9922	0.5270
SE	0.0984	0.1097	0.1196	0.1717	0.2558	0.1991
FA4a	0.4345	0.4897	0.4432	0.7303	0.9368	0.5887
FA10a	0.4344	0.4896	0.4430	0.7302	0.9367	0.5886
df	12.9861	5.9981	6.9888	7.9978	7.9979	3.9970
FA4a - FA10a	0.00012	0.00004	0.00018	0.00005	0.00010	0.00011
ME1	0.0101	0.0062	0.0125	0.0086	0.0108	0.0114
ME3	0.05%	0.02%	0.08%	0.01%	0.01%	0.04%
ME5	0.9989	0.9997	0.9984	0.9997	0.9997	0.9992
ME1 as % FA4a	2.32	1.27	2.83	1.18	1.15	1.94
DA	0.7089	0.8450	0.4506	0.0711	0.5322	-0.0310

Neither the Side x Individual ANOVA nor the replicate measurement scatter plots suggested gross differences in measurement error between groups, and thus that no correcting for this was needed. Similarly, a 3-factor ANOVA of |m2−m1| (Table 5) did not show any differences between sexes, status groups, trait or any interactions between these factors.

Table 5. 3-factor ANOVA of |m2-m1|.

	df	MS	F	p
Sex	2	2.99E-05	0.196	0.823
Status	2	1.26E-04	0.823	0.442
Metacarpal	1	1.12E-04	0.729	0.396
Sex * Status	4	2.15E-04	1.402	0.24
Sex * Metacarpal	2	3.11E-04	2.035	0.137
Status * Metacarpal	2	1.85E-04	1.206	0.304
Sex * Status * Metacarpal	3	5.88E-05	0.384	0.765
Error	87	1.53E-04		

Inspection of scatter plots of trait asymmetry versus trait size (Fig. 11) did not suggest any dependence of asymmetry on trait size. Correlation tests separated for trait-status groups, as well as for trait-sex groups, supported the absence of any significant association between trait asymmetry and trait size but for third metacarpals of status group 1 (Table 6).

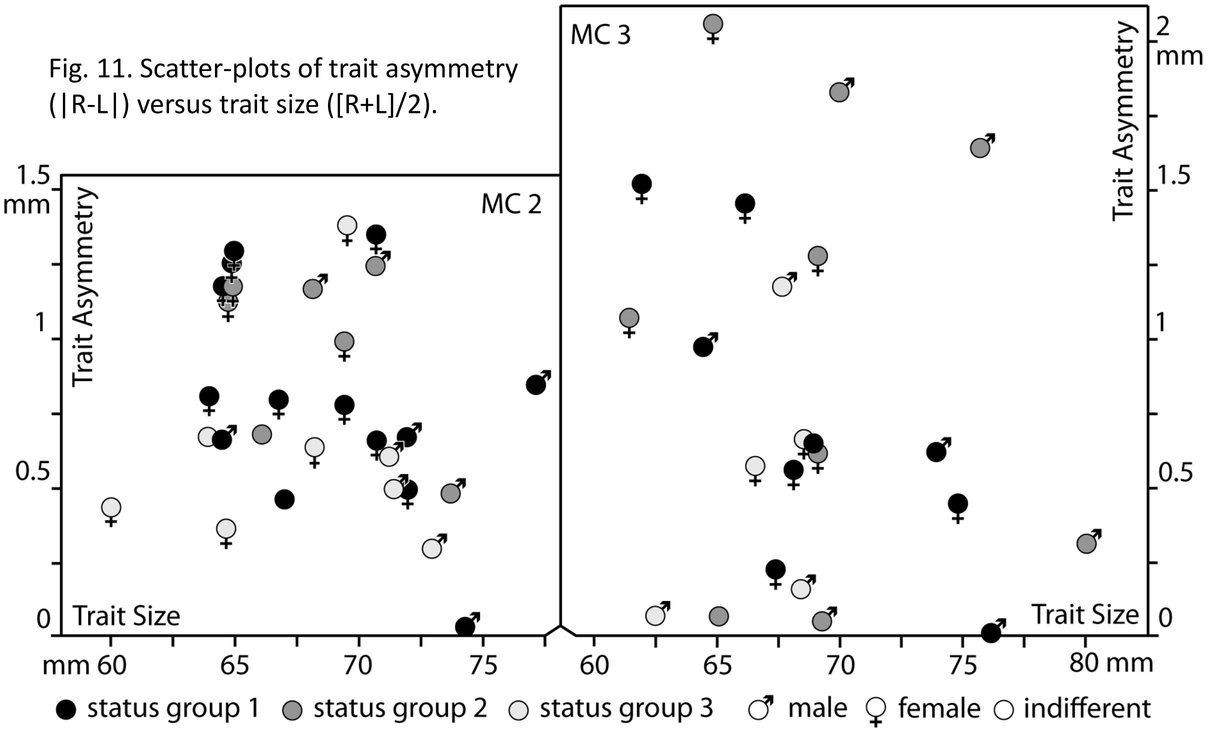

Fig. 11. Scatter-plots of trait asymmetry (|R-L|) versus trait size ([R+L]/2).

