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Fluctuating Asymmetry and Stress in a Medieval Nubian Population

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ABSTRACT Fluctuating asymmetry is commonly used as a bioindicator of developmental stress. This study addresses asymmetry under nutritional/systemic stress in the human craniofacial skeleton and its utility as an indicator of developmental instability. Crania from the diachronic Christian cemeteries at Kulubnarti (Sudanese Nubia) were chosen as a model for nutrition/systemic stress. Previous studies indicate that individuals from the Early Christian cemetery were subjected to greater developmental stress when compared with individuals from the Late Christian cemetery. Therefore, crania from the Early Christian cemetery should display a greater magnitude of fluctuating asymmetry than crania from the Late Christian cemetery. Thirty adult crania of comparable age and sex were selected from each population. Landmark coordinates were digitized in two separate trials and averaged to minimize error. Euclidean distance matrix analysis (EDMA) was used to measure and compare the magnitude of fluctuating asymmetry in each sample. Results indicate that crania from the Early Christian cemetery display greater amounts of fluctuating asymmetry than those from the Late Christian cemetery, as predicted. The degree of fluctuating asymmetry for each linear distance is highly correlated between the cemeteries, suggesting that all humans may share common patterns of fluctuating asymmetry in the skull. In contrast, there is little correlation between magnitude of fluctuating asymmetry and length of linear distance, between-subject variability, or measurement error. These results support the hypothesis that poor nutrition/systemic stress increases developmental instability in the human skull and that increased fluctuating asymmetry constitutes morphological evidence of this stress. Am J Phys Anthropol 132:520–534, 2007.

This study considers fluctuating asymmetry in the craniofacial skeleton as a bioindicator of population health and environmental stress. Developmental stability refers to the ability to produce a given phenotype under specific genetic and environmental conditions and relates to the mechanisms that limit phenotypic variation from minor perturbations that occur during development. These perturbations, also known as "developmental noise," cause random, subtle deviations from symmetry in otherwise bilaterally symmetric structures. The accumulation of these microscopic deviations results in fluctuating asymmetry, a phenotypic character that can be measured macroscopically. Increased levels of fluctuating asymmetry have been used to infer relatively greater levels of developmental noise or "developmental instability," and this relationship is the subject of multiple, recent, comprehensive reviews (e.g., Markow, 1994; Møller and Swaddle, 1997; Polak, 2003).

Because minor perturbations or accidents in development are assumed to produce increased levels of fluctuating asymmetry, early research focused on the positive correlation between fluctuating asymmetry and environmental stress. Elevated levels of fluctuating asymmetry have been documented in animal models subjected to developmental and environmental stresses [nutritional stress (Erway et al., 1970; Sciulli et al., 1979; Swaddle and Witter, 1994); removal of vegetation (Badyaev et al., 2005); extreme temperatures (Siegel and Doyle, 1975; Siegel et al., 1977); noise (Siegel and Smookler, 1973); prenatal chemical treatment (Brown et al., 1989); diabetic fetal environment (Kohn and Bennet, 1986); but see Stub et al., 2002; Kellner and Alford, 2003]. Different mechanisms have been proposed to explain the process by which the generalized phenomenon of "stress" produces increased fluctuating asymmetry. These mechanisms may act to 1) increase the introduction of between-sides variability or 2) reduce inherent buffering capability. For example, the human body requires a given amount of input (energy, nutrients, resources) to develop following an idealized ontogenetic trajectory. Between-sides morphological variability is introduced from multiple sources, including stochastic variation in cell proliferation, migration, and differentiation, and by differences in mechanical loading (discussed in Willmore et al., 2005). Buffering mechanisms act to constrain morphology to the ideal growth trajectory. Ideal bone growth in the skull involves substantial remodeling, requiring the coordination of bone resorption and new deposition in continuous iterations. Inadequate diet and/or high parasitic load may adversely affect the raw materials

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(e.g., amino acids) available for this process. Given reduced raw materials, the body may be unable to maintain optimal levels of remodeling, instead allocating all resources necessary to the minimum threshold of bone growth and remodeling necessary to sustain life. This reduction in the ability to fine-tune morphology effectively increases between-sides variability (fluctuating asymmetry). This is undoubtedly an oversimplified example, but illustrates one possible mechanism for the proposed association of stress and fluctuating asymmetry in the skull.

The apparent correlation with stress has made fluctuating asymmetry a seductive subject for studies of humans, because of its potential for revealing information about the health of past populations. However, the results of such studies have been mixed. Dental fluctuating asymmetry was found to be relatively higher in human samples subject to stress (Bailit et al., 1970; Doyle and Johnston, 1977; Perzigian, 1977), although other researchers using similar methods concluded that fluctuating asymmetry was no higher in the supposedly stressed population (e.g., Black, 1980). These conflicting results may be explained by sampling error (Smith et al., 1982), measurement error (Greene, 1984), and different genotypic backgrounds affecting underlying developmental stability. The level of heterozygosity and genomic coadaptation both appear to affect fluctuating asymmetry (reviewed in Clarke, 1993). It is virtually impossible to control completely for genotypic effects in studies on human samples (but see studies on asymmetry in twins, e.g., Markow and Gottesman, 1989; Pechenkina et al., 2000).

Positive associations between stress and fluctuating asymmetry in humans have been identified using different methodological approaches. Differential levels of stress impacted degree of fluctuating asymmetry in a study of Plains Indian crania using geometric morphometric methods (Kimmerle and Jantz, 2001). A similar geometric morphometric approach to human dental arch morphology identified increased fluctuating asymmetry associated with detrimental environmental conditions (Schaefer et al., 2006). Other studies of fluctuating asymmetry and stress in humans have found increased asymmetry associated with rapid morphological change within a population (Kimmerle and Jantz, 2002), higher odds ratios for dermatoglyphic fluctuating asymmetry and developmental delay (Naugler and Ludman, 1996), and increased asymmetry of epiphyseal fusion in stressed populations (Albert and Greene, 1999). It is clear that fluctuating asymmetry and stress are related, but the full potential of this relationship has not been realized.

The goal of this study was to test the expected positive association of stress and fluctuating asymmetry in skull morphology of a human population. Specifically, I hypothesized that individuals under relatively high levels of nutritional/health stress would display greater overall fluctuating asymmetry in the craniofacial skeleton when compared with a genetically-related group under relatively lower levels of nutritional/health stress. A geometric morphometric analysis is used, because it incorporates information about a large number of characters in a single analysis and is therefore more likely to capture trait-specific fluctuating asymmetry (and by implication developmental instability) when compared with single-trait analyses. Patterns of fluctuating asymmetry, including trait-specificity, are investigated in an effort to identify the characters or regions that are most likely to reflect the effects of developmental instability.

MATERIALS AND METHODS

Study population

Skeletal materials from two diachronic cemeteries at Medieval Kulubnarti, Sudanese Nubia, were used as a model system for differential levels of health and environmental stress in related populations. Kulubnarti is located on a recently-formed island <1 mile in length within the Nile River, south of the Second Cataract and located in a portion of Upper Nubia known as the *Batn el Hajar* ("belly of rock"). The land in this area is harsh, and the banks of the river are steep with no floodplain. Long stretches along the river lack soil, and agriculture is restricted to small, dispersed pockets of alluvium in sheltered areas (Adams, 1977). Archaeological investigations at this settlement revealed two cemeteries: 21-S-46, located on the island, and 21-R-2, which is located on the west bank of the river adjacent to the modern village of Kulb (Adams, 1977). On the basis of associated artifacts and architecture, the "S" cemetery (21-S-46) was dated to the Early Christian period (~550–850 AD) (Van Gerven et al., 1990a, 1995). The "R" cemetery (21-R-2) was originally dated to a broader period, possibly spanning the Early to Terminal Christian periods (~550–1500 AD) (Van Gerven et al., 1990a). Although use of the two cemeteries may have overlapped, they are considered to be diachronic, and are generally referred to as the "Early" (21-S-46) and "Late" (21-R-2) Christian cemeteries (Van Gerven et al., 1995).

For this study, the Early and Late groups are assumed to be related groups subject to different levels of health/environmental stress. Multiple studies indicate that individuals from the Early cemetery were less healthy and subject to more developmental perturbations than those from the Late cemetery (Van Gerven et al., 1981; Hummert, 1983; Hummert and Van Gerven, 1983; Moore et al., 1986; Van Gerven et al., 1990b; Mittler and Van Gerven, 1994). In a comparison of long bone growth between the two groups, the Early group displayed reduced growth after age 8.5 and a reduced adolescent growth spurt relative to the Late group (Hummert and Van Gerven, 1983), although cortical area and endosteal resorption were not found to be substantially different (Hummert, 1983). Comparisons of epiphyseal fusion and dental eruption indicated delayed growth in both groups, and a more pronounced delay in the Early group, which was attributed to greater levels of stress (Moore et al., 1986). The frequencies of enamel hypoplasia (Van Gerven et al., 1990b) and cribra orbitalia (Mittler and Van Gerven, 1994) were also reported to be greater in the Early group than those in the Late group. In addition, mortality rates were generally higher in the Early group than those in the Late group as assessed using both composite life tables (Van Gerven et al., 1981) and regression techniques (Greene et al., 1986).

