

A Cephalometric Comparison of Skulls from Different Time Periods – The Bronze Age, the 19th Century and the Present

Erwin Jonke¹, Katrin Schaefer², Josef W. Freudenthaler¹,
Hermann Prossinger² and Fred L. Bookstein^{2,3}

¹ Vienna University Clinic of Dentistry, Department of Orthodontics, Vienna, Austria

² Institute for Anthropology, University of Vienna, Vienna, Austria

³ Michigan Center for Biological Information, University of Michigan, Ann Arbor, USA

ABSTRACT

The aim of this study was to evaluate secular trends by means of orthodontic measurements on lateral cephalograms. We use roentgenograms from three populations: 22 Bronze Age skulls from a cemetery near Hainburg/Austria, 140 soldiers who served in the Hapsburg Imperial Army in the late 19th century, and 154 contemporary recruits of the Austrian Federal Army. Using conventional morphometric analysis, no statistically significant differences could be established. But applying geometric morphometrics to the 2D-coordinates of the pentagon composed of the landmarks Sella, Nasion, Articulare, Gonion and Menton, some biologically interpretable differences were detected, the size allometry between the 19th- and 20th-century populations being the only notable one. We conclude that landmarks should be digitised directly (and many more of them) and that conventional methods used in clinical orthodontics are inappropriate for addressing the scientific questions approached here.

Key words: cephalometrics, orthodontics, geometric morphometrics.

Introduction

Human growth patterns with many secular trends have been evidenced in numerous studies^{1,2}. For example, generational increases in stature have been de-

scribed previously³. The question we are interested in, and address in this paper, is whether clinical orthodontic measurement techniques can contribute to an-

thropological investigations in a corresponding manner. As the study of the maxilla, mandible and associated parts of the skull is conventionally considered the domain of orthodontics, we ask: are orthodontic measurement techniques adequately powerful to detect secular trends? One orthodontic study has dealt with the issue of secular trends in face size⁴. As studies on morphological changes in the craniofacial skeleton over different time periods^{5,6} are not consistent in their findings and also not in their explanations, we think that comparisons among populations from the same region, spanning a large age range and also environmental change (from the Bronze age until the present), may contribute to clarifying the existing results.

We also augment the issue of secular trends by quantifying other orthodontic features, notably landmark locations derived from distance and angle measurements. By approaching the study of orthodontic features in this way, we suspect that we will find changes on historic and prehistoric time scales, elucidating the possible existence of such trends in a novel way.

Materials and Methods

This paper analysed lateral cephalograms of skulls and of living individuals taken from three collections: 1) 22 skulls from the period 6000 BC–400 AD (the skulls of this »Bronze-Age group«, from an excavated cemetery formerly situated near Hainburg/Donau⁷, are now housed in the Natural History Museum, Vienna, Austria); 2) 140 skulls of soldiers of various ethnic origins who had served in the Hapsburg Imperial Army and died 120–110 years ago (this »19th-century group« was collected by the anatomist Weisbach and the skulls are now in the Natural History Museum, Vienna, Austria); and 3) 154 soldiers conscripted in the present

Austrian Federal Army (this »20th-century group« consisted of recruits born in the years 1970 and 1971).

All x-ray images were made in cephalostats with a film-lens distance of 152 cm. The enlargement factor (107 %) was calibrated by co-imaging a 10 cm long, 2 mm diameter, right-angled wire in the mid-sagittal plane. All cephalograms were scanned and digitised with Gamma[®] Version 3.2d (Slavicek, Klosterneuburg, Austria) software.

The cephalograms of the 162 skulls (Bronze Age, 19th century) were made after implementing the following procedure: 1) the mandible was attached to the maxilla in an optimum occlusal fit; in this position, it was stabilized with dental floss tied at three suitable points. 2) Blue periphery wax (Surgident[®] Heraeus Kulzer Inc., 4315 S. Lafayette Blvd., South Bend, IN 46614, USA) was put between the mandibular condyles and the surface of the temporomandibular joint for further stability and to minimize possible discrepancies between dry skulls and living ones. 3) Then the skull was positioned in the cephalostat. The identification of landmarks in the cephalograms of the *in vivo* subjects was done following standard orthodontic procedures.