This association remained only very weakly significant in Spearman's rank correlation coefficient after sequential Bonferroni correction, and it was moreover negative (variability not increasing with trait size). This and the small sample size of the subgroups, and their values compared to each other, did not warrant a size correction. No dependences could be seen in the trait-sex groups.

Table 6. Results of significance tests (Spearman's rank correlation coefficient, Kendall rank correlation coefficient) of associations between trait size and trait asymmetry for both traits and status groups.

MC	Status		Kendall-Tau-b	Spearman-Rho
2	furnished including metal and prestigious goods (n=14)	τ / ρ	-0.253	-0.336
		p (two-tailed)	0.208	0.240
	furnished not including metal and prestigious goods (n=7)	τ / ρ	-0.143	-0.214
		p (two-tailed)	0.652	0.645
	unfurnished burial (n=8)	τ / ρ	-0.214	-0.214
		p (two-tailed)	0.458	0.610
3	furnished including metal and prestigious goods (n=9)	τ / ρ	-0.611	-0.767
		p (two-tailed)	0.022	0.016 +
	furnished not including metal and prestigious goods (n=9)	τ / ρ	-0.111	-0.117
		p (two-tailed)	0.677	0.765
	unfurnished burial (n=5)	τ / ρ	0.400	0.500
		p (two-tailed)	0.327	0.391

+ significant at 0.1 after sequential Bonferroni correction.

Frequency distributions of right-left differentials showed clear skew for second metacarpals, indicating the presence of directional asymmetry, and a roughly normal distribution for third metacarpals, which was also observed by the statistics (Table 7). After sequential Bonferroni correction individuals of status group 2 showed significant leptokurtosis for second metacarpals, and female individuals exhibited both significant skew as well as leptokurtosis for second metacarpals.

Table 7. Tests for Skew and Kurtosis of (R−L) for traits, and groupings according to either status group or sex (excluding indifferent individuals due to low numbers)

MC	Status / Sex	n	Skew	SE	p	Kurtosis	SE	p
2	pooled	29	-1.018	0.434	*	0.693	0.845	
3	pooled	23	0.166	0.481		-0.621	0.935	
2	status group 1	14	-1.253	0.597		2.071	1.154	
	status group 2	7	-2.190	0.794		4.933	1.587	*
	status group 3	8	-0.539	0.752		2.901	1.481	
3	status group 1	9	0.807	0.717		-0.779	1.400	
	status group 2	9	-0.497	0.717		-0.072	1.400	
	status group 3	5	-0.975	0.913		0.789	2.000	
2	male	10	-0.492	0.687		-0.689	1.334	
	female	16	-1.617	0.564	*	3.534	1.091	**
3	male	10	1.125	0.687		2.776	1.334	
	female	11	-0.224	0.661		-0.298	1.279	

*.** significant at 0.05 (*) and 0.01 (**) after sequential Bonferroni correction.

The Side x Individual ANOVA revealed significant directional asymmetry for second metacarpals of status groups 1 and 2, of which status group 1 remained significant at 0.01 after Bonferroni correction. Though statistical corrections of directional asymmetry are possible, they do not remove the genetic component introduced to the variation through its presence (Palmer & Strobeck, 1992; Graham et al., 1998). An estimate of directional asymmetry (as mean right-left differential) showed it to be larger than FA4a for second but not third metacarpals of all status groups, which, in addition to the small sample size, supports not statistically correcting for it (Palmer & Strobeck, 2003). Thus, no fluctuating asymmetry analyses were conducted for second metacarpals.

Investigating the pattern of directional asymmetry for sex showed that females exhibit highly significant directional asymmetry in their second and significant directional asymmetry in third metacarpals, while males do not (Table 8), which might through its connection to mechanical loading indicate differences in activity. Trait asymmetry (|R−L|) of third metacarpals did not vary between status groups nor between sexes (Table 9).

Table 8. Testing for directional asymmetry separated for trait and sex.