Albert and Greene (1999) addressed relative levels of stress in the Early and Late groups by comparing bilateral asymmetry of epiphyseal fusion between the two samples. Asymmetry was statistically significant ($P < 0.001$) for the Early group, but not the Late group. These results supported previous findings described earlier that the individuals in the Early group were less healthy and/or more affected by environmental stress than those in the Late group.

TABLE 1. Specimens from the Kulubnarti collection used to model health/environmental stress

Early Christian cemetery				Late Christian cemetery			
Males		Females		Males		Females	
Specimen	Age (years)	Specimen	Age (years)	Specimen	Age (years)	Specimen	Age (years)
S236	16	S204	19	R147	16	R61	19
S55	18	S100	23	R141	22	R33	24
S18	21	S213	24	R56	24	R118	26
S222	25	S224	24	R81	24	R29	27
S187	31	S202	26	R145	31	R122	27
S223	31	S185	31	R188	33	R35	31
S86	37	S186	31	R28	34	R58	31
S206	37	S237	31	R3	36	R149	31
S177	38	S171	36	R10	37	R99	36
S200	38	S146	42	R45	37	R119	36
S191	42	S1	42	R1	42	R6	37
S192	42	S21	47	R43	42	R106	38
S84	47	S163	47	R197	42	R114	42
S107	47	S228	47	R46	47	R52	47
S162	47	S212	49	R50	49	R105	49
Mean	34.5	Mean	34.6	Mean	34.4	Mean	33.4

Study sample

The Kulubnarti skeletal collection is housed in the Anthropology Department, University of Colorado, Boulder. Thirty individuals of comparable age and sex were selected from each population (total $N = 60$) (Table 1). Selection criteria were as follows: individuals were adults (defined here as 16 years or older and assumed to have completed adolescent growth spurt); crania exhibited no antemortem abnormalities (e.g., artificial cranial deformation, cleft palate); and crania were complete with no apparent taphonomic distortion or warping. Many individuals in this collection had significant antemortem tooth loss, and they were avoided where possible to limit the potential impact on cranial asymmetry. Nevertheless, to achieve the sample size required for fluctuating asymmetry analyses, a number of individuals were included with complete alveolar resorption. In addition, a number of specimens were excluded from the study, because significant amounts of desiccated soft tissue on these individuals obscured much of the skull.

Sample size has been demonstrated to be an important factor in fluctuating asymmetry analyses (Smith et al., 1982; Palmer, 1994). Therefore, males and females within each sample are pooled. Although sexually dimorphic patterns of fluctuating asymmetry may exist, separating each sample here into sex-specific groups would produce samples of inadequate size ($N = 15$). However, each sample (Early and Late Period groups) contains equal numbers of males and females so as to minimize the effect of sex.

Data collection

Three-dimensional coordinate data from biologically relevant landmarks on the skull were used to quantify and assess craniofacial form in this study (Table 2). Landmarks were chosen to represent all parts of the skull, although the cranial base and face have a much higher density of landmarks when compared with the neurocranium. Coordinate data were collected directly from the dry skulls using a MicroScribe G2 digitizer. Landmark coordinate data from two separate trials were checked for gross error (e.g., swapping right- and left-

TABLE 2. Craniofacial landmarks used in analysis of fluctuating asymmetry

Midline landmarks	
ANS	Anterior nasal spine
BAS	Basion
BRG	Bregma
VSJ	Hormion (posterior midline point on vomer)
INC	Incisive foramen (posterior midline point)
LAM	Lambda
NAL	Nasale
NAS	Nasion
OPI	Opisthion
PNS	Posterior nasal spine
Bilateral landmarks	
AST	Asterion
CAR	Carotid canal (posterolateral point, level with medial border)
DAC	Dacryon (frontal-maxillary-lacrimal junction in orbit)
EFO	Ectocranial foramen ovale (posterolateral point)
EAM	External auditory meatus (superior)
FZJ	Frontomalare orbitale
GPF	Greater palatine foramen (posterolateral point on palate)
IOF	Infraorbital foramen (lateral point)
JUG	Jugular process (anterior point)
MAS	Mastoid process (inferior point, centered on process if necessary)
MXT	Maxillary tuberosity (maxilla-palatine intersection on alveolus)
PTA	Pterion anterior (fronto-spheno-zygomatic intersection)
PTP	Pterion posterior (fronto-spheno-parietal intersection)
SSP	Sphenoid spine (posterior projection behind medial pterygoid plate)
STY	Stylomastoid foramen
TSJ	Temporal-sphenoid junction at petrous
SZM	Zygomatic-maxillary suture (posterior point at lateral inferior orbital fissure)
ZMI	Zygomaxillare inferior
ZMS	Zygomaxillare superior
$K = 48$	

side landmarks) and then averaged to minimize measurement error.

Analysis

Euclidean distance matrix analysis (EDMA) is the morphometric approach used in this study (Lele and Richtsmeier, 1991, 2001). EDMA quantifies form or shape using matrices of interlandmark linear distances. This morphometric approach is invariant to the coordinate system used to represent landmark locations, and as a result, does not rely on the assumptions about variance structure which have been criticized in the context of methods based on the superimposition or deformation of landmarks (Lele and Richtsmeier, 2001; Richtsmeier et al., 2002).

The fluctuating asymmetry application of WinEDMA (Cole, 2003) was used to quantify and compare asymmetry in the Early and Late Period samples (Cole, 2001; Richtsmeier et al., 2005). The variable of interest is the signed asymmetry value ($L - R$) for each bilateral interlandmark linear distance in a given specimen. The distribution of the variable ($L - R$) within a sample provides estimates of the population parameters of directional asymmetry and fluctuating asymmetry. Directional asymmetry for a given interlandmark linear distance is estimated as the mean signed asymmetry ($L - R$) for the sample. Fluctuating asymmetry is estimated as the dispersion of the signed asymmetry ($L - R$); in this case, by the mean absolute (unsigned) asymmetry for the sample, where absolute asymmetry for each individual is the absolute individual deviation from the sample mean signed asymmetry (after Mather, 1953; Van Valen, 1962; Soulé, 1967; Livshits et al., 1988; but see Palmer and Strobeck, 1992).

This algorithm is described more specifically here in the context of a single paired bilateral interlandmark distance (i). However, in application, the algorithm is applied to the matrix of interlandmark linear distances that represents the three-dimensional morphology of a given object. Asymmetry values are defined as univariate terms, and all analyses are performed on matrices of univariate measures. Statistical significance testing is performed using the entire matrix of information for each individual, maintaining the association of within-individual univariate measures and avoiding multiple comparisons issues.

For each individual, a raw (signed) asymmetry metric (RA_i) is calculated as the arithmetic difference between left and right interlandmark linear distances:

$$RA_i = (L - R)_i$$

Symmetric specimens have RA_i values equal to zero, and asymmetric specimens have RA_i values either greater or less than zero. Values farther from zero indicate a greater degree of asymmetry. The mean signed asymmetry value for the sample ($\overline{RA}_i$) is an estimate of the degree of directional asymmetry (DA_i) in the population.

$$DA_i = \overline{RA}_i$$

An absolute (unsigned) asymmetry value (AA_i) is then calculated for each individual, representing the individual deviation from the sample mean asymmetry for that linear distance.

$$AA_i = \left|RA_i - DA_i\right|$$

Fluctuating asymmetry (FA_i) within a sample is defined by the amount of dispersion around the mean signed asymmetry and estimated by the mean absolute (unsigned) asymmetry for the sample ($\overline{AA}_i$).

$$FA_i = \overline{AA}_i$$

In effect, the sample distribution of raw (signed) asymmetry values is "folded" around the sample mean, such that the sample mean functions as zero, and all values are distributed in the positive direction. The most asymmetric observations then have the most positive values, regardless of the original direction of asymmetry.

Fluctuating asymmetry in two samples X and Y may be compared statistically by evaluating the mean absolute asymmetries for distance i in each sample: $\overline{AA}(X)_i$ and $\overline{AA}(Y)_i$. The sample with a higher degree of dispersion around its mean signed asymmetry will have a higher mean absolute (unsigned) asymmetry value ($\overline{AA}_i$) than that of the other sample. For a given comparison, the null hypothesis states that the absolute mean asymmetries are equal (H_0: $\overline{AA}(X)_i - \overline{AA}(Y)_i = 0$). Statistical significance is addressed using the bootstrap method to calculate confidence intervals for the difference $\overline{AA}(X)_i - \overline{AA}(Y)_i$ for a given linear distance (Richtsmeier et al., 2005; following Hall and Martin, 1988). Statistical testing using the bootstrap method involves the generation of multiple test statistics ($\overline{AA}(X)_i - \overline{AA}(Y)_i$) by resampling the existing data to create bootstrap samples randomly and with replacement. In the current set of studies, a distribution of 1,000 test statistics was produced using the bootstrap. Ninety-five percent confidence intervals were obtained using this bootstrap distribution. Fluctuating asymmetry values from two samples are statistically significantly different if this confidence interval does *not* include zero.