The 316 cephalograms were measured by one cephalometric procedure in terms of distances and angles (Table 1). These are a subset of measures that correspond mainly to the McNamara *schema* of analysis⁸, a typical tool for diagnosis and management of patients in the contemporary orthodontic clinical setting.

Data analysis

Two entirely separate analyses of these cephalometric data were carried out.

First, conventional orthodontic measurements (summary descriptive statistics in Table 2) were compared separately by Student *t*-tests and Kruskal-Wallis

analysis of variance among all three groups (Bronze Age, 19th century, 20th century) in pairs.

In a second approach, we reconstructed a digitised coordinate data set for a pentagon of landmark points involved in some

of the computed measurements. Although many angles and distances relative to other landmarks had been measured, only the angles and distances between Nasion, Sella, Articulare, Gonion and Menton allowed a triangulation.

In detail, digitised 2D-coordinates were simulated from the available data as follows (abbreviations are listed in Table 1): Nasion was placed in front of Sella at the measured distance S-N; Articulare was placed at distance S-Ar from Sella along the vector at angle Ar-S-N to the Sella-Nasion line; Gonion was placed under Articulare at distance Ar-Go along a vector at angle S-Ar-Go to the Sella-Articulare line; and Menton was placed in front of Gonion at a distance Ar-Go along a vector making the appropriate angle with the Sella-Nasion line.

We then applied geometric morphometrics methods, a statistical toolkit that is based on Cartesian coordinates of landmark points. The most widely used strategies include Procrustes superimposition^{9,10}, Shape coordinates, Relative Warp

TABLE 1
LANDMARKS USED CONSTRUCTING THE
CEPHALOMETRIC MEASUREMENTS
(AFTER McNAMARA⁸)

Code	Landmark
Se	Sella
Ar	Articulare
Go	Gonion
Me	Menton
Na	Nasion
Gn	Gnathion
A	A-point
B	B-point
MP	Mandibular plane
Uie	Upper incisor incisal edge
Uia	Upper incisor apex
Lie	Lower incisor incisal edge
Lia	Lower incisor apex

TABLE 2
DESCRIPTIVE STATISTICS OF THE CONVENTIONAL MEASURES OF THE SKULLS FROM THE
THREE GROUPS. PAIRWISE COMPARISON YIELDED INSIGNIFICANT DIFFERENCES FOR ALL
MEASURES

Measurement	Bronze Age			19 th century			20 th century		
	X	SD	Median	X	SD	Median	X	SD	Median
Distance (mm)									
S-N	64.59	4.72	65.5	66.3	3.07	66.5	73.35	3.8	73.35
N-Ar	90.11	5.34	91.2	91.25	3.85	91.3	99.21	4.86	38.5
S-Ar	35.07	3.64	35.4	34.6	3.28	34.4	37.42	3.06	37.25
Ar-Go	48.92	5.30	48.8	54.01	4.49	54.1	54.39	5.3	63.95
Me-N	113.4	6.91	112.1	119.0	6.85	119.2	123.0	6.52	122.8
Angle (°)									
GoMe-SN	30.4	6.56	29.3	30.39	6.21	30.0	28.37	6.03	28.2
S-N-A	80.73	4.30	81.0	82.15	4.23	81.8	82.4	3.56	81.7
A-N-B	3.47	2.21	4.0	1.87	2.95	1.6	2.66	2.59	2.85
Ar-Go-Gn	121.5	6.56	120.7	122.5	7.62	122.7	120.9	6.7	121.0
UieUia-SN	97.36	8.30	97.7	100.5	7.51	100.3	104.0	7.55	103.3
LieLia-GoMe	96.49	5.3	95.9	90.56	6.89	89.9	94.6	6.92	94.55