MC	Sex[1]	T	df	p
2	male	2.044	9	0.071
	female	6.520	15	<0.001***
3	male	-1.065	9	0.314
	female	3.683	10	0.004*

[1] excluding indifferent individuals due to low number.
*,*** significant at 0.05 and 0.001 after sequential Bonferroni correction.

Table 9. One-way ANOVA for status groups/sex: trait asymmetry |R-L|.

		df	MS	F	p
Status group	Between groups	2	0.381	0.998	0.386
	Within groups	20	0.381		
Sex[1]	Between groups	1	0.383	0.977	0.335
	Within groups	19	0.391		
		Statistic	df1	df2	p
Status group	Levene	2.347	2	20	0.121
	Brown-Forsythe	1.127	2	17.986	0.346
Sex[1]	Levene	.625	1	19	0.439
	Brown-Forsythe	.959	1	17.553	0.341

[1] excluding indifferent individuals due to low number.

4.2 Articulation facets

4.2.1 2D curves

Re-digitizing showed that placing the curve was well repeatable, yet recreating the images was not: Alignment differences produced a measurement error that significantly contributed to the observed shape variance (F=2.17, p<0.0001***), showing that the alignment procedure was not sensitive enough. To avoid this source of error, placing the curve was repeated in 3D.

4.2.2 3D curves

A Side x Individual Procrustes ANOVA on specimens with repeatedly placed curves showed that the interaction Side x Individual (i.e. FA; Table 10) had a significant effect on size and a highly significant effect on shape in comparison to measurement error (variation caused by curve replication). Investigating shape differences between status groups (Sex x Status ANOVA, Table 11) showed that the attributed status group significantly connects to articular shape.

Table 10. Side x Individual ANOVA of sub-sample of repeats only.

	df	MS	F	p
Centroid Size				
Side	1	6.05E-07	0.885	0.390
Individual	5	2.51E-06	3.667	0.090
Side x Individual	5	6.84E-07	5.750	0.006*
replicate	12	1.19E-07		
Shape				
Side	89	2.62E-05	1.046	0.379
Individual	445	1.49E-04	5.953	<0.001 ***
Side x Individual	445	2.51E-05	8.847	<0.001 ***
replicate	1068	2.83E-06		

*, *** significant at 0.05 and 0.001 after sequential Bonferroni correction.

Table 11. Sex x Status ANOVA with 5000 permutations to elucidate shape differences between groups.

	df	SS	MS	p
Sex	1	0.002	0.002	0.675
Status	2	0.018	0.009	0.009 **
Sex x Status	2	0.013	0.007	0.051 +
Total	35	0.128		

Principal Component Analysis revealed that the first three principal components explain 81% of variance (Fig. 12). A scatter plot (Fig. 13) of the first two principal component scores (accounting for 61% of variation) visualized that though the status groups largely overlap, 1 has a tendency to be more PC1-positive and PC2-negative, and 2 vice versa. Status group 3 meanwhile tends to be both PC1- as well as PC2-positive. It can be seen that group differentiation is subtle, even more so in the following Principal Components, and that the unequal and low numbers for each group, but especially for status group 3 might be problematic. Included in Fig. 13 are articular shapes corresponding to both extremes on Principal Component 1. Warp grids of group-specific shapes (Fig. 14) show that the tendency of proximo-distal flattening apparent in the positive PC1 is much stronger in status group 3 versus the more proximo-distal structured status groups 1 and 2.

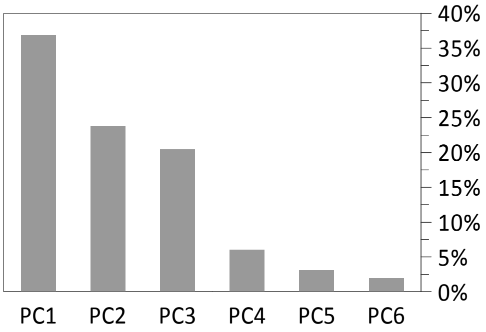

Fig. 12. Proportion of shape variance taken up by principal components.