Antisymmetry refers to a directional component of signed asymmetry in a population that is random with respect to side and is assumed to contain a genetic component (e.g., Van Valen, 1962; Palmer and Strobeck, 1992). If a trait is influenced by antisymmetry, it cannot be used to estimate developmental instability (e.g., Palmer and Strobeck, 1992; but see Graham et al., 1993). Antisymmetry is generally indicated by a bimodal or platykurtic distribution of signed asymmetry ($R - L$) in a population (Palmer, 1994). The distribution of signed asymmetry for each ILD in each sample was tested for departure from normality using combined kurtosis and skewness tests, as recommended by Palmer and Strobeck (1992).

Fluctuating asymmetry is particularly sensitive to measurement error (Greene, 1984; Palmer and Strobeck, 1986; Palmer, 1994). Landmark coordinate data were collected in two trials, allowing me to assess the significance of between-sides variance (fluctuating asymmetry) relative to error variance. A two-way mixed model ANOVA was performed separately for each pair of bilateral distances within each sample (Early and Late Period groups) following Palmer and Strobeck (1986). The significance of fluctuating asymmetry relative to error is estimated by the F-ratio of mean squares of the individual $\times$ side interaction term and the error term. In this case, where statistical analysis was performed separately

on each of the 361 bilateral distances, a conservative Bonferroni correction was applied, reducing the critical value from $\alpha = 0.05$ to $\alpha/n = 0.00014$. In the Early Period group, 10 linear distances had nonsignificant fluctuating asymmetry values (P-values ranged from 0.00025 to 0.42918 for these 10 distances). Each of these distances included dacryon as an endpoint. In the Late Period group, six linear distances had nonsignificant fluctuating asymmetry values (P-values ranged from 0.00019 to 0.06478 for these six distances), one of which was also found to be nonsignificant in the Early Period group. The 15 distances that were found to have nonsignificant fluctuating asymmetry estimates in either sample in this analysis were excluded from discussion and interpretation of all results.

RESULTS

Fluctuating asymmetry differences in the Early and Late Periods

Previous studies have demonstrated that the Early Christian Period group was under greater health/environmental stress when compared with the Late Christian group (Hummert, 1983; Hummert and Van Gerven, 1983; Sandford et al., 1983; Van Gerven et al., 1985, 1990b; Moore et al., 1986; Mittler and Van Gerven, 1994; Sandford and Kissling, 1994; Albert and Greene, 1999). On the basis of this demonstration of differential levels of stress, I expected the Early Period group to display relatively greater magnitude of fluctuating asymmetry when compared with the Late Period group. Estimates of directional and fluctuating asymmetry were obtained for each bilateral interlandmark linear distance (ILD = 361) in the Early and Late Period groups. Differences in fluctuating asymmetry were calculated for each bilateral linear distance as the signed difference between fluctuating asymmetry (FA) estimates for the Early and Late Period groups ($FA_{Early} - FA_{Late}$). As noted previously, the fluctuating asymmetry estimates were the average absolute asymmetry for each distance after correction for directional asymmetry, and statistical significance of each difference was determined using the bootstrap method. Fifteen of 361 distances had nonsignificant levels of fluctuating asymmetry. Of the 346 remaining distances with significant fluctuating asymmetry, more than half of the bilateral linear distances showed higher estimates of fluctuating asymmetry in the Early Period group than in the Late Period group (194/346 in the Early Period, compared with 152/346 in the Late Period).

The Early Period group also had more linear distances with statistically significantly greater levels of fluctuating asymmetry than that of the Late Period group. Approximately 11% of all bilateral interlandmark linear distances (39 out of a total 346 linear distances) showed statistically significantly different levels of fluctuating asymmetry between the Early and Late Period groups ($\alpha = 0.05$) (Fig. 1). Of these, 62% (24/39) were more asymmetric in the Early Period group, which is known to have been subjected to higher magnitudes of health stress. Thirty-eight percent (15/39) of the significantly different linear distances were more asymmetric in the Late Period group, which was subjected to relatively lower magnitudes of stress. These results support the hypothesis that the more-stressed Early Period group would display a greater overall magnitude of fluctuating asymmetry, and by implication greater developmental instability, when compared with the less-stressed Late Period group.

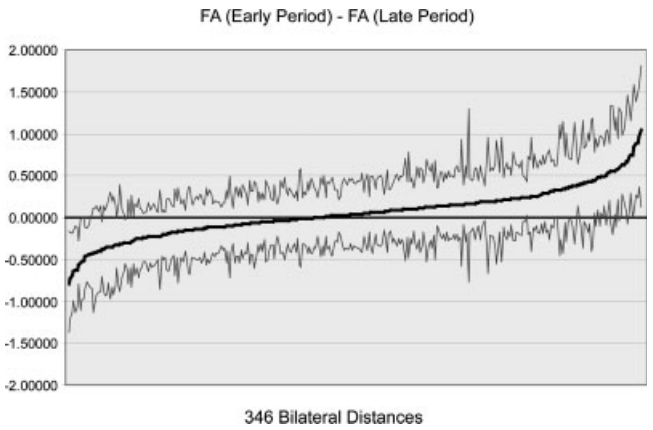

Fig. 1. Differences in fluctuating asymmetry in the Early and Late Period groups. This graph shows the distribution of the differences in magnitude of fluctuating asymmetry ($FA_{Early} - FA_{Late}$). Each data point on the x-axis represents one of 346 bilateral interlandmark linear distances. The black line indicates the value of $FA_{Early} - FA_{Late}$ for each linear distance. Gray lines indicate the upper and lower limits of a 95% confidence interval for $FA_{Early} - FA_{Late}$. When the confidence interval does not include zero, a significant difference in magnitude of fluctuating asymmetry exists between the Early and Late Period groups for that particular linear distance.

Localization of significant fluctuating asymmetry differences

To further investigate the biological processes underlying these differences in fluctuating asymmetry, localization of the significant differences was considered. Figure 2 illustrates linear distances that had significantly more fluctuating asymmetry in either the Early Period group or the Late Period group. One way to discern patterns among large numbers of linear distances is through the identification of landmarks that act as endpoints for multiple linear distances of interest. In the Early Period group, the landmark pterion posterior (PTP) was involved in a number of linear distances that had significantly more fluctuating asymmetry than that in the Late Period group. Seven of the 28 linear distances involving PTP had greater fluctuating asymmetry in the Early Period group, but the landmark was not involved in any linear distances that were more asymmetric in the Late Period group. These significantly different linear distances fanned out inferiorly from PTP into the face and anterior cranial base, consistent with a highly variable superior extension of the greater wing of the sphenoid over the coronal suture. The jugular process (JUG), lambda (LAM), and the greater palatine foramen (GPF) were also involved in multiple (four or more) linear distances with significantly more fluctuating asymmetry in the Early Period group.

In contrast, only one landmark was an endpoint for multiple linear distances that had significantly more fluctuating asymmetry in the Late Period group relative to the Early Period group. Six linear distances extending from asterion (AST) anteriorly toward the face were significantly more asymmetric in the Late Period group. This result indicates that the anteroposterior position of asterion was the primary factor in the small number of linear distances that were significantly more asymmetric in the Late Period group.