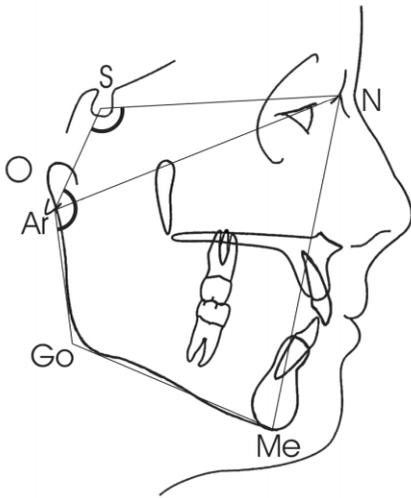


Fig. 1. A sagittal section drawing of a lateral headfilm, illustrating the landmarks used in this study. Landmark codes as in Table 1.

Analysis¹¹, and visualization by Thin Plate splines (see definitions in the Appendix). The analyses and graphics were computed using S-Plus[®].

A standard geometric morphometric analysis^{12–14} starts with the construction of Procrustes shape coordinates (the set of vectors connecting the landmarks of a specimen to corresponding landmarks in the consensus configuration after a Procrustes fit), along with Centroid Size (the factor divided out in the course of size-standardization). Statistical computations include comparison of group mean shape differences, relative warp (principal components for Procrustes-registered shape co-ordinates) analyses separately by group and pooled, and close study of allometry (regressions of the shape coordinates on Centroid Size) by group and pooled.

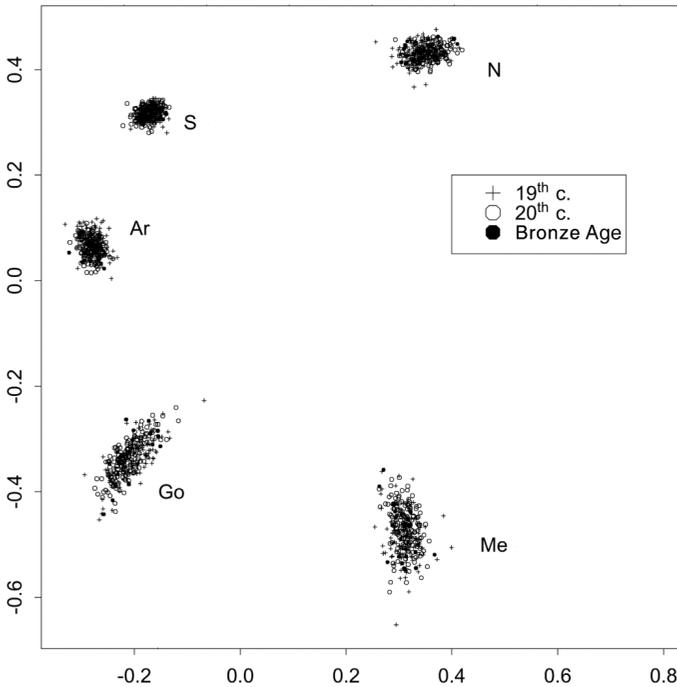


Fig. 2. Scatters of the Procrustes-fitted points of all the specimens. Landmark codes as in Table 1.
• Bronze Age specimens; + 19th-century sample; o contemporary cases.