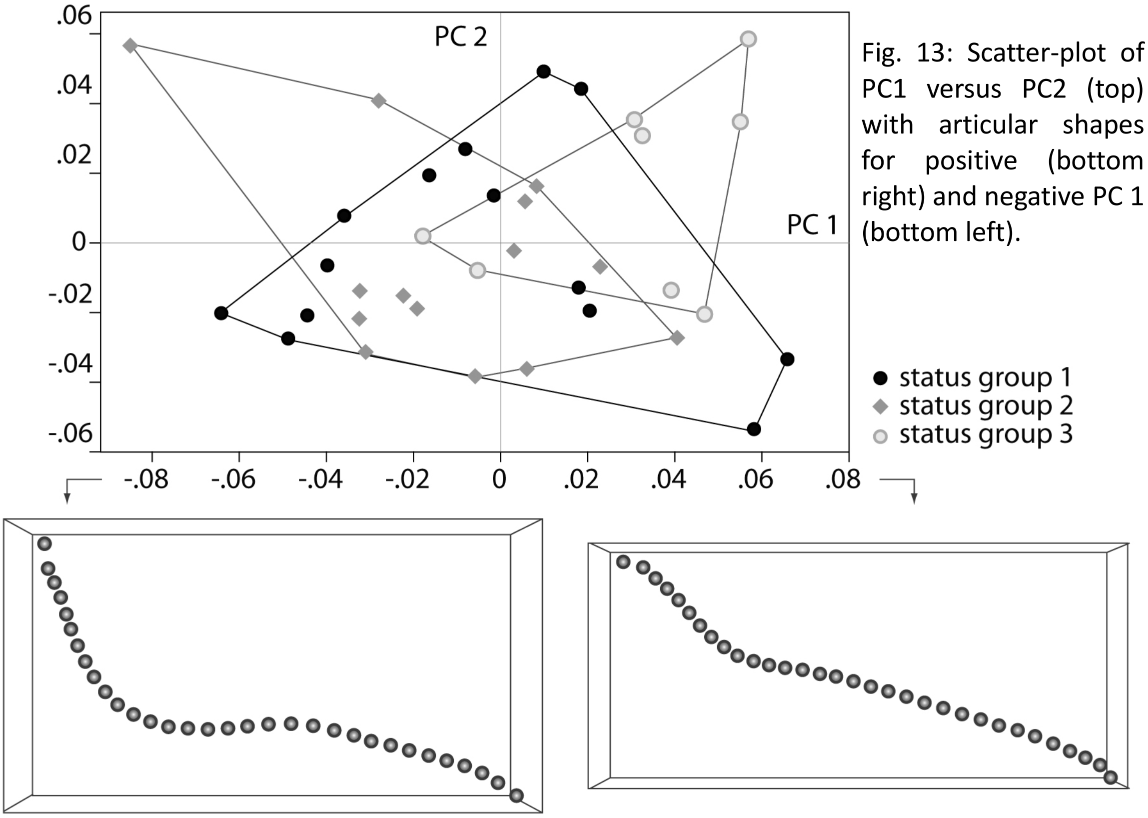

Fig. 13: Scatter-plot of PC1 versus PC2 (top) with articular shapes for positive (bottom right) and negative PC 1 (bottom left).

The Sex x Status ANOVA for FA 18 did not reveal any significant effect of sex or status on the fluctuating asymmetry of the curves.