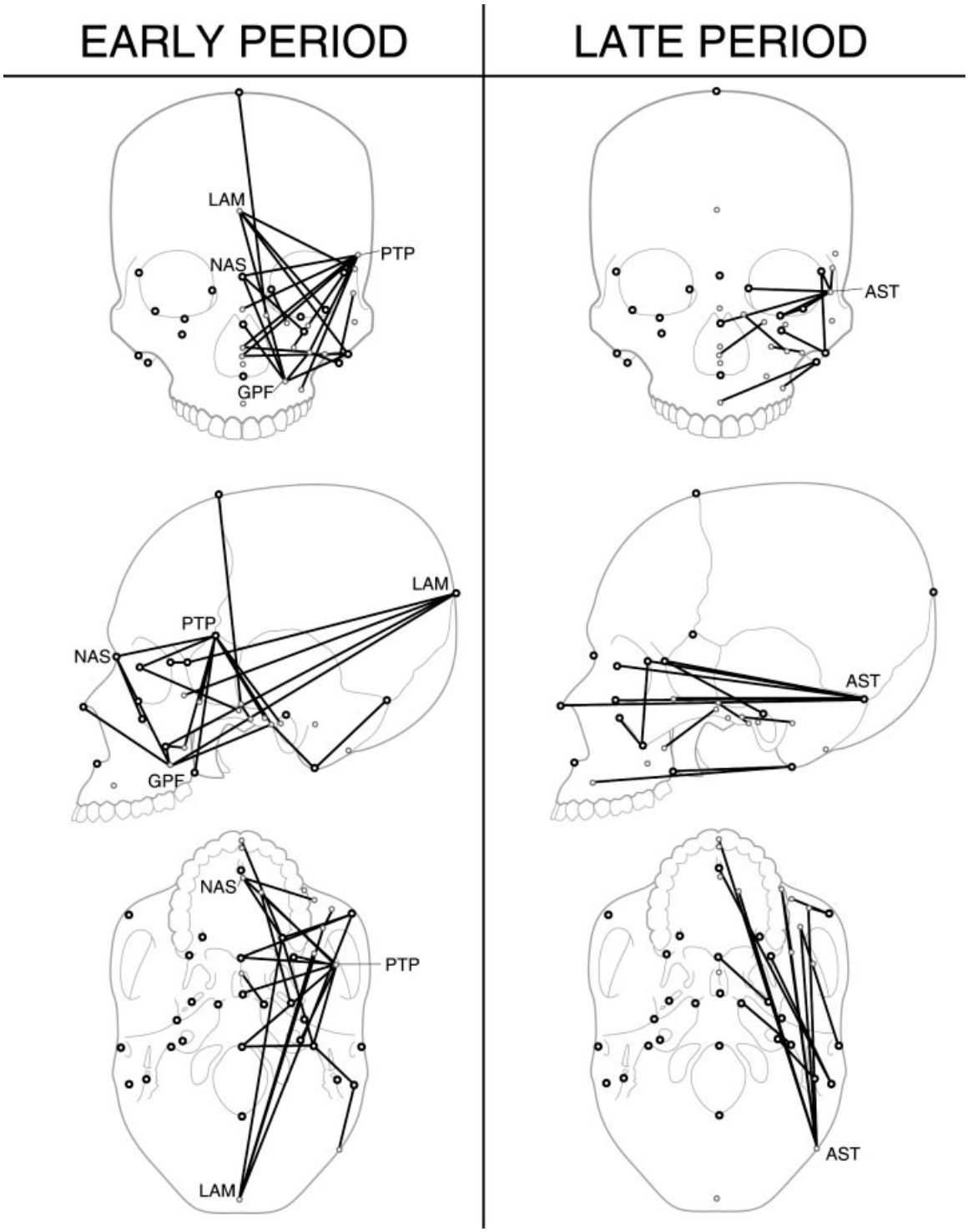

Fig. 2. Linear distances with significantly different levels of fluctuating asymmetry in the Early and Late Period groups ($\alpha = 0.05$). The left column shows linear distances with significantly more fluctuating asymmetry in the more-stressed Early Period group. The right column shows linear distances with significantly more fluctuating asymmetry in the less-stressed Late Period group. In order to convey 3D relationships, all significant distances are illustrated in each one of the three views of the skull. Bold landmarks are those that are actually visible in a given view.

Patterns of asymmetry in each group

Specific patterns of asymmetry were investigated further to elucidate the biological implications of asymmetry in the human skull. These results are descriptive and do not involve statistical testing. For the set of all linear distances, directional asymmetry ($L - R$) ranged from −1.51 to 1.29 mm in the Early Period group and −1.51 to 0.98 mm in the Late Period group (Fig. 3). There was a slight trend toward right-side dominance in

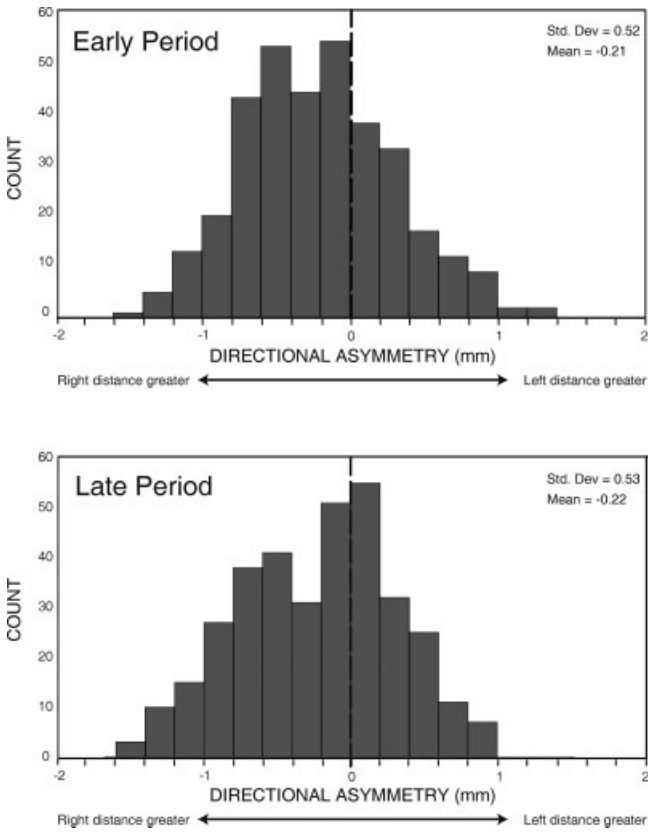

Fig. 3. Distribution of directional asymmetry values. These histograms illustrate the distribution of directional asymmetry values ($L - R$) for the 346 bilateral linear distances in the Early and Late Period groups. A dotted line indicates the axis of symmetry at a directional asymmetry score of zero. In both samples, the mean directional asymmetry was slightly less than zero and negative values were slightly more extreme, indicating a modest right-side bias.

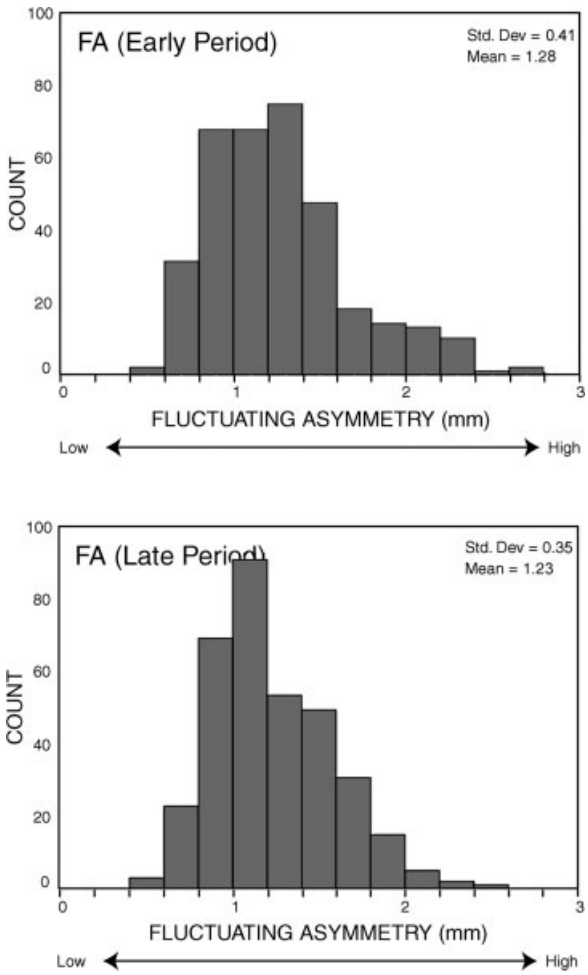

Fig. 4. Distribution of fluctuating asymmetry values. These histograms illustrate the distribution of fluctuating asymmetry values for the 346 bilateral linear distances in the Early and Late Period groups. The fluctuating asymmetry estimate for each bilateral linear distance is determined by centering the signed asymmetry distribution ($L - R$) at the sample mean (the estimate of directional asymmetry in the sample), and calculating the mean absolute deviation of all individuals from the sample mean for that linear distance.

both the Early and Late Period individuals [$(L - R) < 0$]. Right-side dominant values were slightly more frequent (68% in the Early Period and 63% in the Late Period) and more extreme. However, almost all directional asymmetry values in both the Early and Late Period individuals (93% and 92%, respectively) were within 1 mm of perfect symmetry, indicating that directional asymmetry was minimal overall.

Fluctuating asymmetry estimates for the set of all linear distances ranged from 0.58 to 2.75 mm in the Early Period group and 0.50 to 2.44 mm in the Late Period group (Fig. 4). The ranges of fluctuating asymmetry were similar in the two groups, and suggest that some linear distances may display greater amounts of fluctuating asymmetry than others.