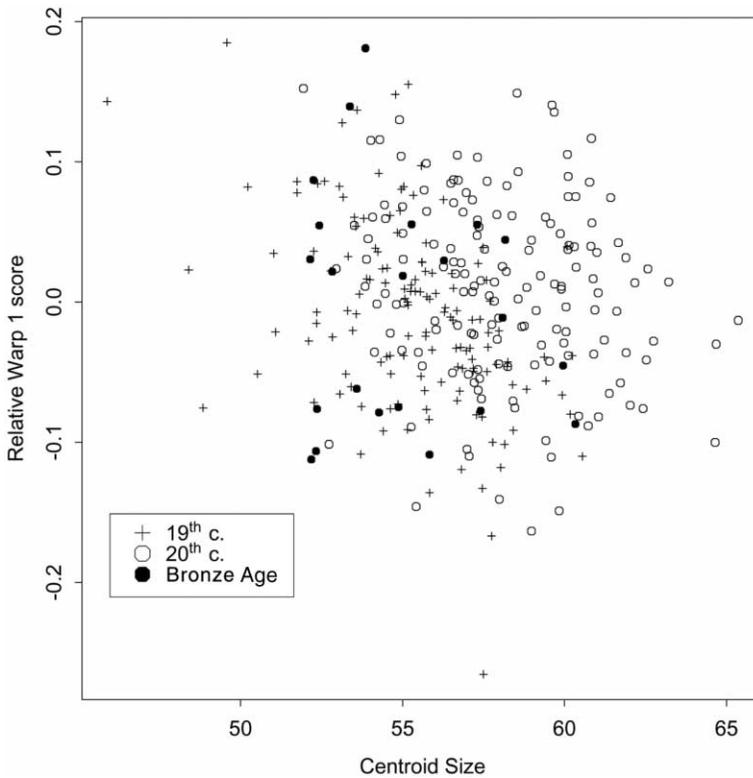


Fig. 3. Centroid Size (abscissa) vs. 1st Relative Warp (ordinate) for all 316 configurations.
 • Bronze Age specimens; + 19th-century sample; o contemporary cases.

Results

Conventional morphometrics

After statistical correction for multiple comparisons (Bonferroni correction), no measured quantities were significantly different between any pairs of groups in Table 2.

Geometric morphometrics of five landmarks

Any geometric morphometric analysis should begin with a careful scan of the »digitised« data for outliers and atypical cases. Figure 2 shows the shape coordinate scatters for the five landmarks together. All scatters seem well-behaved,

with no obvious outliers. The distribution of Centroid Size (see abscissa, Figure 3) is likewise well-behaved.

Mean differences

Centroid size: mean Centroid Sizes for the three groups are 55.01 (Bronze Age), 55.30 (19th century), and 58.17 (20th century), with within-group standard deviations of around 2.5. The 20th-century population is significantly different from the other two, which do not differ from one another.

Pentagon shape: mean shapes of the five-landmark set of shape coordinates for the 19th-century and 20th-century populations differ by permutation test be-