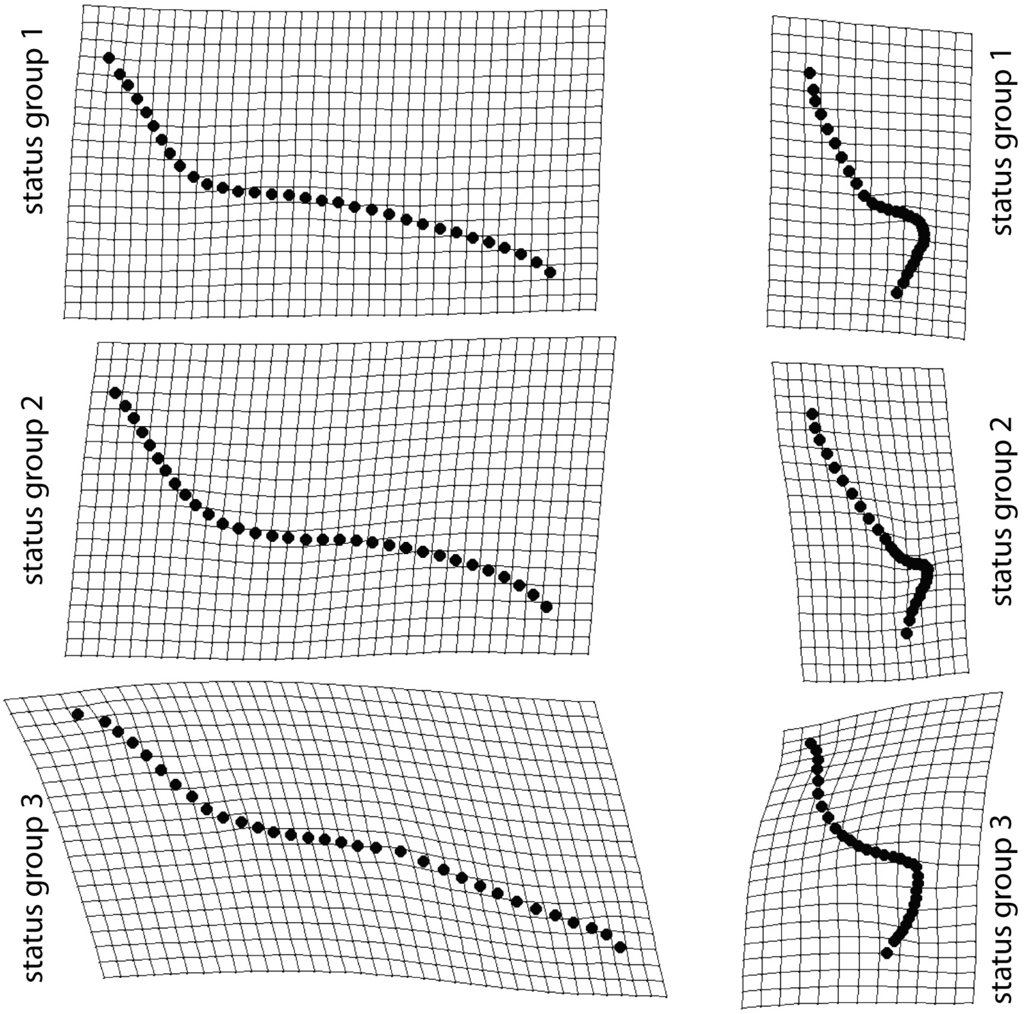

Fig. 14. Y-Z and Y-X warpgrids of deposit groups

4.2.3 *Ridge lengths*

Due to the small number of replicate measurements, scatter plots of replicate measurements did not yield much information. No extreme values could be detected investigating replicate measurement differentials. One potentially anomalous individual for (R−L) was observed and Grubbs' test applied (mean=0.0033, SD=0.0114, n=18). It was not found a significant outlier (R−L=0.03, Z=2.344, p>0.05).

The Side x Individual ANOVA for replicate measurements revealed a very weakly significant interaction of Side x Individual after sequential Bonferroni correction (Table 12). The small number of individuals with replicate measurements, especially in light of the weak significance of fluctuating asymmetry in comparison with measurement error, cautions against all of the following test results.

Table 12. Side x Individual ANOVA for replicated measurements.

	df	SS	MS	F	p
Side	1	0.000058	0.000058	2.899	0.137
Individual	6	0.002294	0.000382	18.132	0.001 **
Side x Individual	6	0.000127	0.000021	3.281	0.047 +
Error	10	0.000064	0.0000064		

+,** significant at 0.1 (+) and 0.01 (**) after sequential Bonferroni correction.

As of testing for heterogeneity of variances, no significant differences could be observed in measurement error between status groups (ANOVA: df=2, MS=4.822E-7, F=0.120, p=0.889). Frequency distributions of right-left differentials were roughly normally distributed. No significant kurtosis or skew could be seen in status groups, and only weakly significant leptokurtosis for females after sequential Bonferroni correction (Kurtosis=2.981, SE=1.481, p=0.0441+).

The Sex x Status ANOVA of (R−L) did not suggest the presence of directional asymmetry (Table 13), neither did investigating trait asymmetry yield any differences in asymmetry between status-groups or sexes (Table 14).

Table 13. Test for directional asymmetry: Sex x Status ANOVA of (R-L).

	df	MS	F	p
Status	2	1.47E-05	0.089	0.915
Sex	1	1.04E-04	0.634	0.442
Status x Sex	2	1.42E-05	0.086	0.918
Error	12	1.65E-04		

Table 14. One-way status group/sex ANOVA of trait asymmetry as |R-L|.

		df	MS	F	p
Status-group	Between groups	2	6.98E-05	1.178	0.335
	Within groups	15	5.92E-05		
Sex	Between groups	1	1.85E-07	0.003	0.958
	Within groups	16	6.42E-05		
		Statistic	df1	df2	P
Status-group	Levene	1.159	2	15	0.340
	Brown-Forsythe	1.103	2	9.658	0.370
Sex	Levene	3.050	1	16	0.100
	Brown-Forsythe	0.003	1	10.300	0.961