Figure 5 illustrates linear distances for which the magnitude of fluctuating asymmetry was relatively high. Most linear distances with high levels of fluctuating asymmetry involved the landmark pterion posterior (PTP). Asterion (AST) was also an endpoint for linear distances with high fluctuating asymmetry in both groups. In the Early Period group, mediolateral asymmetry of nasion (NAS) was notable. This is a result of how the landmark was located. All landmarks defined by sutural intersections were located at the actual intersection of sutures. So, for example, nasion was located at the intersection of the internasal suture with the frontonasal suture, rather than at a perceived midline. The patterns of linear distances with high fluctuating asymmetry are similar between in the Early and Late Period groups, and appear to involve laterally located, primarily neurocranial structures.

Figure 6 illustrates linear distances for which the magnitude of fluctuating asymmetry was relatively low. Ten of the 15 distances excluded from analysis as having nonsignificant fluctuating asymmetry were noted to have very low levels of fluctuating asymmetry (<0.75 mm). This meant that fluctuating asymmetry was nonsignificant relative to measurement error, which can artificially *increase* estimates of fluctuating asymmetry. However, we are able to conclude that fluctuating asymmetry in these linear distances is of low magnitude. For this reason, all linear distances noted to display low fluctuating asymmetry are included in Figure 6, regardless of the

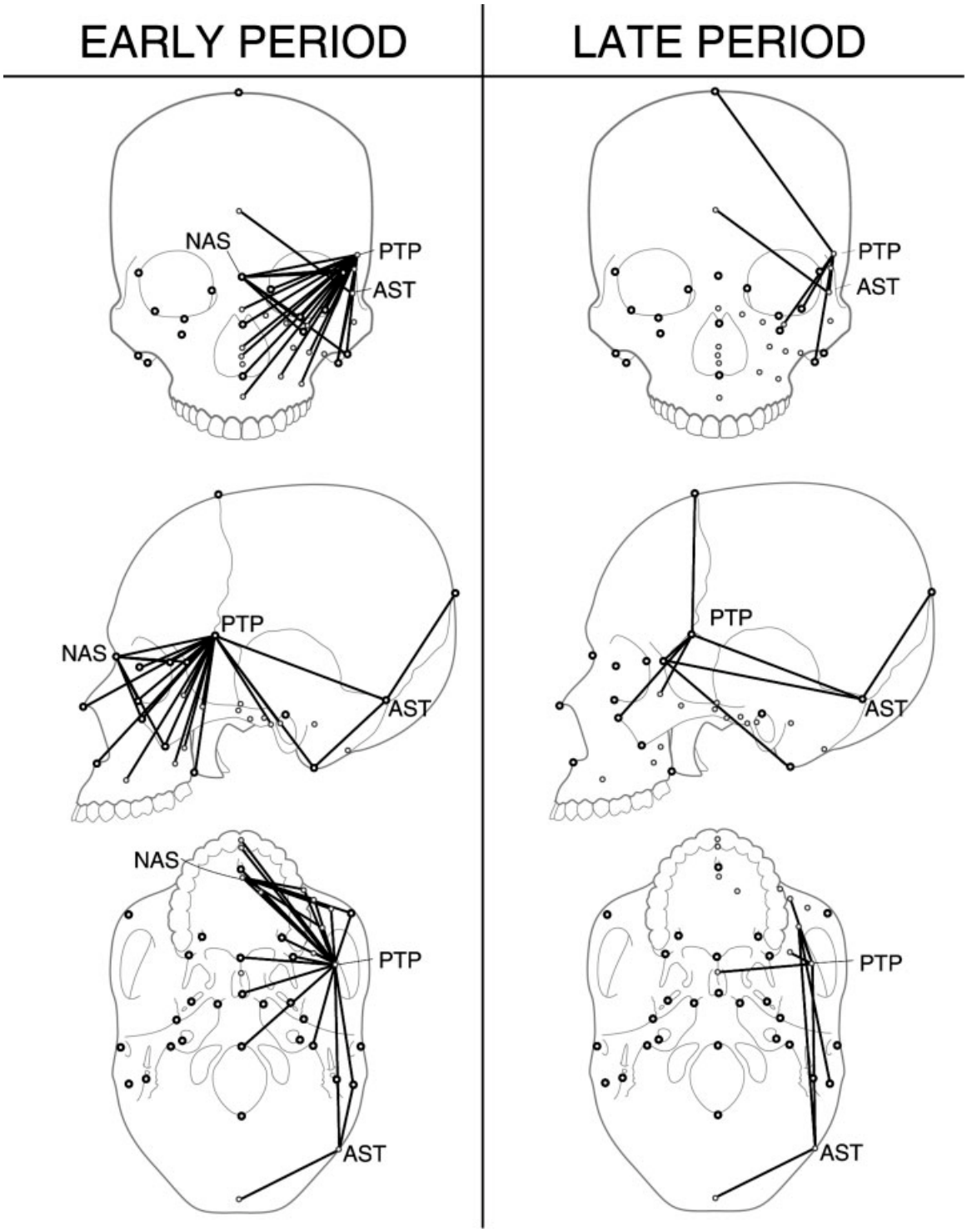

Fig. 5. High fluctuating asymmetry values. The linear distances shown in this figure had relatively high fluctuating asymmetry estimates (>2.0 mm). Values were calculated separately for the Early and Late Period groups.

statistical significance of the level of fluctuating asymmetry relative to error. In both the Early and Late Period groups, the landmarks dacryon (DAC) and the sphenoid spine (SSP) are included in most of the linear distances with relatively low levels of fluctuating asymmetry. In addition, most linear distances involving zygomaxillare superior (ZMS) in the Early Period group and linear distances involving the greater palatine foramen (GPF) in the Late Period group also tended toward low levels of fluctuating asymmetry. Note that these linear distances almost all involve midline landmarks as well, and that DAC, SSP, ZMS, and GPF are located relatively

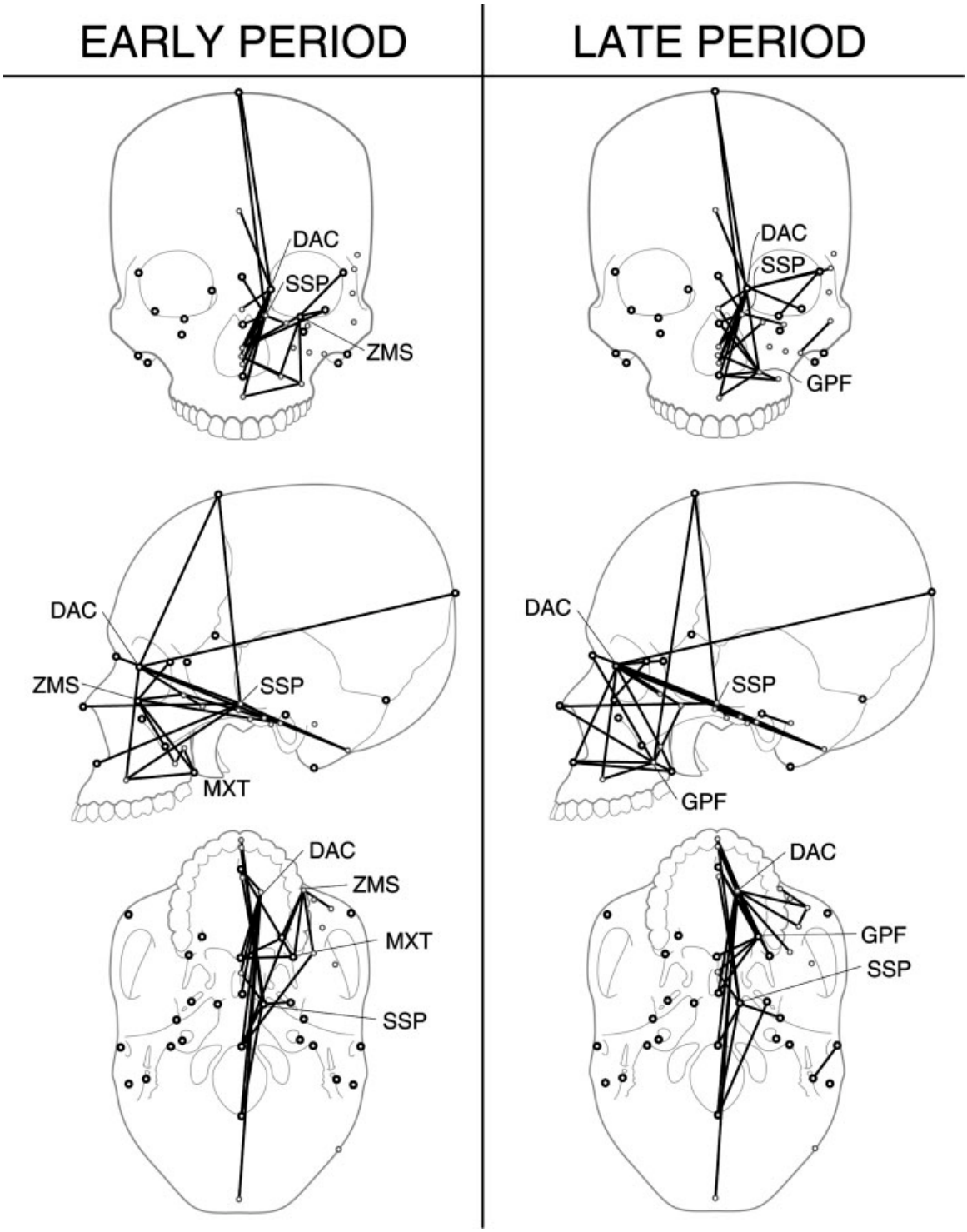

Fig. 6. Low fluctuating asymmetry values. The linear distances shown in this figure had relatively low fluctuating asymmetry estimates of less than 0.75 mm. Values were calculated separately for the Early and Late Period groups. Distances illustrated in this figure include 10 linear distances where low fluctuating asymmetry values were exceeded by measurement error variance.

close to the midline. This result suggests that variation of structures close to the midline, demonstrated here in the ethmoid, maxillary and, basisphenoid regions, is constrained to symmetry in both groups. Linear distances on the palate also had relatively low fluctuating asymmetry and are located relatively close to the midline.