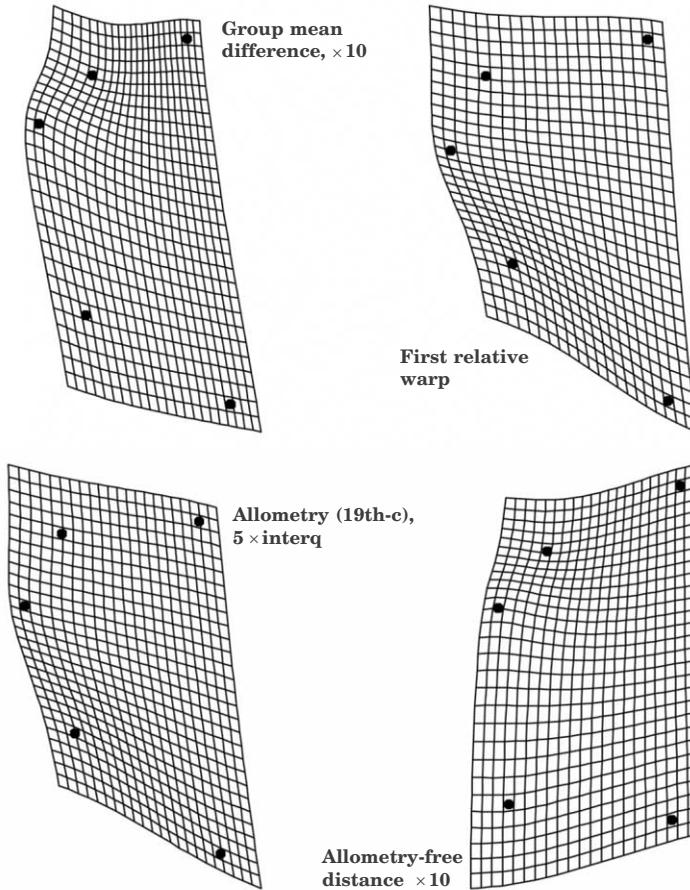


Fig. 4. Comparison between the 19th- and the 20th-century group, visualised by thin plate spline deformation grids to a convenient scale (as labelled). »Group mean difference« shows mean 19th-century shape deformed into mean 20th-century shape, exaggerated tenfold for visibility; »First relative warp« is effectively the same in both groups; »Allometry for the 19th-century group« shows five times the deformation of the average of the 19th-century specimens of less than average size to the average of those of greater than average size; »Allometry-free difference« is the allometry-free component of the group mean difference.

yond the 0.001 level (the observed Procrustes distance between group means is not exceeded in 2,000 random permutations of group label over these 294 cases). The prehistoric group does not differ significantly from either of these. Figure 4, which collects all our findings as deformation grids, begins (at upper left) with

the deformation of the mean 19th-century pentagonal shape into the mean 20th-century shape, exaggerated tenfold for visibility.

Relative warp analysis

The standard relative warp analysis of the full data set of 316 pentagons extracts