5 Discussion

Connecting socio-economic data to fluctuating asymmetry scores can elucidate the relationship between living conditions and socio-economic situation, showing whether asymmetry levels, and thus stress pressure, differ within a population. Homogeneous asymmetry levels such as we have found in third metacarpals indicate a homogeneous general stress pressure, and thus a rather stable economic situation of the population as a whole. This gains support from population parameters indicating both better health and less inner-population tension than in contemporaneous populations (Spannagl-Steiner et al., 2011, Krenn-Leeb, personal communication). Focusing on the sub-sample used in this study, it is notable that a slight difference could be seen in health parameters across status groups, with status group 1 including more individuals without pathology and individuals of fewer pathologies than status group 3. Though pathology patterns differed for males and females, they in general suggested an overall equal health. This indicates that subtle differences in various stress pressures might exist between groups, which were not reflected in the analysis of fluctuating asymmetry and must be confirmed by further investigation upon the completion of ongoing analysis of health parameters of the whole population.

Another possible explanation for seemingly homogeneous stress-pressure across subgroups is a temporal shift of “status” through the course of an individual´s life: While fluctuating asymmetry is a function of developmental stress-pressure, and thus mainly indicates the socio-economic position during periods of development, funerary deposits reflect the socio-economic position at the end of an individual´s life. In societies that base “status” increasingly on achievement, individuals might differ in their socio-economic positions between these two points in their lives, and subgroups based on the socio-economic position of the dead might appear to be equally stress-affected when they are actually comprised of a mix of developmentally differentially stressed individuals. These homogeneous levels would therefore not necessarily indicate the economic situation of the population. For the population of Hainburg-Teichtal, both population and health parameters (see above) as well as studies suggesting the heritability of status in Bronze Age Europe (Gilman et al., 1981) make such a temporal shift of an individual´s socio-economic position seem unlikely. Nonetheless, to completely rule out this possibility, data from further research on parameters on which “status” is based is necessary.

Both analysis of maximal length measurements as well as the landmark-based approach to proximal joint structuring showed significant amounts of fluctuating asymmetry in comparison to measurement error as well as the absence of directional asymmetry or antisymmetry in third metacarpals. Fluctuating asymmetry levels, however, did not differ significantly between deposit groups for either method employed, while the shape of proximal surfaces did.

Right-left differential distributions of maximal length measurements in second metacarpals show a clear tendency of greater metacarpal length on the right side that might be based on both genetic as well as biomechanical factors (Plato et al., 1980; Roy et al., 1994; Mays, 2002; Özener, 2010). It must be noted that although no similar significant effects were apparent for third metacarpals, the small sample size is a serious confounding effect on more subtle as well as more complex patterns of bilateral asymmetries. The tendency of greater development in second metacarpals varied between deposit groups, with status group 1 exhibiting significant directional asymmetry and status group 2 exhibiting a trend only. The appearance of directional asymmetry also differed between sexes: While females had both directionally asymmetric second and third metacarpals, males did not. This would indicate differences in activity patterns both between status groups, which is also implied by differences in joint morphology between those groups, as well as between sexes. This seems reasonable insofar as differentiation in socio-economic status is often based on occupation which differs in manual loading (e.g. manual labour against non-manual labour), and there is evidence for sex/gender-based differentiation both regarding funerary modes (orientation, attire, grave goods) as well as activities of Early Bronze Age communities (Sládek, Berner, Sosna, & Sailer, 2007).

These results must be seen in the light of the limitations of this study, which, based on the preservation of the specimens, lie mainly in the small sample size, but also in the severely limited choice of traits. The small sample size – Palmer (1994) suggest a minimum sample size of 30 – makes estimates of variance problematic, leads to decreased statistical powers of tests (e.g. ANOVA) as well as to difficulties ascertaining (non-)normality. Additionally, fluctuating asymmetry is a subtle effect to be discerned in the first place – between-sides differences are usually smaller than 5%, and often even smaller than 1% of trait size (Palmer, 1994).

The availability of more traits would have provided higher stability accompanied by either complex (Livshits, Yakovenko, Kletselman, Karasik, & Kobyliansky, 1998) or multiple traits (Leung et al., 2000), since the "impacts of [fluctuating asymmetry] in one set of paired structures may magnify size differentials elsewhere" (Emlen et al., 1994, p. 84).