Correlation of asymmetry under different levels of stress

Up to this point, asymmetry has been considered separately in the Early and Late Period groups. However, patterns exist that appear to be shared between the two

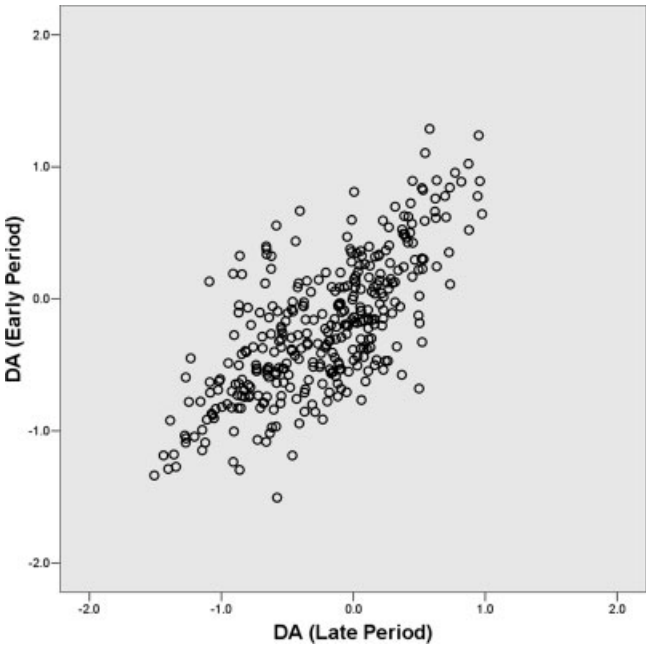

Fig. 7. Correlation of directional asymmetry values in Early and Late Period groups.

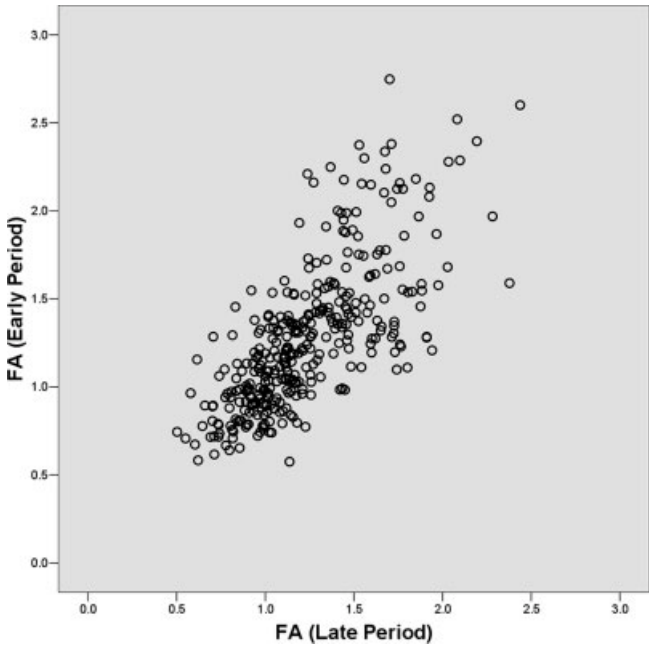

Fig. 8. Correlation of fluctuating asymmetry values in Early and Late Period groups.

groups. Directional asymmetry values for the set of all bilateral linear distances are strongly correlated between the Early and Late Period groups ($r = 0.715$; $P < 0.01$) (Fig. 7). Most linear distances with positive directional asymmetry ($L - R$) in the Early Period group are also positive in the Late Period group (meaning that those linear distances are greater on the left side of the skull in both groups). Similarly, most linear distances with negative directional asymmetry in the Early Period group are also negative in the Late Period group (meaning that those linear distances are greater on the right side in both groups).

Fluctuating asymmetry values for the set of all bilateral linear distances were also highly correlated ($r = 0.726$; $P < 0.01$) (Fig. 8). This correlation of fluctuating asymmetry values in the Early and Late Period groups provide strong evidence for the existence of biological processes influencing craniofacial asymmetry that are common to all humans, independent of sex. To determine the validity of this observation, it was first necessary to address other possible factors that might have influenced the correlation of fluctuating asymmetry values: 1) length of linear distance, 2) overall variability of the linear distance, and 3) measurement error. The issue was whether the correlation of fluctuating asymmetry values in the Early and Late Period groups were significant, independent of the influence of these three factors.

The relative length of each linear distance was potentially a confounding factor in the observed correlations. A positive association between the size of a character and its fluctuating asymmetry has been noted in the literature (e.g., Palmer and Strobeck, 1986). The linear distances illustrated in Figure 5, comprising those linear distances with fluctuating asymmetry estimates greater than 2.0 mm, appear to be relatively longer, suggesting that length of linear distance may be positively associated with the observed level of fluctuating asymmetry. If the length of a given linear distance was correlated with the magnitude of fluctuating asymmetry, then one would expect the asymmetry values for all linear distances to be correlated in the Early and Late Period groups (i.e., regardless of the level of stress, as the linear distance increases in length, so does the magnitude of asymmetry). For this analysis, *Length* of each interlandmark linear distance was determined separately for the Early and Late Period groups and estimated by the average of the right- and left-side linear distances across all individuals in the sample.

Interindividual variability was another potentially confounding factor in the observed correlations. The relationship between interindividual and intraindividual variability is debated in the context of whether canalization and developmental stability are similar or independent processes (e.g., Debat et al., 2000; Willmore et al., 2005). If these mechanisms are related, then the overall variability of a linear distance may be a factor in the observed levels of fluctuating asymmetry. If the variability of a given linear distance were correlated with the magnitude of fluctuating asymmetry, then one would expect the asymmetry values for all linear distances to be correlated in the Early and Late Period groups (i.e., regardless of the level of stress, linear distances with greater overall variability will display greater levels of asymmetry). For this analysis, *Variability* of each interlandmark linear distance was determined separately for the Early and Late Period groups and estimated by taking the average length for each individual and calculating the standard deviation across all individuals.

Finally, measurement error could have been a confounding factor in the correlations observed between the sexes in fluctuating asymmetry values for all linear distances. If the amount of error associated with a given linear distance significantly influenced the magnitude of observed fluctuating asymmetry, then one would expect the asymmetry values for all linear distances to be correlated in the Early and Late Period groups (i.e., regard-

TABLE 3. Partial correlations for fluctuating asymmetry values in the Early and Late Period groups and their respective estimates of linear distance length, variability, and measurement error

	Zero-order correlations	Partial correlations
Fluctuating asymmetry[a] *in Early Period (higher stress)*		
Length (Early)[b]	0.240	−0.096
Variability (Early)[b]	0.418	0.234
Error (Early)[b]	0.585	0.323
FA (Late)[b]	0.741	0.536
Fluctuating asymmetry[b] *in Late Period (lower stress)*		
Length (Late)[b]	0.238	−0.011
Variability (Late)[b]	0.322	0.122
Error (Late)[a]	0.431	0.245
FA (Early)[a]	0.741	0.637

[a] Fourth-root transformation.
[b] Square-root transformation.

less of the level of stress, as the amount of measurement error in a linear distance increases, so does the magnitude of asymmetry). *Error* was determined separately for the Early and Late Period groups and was estimated for each linear distance as the average across all individuals of the standard deviation of the signed asymmetry values ($L - R$) for the two trials.