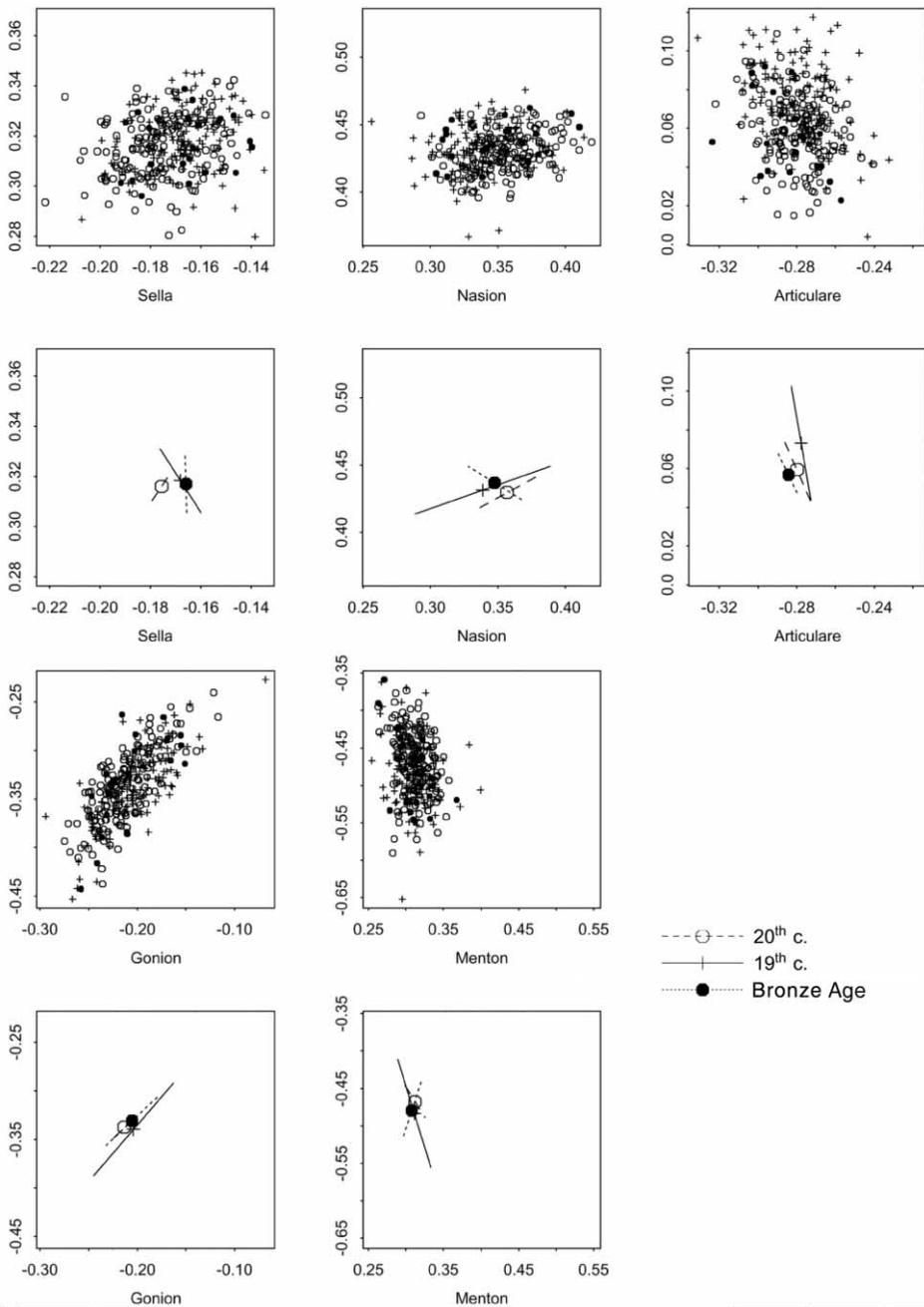


Fig. 5 Allometric regressions, landmark by landmark, in terms of the complete pentagon of shape coordinates (Figure 1 and Figure 2). The second and fourth rows show four times the shift from the mean location for the smaller half of the subsample to the mean for the larger half.

components with eigenvalues 1.44, 0.27, Only the first is likely to have any meaning. The two larger groups differ significantly in mean score on this first relative warp, but the magnitude of the difference is less than one-third as great as for Centroid Size (which we will declare to be the factor underlying this relative warp: see below). Figure 3 scatters the RW1 score against Centroid Size, with group coded by plotting symbol. There is clearly a regression here ($r = -0.45$ in the 19th-century subsample, -0.19 in the moderns), but most of the variation remains unexplained. Figure 4 displays this single relative warp in the form of a deformation grid to a convenient scale.

Size allometry

There is significant size allometry in the two larger groups separately. The second and fourth rows of Figure 5 show the allometric regressions separately by landmark. In terms of the complete pentagon of shape coordinates, these two allometric patterns are different between our two larger groups; *but they point in the same direction of shape space*, differing only in the overall amplitude of this size effect ($P \sim 0.40$ for the hypothesis of group differences in the directions of these vectors). As is evident from the lengths of the solid versus dashed lines in the figure, the overall allometric regression is stronger for the 19th-century sample. (Dotted line: regression for the prehistoric group, which is less stable owing to its smaller sample size.)

Evidently, the effect of this shared size factor in either of the large samples is oblique to the sample mean difference at most of the landmarks. The cosine of the angle between pooled within-group size allometry and 19th- to 20th-century mean difference is 0.818. (By contrast, that between size allometry and RW 1 is 0.928.) Even so, size allometry explains $0.818^2 \sim 67\%$ of the group mean shape difference.

(In view of these large sample sizes, however, what remains is still statistically significant by permutation test.)

Figure 4 shows all the grids involved in these comparisons: RW1, group mean difference, size allometry, and allometry-free mean difference. Relative warp 1 and size allometry are strikingly similar, both emphasizing change of gonial angle and the ratio of anterior to posterior facial height. The actual group mean difference differs from both in changing this ratio considerably less than a different ratio, facial height to facial depth. There is also considerable discrepancy in changes of cranial base shape. The contrast is clarified by the grid at lower right in the figure, which shows the »allometry-free« component of group mean difference, representing, more or less, the mandibular hypertrophy without the open bite. This pattern, combining an opening of the cranial base angle with ramal hypertrophy and a closing of the gonial angle, seems not to correspond to any familiar biological factor of facial shape.

Discussion

Our discussion of these findings will touch on three themes: noncomparability of the subgroups, inefficiency of conventional cephalometric approaches for scientific work, and implications for combinations of modern and archaic samples in a range of scientific projects.