Working with a 3D image without practical depth perception impeded the reliability of landmark placement, which contributed to the a priori limited availability of well-defined 3D landmarks, but allowed working with the entire volume, including the inside of objects, as its major advantage. Both the absence of reliable landmarks preserved in all specimens as well as the difficulty of bone alignment were major issues that prevented the investigation of other parameters like average intramedullary width, total metacarpal width, cross-sectional area and polar second moment of area for different sections as well as obtaining morphometric parameters derived from them (e.g. shape of cross sections). These would be most interesting for analysis of activity patterns as diaphyseal dimensions reflect bone strength and thus functional use more than bone length does, which has a reduced potential for plasticity as a more functional trait (Ruff & Jones, 1981; Trinkaus, Churchill, & Ruff, 1994; Özener, 2007).

Processes including a threshold (e.g. µCT data export and surface generation), also induce a problematic factor since a threshold reduces the sharpness, and thus the defining aspect, of rims. This effect is especially pronounced in finer and more delicate structures.

Another question is whether isolated curves defined by only two landmarks as endpoints are suitable for approaching proximal joint structuring (and specifically whether those two landmarks are well-defined enough). It is clear that using the whole joint surface, as well as using the whole structure of a specimen, which is prevented by the state of preservation in this sample, would be more suitable in more complete specimens.

Including adult individuals only also biases a sample insofar as environmentally induced morphological variation is decreased in adults – most stressed individuals will never have reached adulthood, and those that did might have adjusted in the process (e.g. catch-up growth, Goodman & Martin, 2002) – bone might remodel, while for example enamel might not. To include sub-adult individuals, a differentiation in fluctuating asymmetry analyses would be necessary for different age groups due to the relationship between growth processes and fluctuating asymmetry. This is often not warranted in non-recent populations due to the small sample size across age groups.

Considering the sample size, no comparison could be made between sexes and status groups at the same time, which is questionable insofar as sexes might not only differ in their socio-economic position and activity patterns (a tendency of which is seen through differences in pathologies and trauma noted in this sample, as well as in directional asymmetry), but also in canalization and sensitivity to environmental changes (overview of studies see, Barrett, 2005).

Due to the scarcity of settlement structures, activity differences between social groups as well as sexes are not well known for the Wieselburg culture. During the Copper Age elites were directly concerned with metal and metallurgical processing (e.g. smelting, forging), while during the Bronze Age this shifts to elites controlling metal manufacture rather than actively crafting. The Wieselburg culture was in general less influenced by the advent of metallurgy, and as a rather rural population neither used nor traded metals as much as other groups did, hence the comparatively fewer metal items. Yet numerous indications point to active trade that must have included other trading goods: The importance of vessels is shown by findings of complex assemblages that include various types. This might also hint at another kind of product, namely such that would be kept and traded in those vessels (e.g. liquids but also grains).

Another trading good could be seen in textiles whose production is indicated by loom weight findings. In the Early Iron Age Hallstatt culture, elaborate textiles constituted an important trade good with Southern European groups, and their production thus formed a part of the occupation of elites. It is therefore very likely that the growing importance of textiles must have had their advent in Bronze Age cultures, and that this activity might, in addition to being thus status-related, also be a sex/gender-specific occupation. (Krenn-Leeb, personal communication)

Strontium Isotope Analysis of this and contemporaneous populations is ongoing to address questions of mobility and change of residency (Krenn-Leeb, 2011) – individuals probed so far showed a local origin in 86% of the cases (Irrgeher, Weiß, Krenn-Leeb, Teschler-Nicola, & Prohaska, 2011). Non-locality has also been noted in funerary structures (usually conforming with those of the Únětice culture), suggesting a differentiation in cultural identity that also influenced individuals during their lifetime. Comparing asymmetries between local and non-local groups would allow another interesting insight into population functioning, especially social group membership, social preferences and social marginalisation of individuals of certain identity groups. Especially interesting in this light is the analysis of deviant burials at settlement edges (Krenn-Leeb & Teschler-Nicola, 2013) that will elucidate whether "deviating" is (also) linked to a status as a foreigner.

Indications of migration background and different cultural identities within the population thus reflect interregional contact as well as intermixture, which raises the question of whether genetic differences might have influenced both the formation of asymmetries and joint structuring. This thought is supported by the findings of Pellegrini et al. (2011): Geographical barriers like the Danube or the Wienerwald impact this and surrounding populations strongly enough to elicit differences in morphology – the geographical distance is related to morphological distance as seen in cranial morphology. Thus a comparison across populations, especially of the groups of Wieselburg, Únětice and Unterwölbing, would be beneficial to the interpretation of my results.

Other interesting mortuary features in such populations that could be included in group classification would be grave orientation, grave dimension and degree of flex (Saxe, 1971), though these are probably structures not well-suited for the necropolis of Hainburg-Teichtal that allows for more variation in funerary deposition than contemporaneous communities.