Multiple regression analysis was used to test the correlation of fluctuating asymmetry values in the Early and Late Period groups, given the group-specific factors of Length, Variability, and Error. Two analyses were conducted, in which data points represented each of the 346 linear distances under consideration. In the first analysis, fluctuating asymmetry in the Early Period group was the dependent variable, and Length, Variability, and Error in Early Period group were independent variables. Fluctuating asymmetry in the Late Period group was included as an additional independent variable. In the second analysis, fluctuating asymmetry in the late Period group was the dependent variable, and Length, Variability, and Error in the Late Period group were independent variables, along with fluctuating asymmetry of the Early Period group. The goal of this design was to test the predictive value of fluctuating asymmetry values in one group for fluctuating asymmetry in the other group, holding constant the factors of group-specific Length, Variability, and Error. Multiple regression analysis makes the assumption that variables are normally and symmetrically distributed. The distributions of most of the variables included in these analyses (fluctuating asymmetry values, length of linear distances, variability, and measurement error values) were significantly positively skewed. These data were transformed using the square root function to achieve normal, symmetric distributions. A fourth-root transformation was applied to fluctuating asymmetry in the Early Period group and to Error in the Late Period group to obtain a normal distribution. Results obtained using these transformed data were almost identical to results obtained using the raw data.

Partial correlations reported in the multiple regression analysis demonstrated that asymmetry values are highly correlated between the Early and Late Period groups, independent of the variables Length, Variability, and Error (Table 3). There was moderate to minimal zero-order correlation between fluctuating asymmetry values and Length, Variability, and Error values. In addition, the partial correlations for these factors were relatively low ($-0.096 \leq r \leq 0.323$). In contrast, the partial correlation for fluctuating asymmetry between the Early and Late Period groups, controlling for those confounding factors, remained relatively stronger ($r = 0.536$ and 0.637, for the Early and Late Period groups, respectively). These results demonstrate that the observed correlation of asymmetry values between the higher-stressed Early Period group and the lower-stressed Late Period group is a result of common biological processes and differential levels of developmental instability in the skull operating in both populations, rather than a byproduct of size, interindividual variability, or measurement error.

DISCUSSION

In this comparison of craniofacial fluctuating asymmetry, the Early group was found to have greater overall fluctuating asymmetry in the craniofacial skeleton when compared with the Late group, as originally hypothesized. A majority (56%) of the 346 bilateral linear distances under consideration here had estimates of fluctuating asymmetry that were greater in the Early group than that in the Late group. In addition, among the linear distances with statistically significantly different levels of fluctuating asymmetry between the two groups, a majority (62%) had greater fluctuating asymmetry in the Early group. These results are consistent with previous research, indicating that the Early group was generally less healthy and more affected by environmental stress when compared with the Late group.

The conclusion that the more-stressed Early Period group had a greater number of distances (62%) with significantly greater fluctuating asymmetry was consistent with the expected association of stress and fluctuating asymmetry. However, many linear distances with significantly different levels of fluctuating asymmetry (38%) were *more* asymmetric in the healthier Late group. It is difficult to determine whether the observed proportions represent something more meaningful than a random deviation from a binomial distribution. Simple comparisons to expected frequencies (e.g., χ^2 values) are inappropriate here because of the interdependence of linear distances sharing common endpoints. Therefore, the interpretation is limited to the conclusion that these data support the hypothesized association of stress and fluctuating asymmetry.

Ideally, for statistical comparison, a single index would summarize the fluctuating asymmetry characteristic of an entire organism (or sample of organisms). However, this study has demonstrated that fluctuating asymmetry is trait-specific, meaning that the success of any single index for estimating fluctuating asymmetry is dependent on the appropriate choice of component traits. Consider, for example, how the results of the current study would have been impacted if either of the landmarks pterion posterior (PTP) and asterion (AST) had been excluded.

The identification of statistically significant differences in magnitude of fluctuating asymmetry, and by implication differences in developmental instability, allowed me to localize asymmetries in the human skull associated with responses to stress. Pterion posterior, nasion, lambda, dacryon, and the greater palatine foramen were all involved in multiple linear distances that had significantly more fluctuating asymmetry in the more highly stressed Early group. In contrast, among the smaller number of linear distances with significantly more fluctuating asym-

metry in the less-stressed Late group, asterion was the only landmark involved in multiple linear distances. One interpretation for these findings is that fluctuating asymmetry values for certain landmarks are more sensitive indicators of stress than others. These results suggest that the former set of landmarks (pterion posterior, nasion, lambda, dacryon, and the greater palatine foramen) are good estimators of developmental instability, because they produced the expected results in this analysis. In contrast, asterion may not be a good estimator of fluctuating asymmetry, because it did not produce the expected results and instead showed significantly more fluctuating asymmetry in the less-stressed Late group. This interpretation relies on *a priori* expectations, but provides a foundation for further investigation of the sensitivity of particular landmarks to differential levels of health and environmental stress.

Results of this study also demonstrated a clear correlation between the Early and Late Period groups in fluctuating asymmetry values for each bilateral linear distance. This common pattern was not strongly correlated with length of linear distance, interindividual variability, or measurement error, and therefore provided evidence of underlying biological processes that are common across differential levels of health and environmental stress. Landmarks close to the midline and in the face displayed the most symmetry. In contrast, landmarks with the most fluctuating asymmetry were located on and around the neurocranium and generally farther from the midline. Fluctuating asymmetry of the landmark nasion in the Early group was a notable exception. Marked convolutions in the sutural pattern at nasion were noted during landmark collection for the Kulubnarti material, and these results suggest that magnitude of these midline deviations was greater in the Early group.

Different explanations have been offered in the literature for the apparent differential expression of fluctuating asymmetry in various traits. The developmental stability of a given character is expected to be positively correlated with the functional importance of symmetry in that character (Palmer and Strobeck, 1986). Natural selection should act to reduce fluctuating asymmetry in traits that are functionally important for the fitness of an organism (referred to here as the "functionality hypothesis"). For example, fluctuating asymmetries of traits important for locomotion have been reported to be lower than that of other traits, based on the optimal energetic efficiency of limb symmetry (Gummer and Brigham, 1995; Trivers et al., 1999). The functional importance of symmetry in the skull is less clear. In a study that failed to find congruence between inter- and intraindividual variation in the mouse skull, the authors cited a number of studies on fluctuating asymmetry in functionally important traits and stated "[t]here is no evidence that the size and shape symmetry of the skull may have such a crucial importance in terms of fitness and its developmental homeostasis" (Debat et al., 2000, p. 429). However, symmetry in the masticatory apparatus has been shown to be important for proper function of the temporomandibular joint in humans. Although different in character from the function of locomotor traits, the functional importance of craniofacial symmetry cannot be discounted.

In the current study, landmarks in the face located close to the midline displayed the least amount of fluctuating asymmetry (dacryon, the sphenoid spine, zygomaxillare superior, and the greater palatine foramen). In contrast, landmarks on the cranial vault showed the greatest amount of asymmetry (pterion posterior and asterion), particularly in those linear distances extending to neurocranial midline landmarks (nasion, bregma, and lambda). Following the functionality hypothesis for differential levels of fluctuating asymmetry, these results suggest that the landmarks noted on the face close to the midline are of greater functional importance than those on the cranial vault. In addition, the positions of certain landmarks are intimately related to underlying structures, and therefore, variability at these landmarks is constrained by the variability of those structures. In contrast, other landmarks are only loosely integrated with underlying structures, and functional integrity can withstand greater amounts of variability. For example, the landmark dacryon represents the junction of relatively blunt sutures between the frontal, maxilla, and lacrimal bones. Variations in the position of this landmark are indicative of variation in the position of these bones and related soft-tissue structures (e.g., the nasolacrimal duct). Small deviations in position are likely to affect function, even if only to a small degree. In contrast, the landmark pterion posterior represents the junction of a beveled suture where the greater wing of the sphenoid overlaps the coronal suture. The function of this area is to support and protect the endocranial contents (i.e., brain) and to serve as the proximal attachment for the temporalis muscle. The exact position of the sphenoparietal suture on the external surface of the skull probably does not influence the form or function of the underlying brain. Similarly, the origin of the temporalis muscle covers frontal, parietal, and sphenoid bone in the pterion region, and the precise location of pterion posterior at the intersection of these bones is unlikely to affect function of the muscle. Changes of 2–3 mm in the superior extent of the greater wing of the sphenoid probably do not significantly affect overall functionality at this landmark. In fact, the high variability of the sutures at pterion has been noted in the literature (e.g., White, 1991). The results of the current study appear to be consistent with the functionality hypothesis.