Comparability of the two large samples. Our principal finding is the consistency of size allometry between these 19th-century and 20th-century samples. It is well-known that contemporary people are larger than their ancestors¹⁵, presumably owing to improved nutrition, better medical care, and other socio-economic effects: changes that are sociological, not biological. Even though the individuals in the groups studied here may not be representative of their contemporary popula-

tions, the observed size shift is substantial, accounting for two-thirds of the group mean shape difference. There is, however, a difference in the intensity of this allometry between the samples, for which some further explanation might be sought. Further work would require access to putative causes of the mean size difference or speculations regarding that difference in intensity of size allometry. The remaining one-third of empirical shape variation, borne by the inscrutable grid pattern at lower right in Figure 4, is perhaps an accumulation of various factors, such as differences in military recruitment practices, ethnicities, age effects, artefacts of cephalometric positioning in dried materials, or orthodontic treatment in the moderns. As it corresponds to no known biological factor, we see no useful purpose to be served by its further analysis in so heterogeneous a sample of convenience as this.

Conventional cephalometric »analysis« made no useful contribution. This point is not new with this paper – one of us published it a quarter of a century ago¹⁶, and it has been a provocation to the orthodontic literature ever since. Recall that the findings of the suite of conventional measures, Table 2, were *entirely null*. No group differences were manifest in these data taken one variable at a time. An analysis designed for diagnosis and treatment of contemporary adolescents has no necessary relationship to the information borne in the cephalogram for more fundamental scientific purposes, like this multi-century comparison. It is not that the »analysis« was noise – the information it contains was precisely what we used to simulate the digitising of the landmark »coordinates« that led to the significant and successfully interpretable Procrustes analyses here – but that the *schema* of the measurement, the list of individual distances and angles, is not an appropriate tool for scientific analyses,

because, among other reasons, morphometric differences (allometry, size, shape, etc.) are not subtle but rather fundamental effects and have to be captured by the method applied.

In the present data set, the role of the cephalometric »analysis« was in effect to serve as an indirect digitisation of five landmark locations. In that case, there could have been a great many more than five shape coordinate pairs – we could have commented on group differences or allometric trends in a variety of dental landmarks, for example, none of which contributed to more than one of the measures like those in Table 1, and hence none of which could be »digitised« like the large pentagon we used.

All the methods exploited here exist in versions for 3D data exactly paralleling these versions for 2D data. Some landmark points can be viewed in both lateral and postero-anterior cephalogram. The resulting analyses, by including information oblique to the lateral film, would greatly enrich the interpretability of any findings that emerge. There are also methods available for the Procrustes analysis of entire skeletal surfaces, including landmark points but also ridge curves and the smooth shells between^{17,18}. These would greatly enhance the visualization of large-scale processes such as normal growth or evolutionary change, at the cost of somewhat obscuring the small-scale features that are the subject of clinical orthodontic attention.

There are implications for prehistoric, palaeoanthropological and historical studies. Applications of geometric morphometric methods to historical or anthropological questions need to attend more carefully to issues of sample accrual. The role of Centroid Size is not limited to the Procrustes scaling it provides. It shapes the report of findings in at least the two further ways reported here: differences of size distribution among samples, and the

partition of shape differences into its allometric and non-allometric parts, with appropriate attention paid to both within-group and among-group factors of each (see reference 19). Furthermore, any reconstructed censoring of samples, at the time of the specimen's life or the time of the study's execution, can interact with these size and size allometry effects just as it can with the more familiar range of purported findings of Procrustes shape coordinates per se. The present study, for instance, might be elucidated by comparisons between conscription patterns of the 19th-century Hapsburg Imperial (*Gesetz der Erfüllung der Wehrpflicht, 1868*)²⁰ and 20th-century Austrian armies (*Bundesgesetzblatt Nr. 368, 1975*)²¹.