It remains open how much of fluctuating asymmetry is actually due to environmental perturbations, and how much to the "nonlinear dynamics of developmental processes" (Graham et al., 1994, p. 137) – how to "distinguish noise from deterministic chaos" (ibid.). Fluctuating asymmetry is such an interesting character for a number of reasons: The ubiquity of symmetry in all organisms and its reliability (Graham et al., 2010) as well as being not very susceptible to short-term stress give it an advantage over other measurements of developmental instability. Measuring general rather than specific stress also has an advantage – while individuals with time- or disease-specific stress markers can be said to be both less as well as more healthy than individuals that do not; since they show both evidence of stress as well as evidence of surviving long enough to develop a specific response (Wood et al., 1992), it is far less likely that individuals might die before exhibiting fluctuating asymmetry due to the level of general stress being different from both disease-specific and temporary intense stress.

Likewise open remain the interactions of genetic and environmental factors in the formation of directional asymmetry, and the actual impact of mechanical loading on different skeletal parameters like maximum bone length, especially in the face of unequal distribution of loads (Trinkaus et al., 1994; Mays, 2002; Özener, 2007, 2010; Sládek et al., 2007).

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7 Abstract

Asymmetry is a universal feature characterizing biological systems that occurs in different forms: While fluctuating asymmetry represents the result of developmental perturbations, differentiating organisms according to their developmental stability, directional asymmetry is both said to be genetically determined as well as influenced by biomechanical loading. Both asymmetries can thus be seen as a function of the socio-economic position of an individual, which is influenced by their manual occupation, and forming the basis of differential stress of that individual. In the Early Bronze Age population of Hainburg-Teichtal such a socio-economic differentiation, expressed through the composition of funerary deposits, was connected to measures of asymmetry: Asymmetry scores of 3D-µCT-Data included maximal lengths of second and third metacarpals and GMM-analysis of a proximal joint structure in third metacarpals. Homogeneous fluctuating asymmetry values across status groups indicated homogeneous stress pressure, and thus a rather stable economic situation of the population as a whole. Significant differential directional asymmetry of status groups as well as sexes, combined with significantly status-dependent joint shape variation suggest differences in activity patterns across these groups.

8 Zusammenfassung (German abstract)

Asymmetrie ist ein charakteristisches Merkmal biologischer Systeme, welches in verschiedenen Formen auftreten kann: Während fluktuierende Asymmetrie als Ergebnis zufälliger Entwicklungsperturbationen häufig als Maß für organismische Entwicklungsinstabilität herangezogen wird, reflektiert direktionale Asymmetrie einerseits eine genetisch determinierte Tendenz größerer Merkmalsausprägung einer Seite als auch Belastungsmuster im Maß ihrer Ausprägung. Beide Asymmetrien können daher als Funktion der sozioökonomischen Situation des Individuums betrachtet werden, die die Grundlage unterschiedlicher Stress-Levels zwischen Individuen bildet, sich aber auch an der manuellen Tätigkeit festmacht. In der frühbronzezeitlichen Population von Hainburg-Teichtal zeigt sich durch Reichhaltigkeit und Form der Grabbeigaben eine solche sozioökonomische Differenzierung, die mit Asymmetrie-Messungen in Verbindung gebracht wurde: 3D-Maße der µCT-Daten umfassten maximale Längen zweiter und dritter Metacarpalknochen, sowie GMM-Analyse einer Gelenkflächenstruktur dritter Metacarpalia. Dabei konnte kein Zusammenhang zwischen „Status“ und fluktuierender Asymmetrie nachgewiesen werden, was auf homogene Stress-Levels innerhalb der Population, und damit auf eine stabile Versorgung, hindeutet. Jedoch legt eine signifikante status-, sowie geschlechtsabhängige direktionale Asymmetrie, als auch die verschiedenartige Gelenkflächenform der Statusgruppen Unterschiede der manuellen Tätigkeit dieser Gruppen nahe.

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EDUCATION

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EXTRACURRICULAR ACTIVITIES

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2009 & 2010 Participation in the Willendorf II excavations (Max Planck Institute for Evolutionary Anthropology, Leipzig; University of Vienna); Willendorf, Austria

2008 Participation in the Mongol-American Archaeology Project (University of Pennsylvania, National Museum of Mongolian History); Khovd, Mongolia

2007 Contributing to research projects at the tropical field station La Gamba, Costa Rica

2005 Volunteer for an ecological and social project with the Fundation Aliñambi; Tena, Ecuador

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