Another explanation for differential levels of fluctuating asymmetry in different craniofacial traits is related to signaling and sexual selection. Facial symmetry is positively correlated with perceived attractiveness and is thought to signal developmental stability and reproductive fitness (Grammer and Thornhill, 1994; Thornhill and Gangestad, 1996; Swaddle, 1998). On the basis of this relationship, natural selection should act to reduce fluctuating asymmetry in those traits for which the degree of symmetry (or asymmetry) is most visible (referred to here as the "signaling hypothesis"). "Only traits that are detected by the receiver can be considered signals" (Uetz and Taylor, 2003, p. 214). Asymmetry close to the midline in the face is more readily visible than the same degree of absolute asymmetry in more lateral structures on the neurocranium. Therefore, one would expect facial landmarks close to the midline (e.g., dacryon and the premaxilla-maxillary junction) to be constrained to very little fluctuating asymmetry, whereas neurocranial landmarks far from the midline (e.g., asterion and pterion posterior) could cope with higher magnitudes of fluctuating asymmetry with no concomitant increase in asymmetry of visible soft tissue structures.

In the current studies, linear distances involving facial landmarks close to the midline tended to display rela-

tively low levels of fluctuating asymmetry. Of particular interest were landmarks around the orbit. The bony structure of the orbit provides the substrate for the soft tissue structures of the eye and palpebral fissures. Asymmetry in the eye is readily apparent, and presumably, underlying asymmetry of the bony orbits would also be apparent. The signaling hypothesis predicts that symmetry in the orbits is adaptive and that these structures should be relatively more stable than other characters. The landmark dacryon (at the intersection of the frontal, lacrimal, and maxillary bones) was an endpoint for a high proportion of linear distances with low fluctuating asymmetry. In addition, zygomaxillare superior (on the orbital rim) was involved in multiple linear distances with low fluctuating asymmetry. These results demonstrate that fluctuating asymmetry in the bony orbit is relatively low.

In contrast, relatively high levels of fluctuating asymmetry were noted in the neurocranial landmarks pterion posterior and asterion. These landmarks constitute the intersections of osteogenic fronts that create a continuous surface on the neurocranium. The precise location of the landmark does not appear to affect overlying soft tissue structures, and fluctuating asymmetry at these landmarks is not likely to result in visible asymmetry. Therefore, the results of the current studies are consistent with the signaling hypothesis, as described earlier.

Finally, morphological traits of greater complexity are expected to display lower levels of fluctuating asymmetry relative to simple traits (referred to here as the "complexity hypothesis") (Soulé, 1982; Livshits et al., 1998; Aparicio and Bonal, 2002). This expectation is based on simple mathematical principles involving the fluctuating asymmetry phenotype and does not make any assumptions about differential levels of underlying developmental instability. For purposes of illustration, consider a complex structure made up of component parts: a digital ray consisting of metacarpal, proximal, middle, and distal phalanges. The length of the digital ray is a complex trait, and each of the four bones is a simple trait. Assume that developmental noise introduces random asymmetry at each bone equal to 1 mm. If the direction of asymmetry in each developmental unit is truly random (in accordance with the definition of fluctuating asymmetry), then generally two of the four bones will be larger on the right side and the other two will be larger on the left side. The combined right- and left-side biases among the four bones effectively cancel each other out and the right and left digital rays (the complex trait) are therefore symmetric. Although this example is overly simplistic, it demonstrates the mathematical basis for the complexity hypothesis. In addition, if the direction of asymmetry within the component parts of a complex trait is correlated, asymmetry of the complex trait will be higher than if the component parts are uncorrelated, because a correlation among component parts indicates that the direction of asymmetry is not entirely random. This hypothesis involves the etiology of fluctuating asymmetry, distinct from the level of developmental instability. In other words, given two traits subject to equivalent levels of developmental instability, the more complex trait is expected to show less fluctuating asymmetry than the simple trait.

The definition of component parts for the identification of simple versus complex traits is somewhat arbitrary. In the context of the human skull, developmental units exist at many levels. For example, the embryonic frontonasal prominence and branchial arches could be considered the component parts of cranial traits. However, because asymmetry of the bony skeleton is considered here, I adopted osteogenic sites as the component parts from which to judge the complexity of linear distances. Linear distances crossing only one or two osteogenic sites are relatively simple traits, and those that cross multiple osteogenic sites are relatively complex traits. Linear distances in the neurocranium should generally be simple traits, because the entire cranial vault is formed from only five osteogenic sites (two in the squamous frontal bone, one in each parietal bone, and one in the squamous occipital). In contrast, linear distances in the facial skeleton should generally be more complex traits, because most bones in the face are formed from multiple osteogenic sites.

In the current study, the involvement of cranial vault landmarks in linear distances with relatively high fluctuating asymmetry, and that of facial landmarks in linear distances with relatively low asymmetry, initially suggests that the complexity hypothesis might accurately explain the observed results. However, upon closer inspection, linear distances with relatively high fluctuating asymmetry extend from the cranial vault landmarks to landmarks in the face and cranial base, crossing many osteogenic fronts. Therefore, the complexity hypothesis does not adequately explain the observed results in the current studies.

As discussed earlier, the patterns of differential fluctuating asymmetry observed in the current study were most consistent with two of the proposed hypotheses for trait-specific expression of fluctuating asymmetry: the functionality hypothesis and the signaling hypothesis. It may be difficult to distinguish between these two hypotheses in the context of the craniofacial skeleton, because of the difficulty in isolating portions of the skull expected to be important exclusively for function or signaling. However, based solely on the results of the current study, the signaling hypothesis best explains the observed differential in fluctuating asymmetry values. Low asymmetry values were noted for linear distances involving landmarks in the face and close to the midline. These landmarks were considered to be important for both function and signaling. In contrast, linear distances involving landmarks in and around the cranial base showed moderate levels of fluctuating asymmetry and were not noted to be particularly low. These landmarks are defined predominantly by neurovascular foramina (the carotid canal and foramen ovale). Basicranial morphology is generally thought to display little variability, and from this one might infer functional importance of these structures. The lack of relatively low fluctuating asymmetry values in this region is not consistent with the functionality hypothesis, which predicts low asymmetry values in the basicranium, based on the functional importance of its morphology. However, the high fluctuating asymmetry values observed in the basicranium (relative to the face) are consistent with the signaling hypothesis, which predicts relatively higher fluctuating asymmetry in the nonvisible basicranium, relative to the visible structures of the facial skeleton.

Additional work is required to test the applicability of these hypotheses. I expect that the differential levels of fluctuating asymmetry in various craniofacial characters reflect some combination of the explanations described earlier. For example, in the orbit, symmetry of the landmark dacryon may have functional importance, because

of its relationship with the nasolacrimal duct and other soft tissue structures. However, landmarks on the orbital rim (frontozygomatic junction and zygomaxillare superior) may be more important for signaling, because of their impact on symmetry of the soft tissues around the eyes. One approach would be to compare fluctuating asymmetry of more detailed data from the face and masticatory apparatus. I expect symmetry in landmarks around the lingual alveolar ridge and on the hard palate to be more important for masticatory function than for signaling. In contrast, landmarks around the cheekbones, nasal aperture, and orbital rims are predicted to be important for signaling (although it is impossible to exclude their functional importance). If landmarks from both areas display fluctuating asymmetry values that are relatively low, then both the functionality and signaling hypotheses may be valid. On the other hand, if landmarks in one area have significantly lower fluctuating asymmetry values than those in the other area, these results would provide stronger support for the respective hypothesis.

CONCLUSIONS

Fluctuating asymmetry is commonly used as a bioindicator of developmental instability. Although asymmetries in the human craniofacial skeleton have been the subject of research throughout the last century, surprisingly little effort has been made to measure fluctuating asymmetry in the human skull. Early anthropological studies focused on odontometric analyses of asymmetry in humans, but methodological criticisms based on sample size and error detracted from the strength of this research.

The current study takes advantage of recent developments in geometric morphometric methods for the analysis of fluctuating asymmetry based on three-dimensional landmark coordinate data. This research addresses fluctuating asymmetry in the context of the human craniofacial skeleton and considers the effects of nutrition/systemic stress. In a comparison of two related samples under differential levels of health and environmental stress, fluctuating asymmetry was found to be relatively higher in the sample under a higher level of stress.

One of the most intriguing results of this research was the discovery of concordance between the samples in fluctuating asymmetry values across all linear distances considered here. Laterally located landmarks on the neurocranium tended to display higher levels of fluctuating asymmetry, and those located on the face and close to the midline tended to display lower levels. This evidence for differential levels of fluctuating asymmetry within the craniofacial skeleton supports the idea that developmental instability is trait-specific.

Asymmetry is a form of morphological variation that is frequently overlooked. However, within-individual variation may contribute substantially to overall variation in a population. This study has demonstrated that fluctuating asymmetry may effectively be used to estimate and compare developmental instability in natural populations, specifically in the context of the human skull. Results presented here provide support for the use of fluctuating asymmetry to estimate health and environmental stress in archaeological and medical anthropological research. Finally, this research indicates that the degree of fluctuating asymmetry is trait-specific in the human skull. These results provide unique information about the differential variability in the craniofacial skeleton and are relevant to studies of human evolution, adaptation, growth, and development in both living and past populations.

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