That is the negative message of this analysis. The positive message is that the contemporary methods of geometric morphometrics have progressed far enough beyond the standard anthropometrics of the applied craniofacial sciences to make a material difference for the strength of the associated scientific research findings. Within a large suite of familiar distances and angles showing no group differences whatever, we were able to find enough geometric information that, properly rearranged (into shape coordinates), a signal emerged of strikingly high amplitude: a signal, to be sure, dealing with size, size shift, and size allometry effects, but a signal nonetheless. Analyses of conventional cephalometric measures should

be replaced by digitized coordinates of landmarks (and semilandmarks)^{18,22,23} whenever the context is one of a scientific investigation. That is not to say that landmark coordinate data are a panacea. In the present study, the Bronze Age sample size was simply too small for any findings whatever to be reported, by scalars, shape coordinates, Centroid Size, or any other approach.

In their everyday practice, orthodontists will continue to rely on traditional measurements for both diagnosis and individual treatment planning, but where multiple explanations are to be combined (here, secular change, size allometry, and principal components, as in Figure 4), it is best to turn to the methods that were developed for precisely such scientific contexts, not the essentially case-by-case world of clinical orthodontics.

Acknowledgements

We thank Otto Vysložil, Klosterneuburg, and Markus Bernhard, Institut für Anthropologie, Vienna, for help with organising the data, Maria Teschler-Nicola, Natural History Museum, Vienna, for permitting access to those skulls in her custody that were used in this study, two anonymous referees for their valuable comments on an earlier version of this paper, and Horst Seidler, Institut für Anthropologie, Vienna, for having brought this group together.

REFERENCES

1. WOLANSKI, N., *Coll. Antropol.*, 2 (1978) 69. —
2. ULJASZEK, S. J., F. E. JOHNSTONE, M. A. PREECE (Eds.): *The Cambridge encyclopaedia of human growth and development.* (Cambridge University Press, Cambridge, 1998). —
3. BODZSAR, E. B., A. ZSAKAI, *Coll. Antropol.* 26 (2002) 477. —
4. SMITH, G. B., S. M. GARN, W. S. HUNTER, *Angle Orthod.*, 56 (1986) 196. —
5. CARLSON, D. S., *Am. J. Phys. Anthropol.* 45 (1976) 467. —
6. VARELA, J., *Europ. J. Orthod.*, 14 (1992) 31. —
7. GEYER, E., *Skelette aus dem frühbronzezeitlichen Reihengraberfeld bei Hainburg a.d. Donau.* In: BENINGER, E., F. MÜHLGHOFER, E. GEYER (Eds.): *Das frühbronzezeitliche Reihengraberfeld bei Hainburg-Teichtal* (*Mitt. d. Anthropol.* 60, 1930). —
8. MCNAMARA, J. A.: *An atlas of craniofacial growth.* Monograph No. 2. (University of Michigan, Ann Arbor, 1974). —
9. GOODALL, C. R., *J. R. Stat. Soc. B35* (1991) 285. —
10. ROHLF, F. J. J. *Classif.*, 16 (1999) 197. —
11. BOOKSTEIN, F. L.: *Morphometric tools for landmark data: Geometry and biology.* (Cambridge University Press, Cambridge, 1991). —
12. MARCUS, L. F., M. CORTI, A. LOY, G. J. P.

- NAYLOR, D. E. SLICE (Eds.): Advances in morphometrics. (Plenum Press, New York, 1996). — 13. DRYDEN, I. L., K. V. MARDIA: Statistical shape analysis. (Wiley, Chichester, 1998). — 14. SCHAEFER, K., H. SEIDLER, F. L. BOOKSTEIN, H. PROSSINGER, D. FALK, G. CONROY, In: FALK, D., K. R. GIBSON, (Eds.): Evolutionary anatomy of the primate cerebral cortex. (Cambridge University Press, Cambridge, 2001). — 15. LINDGREN, G., In: ULJASZEK, S. J., F. E. JOHNSTONE, M. A. PREECE (Eds.): The Cambridge encyclopaedia of human growth and development. (Cambridge University Press, Cambridge, 1998). — 16. MOYERS, R. E., F. L. BOOKSTEIN, Am. J. Orthodont., 75 (1979) 599. — 17. ANDRESEN, P. R., F. L. BOOKSTEIN, K. CONRADSEN, B. ERSBØLL, J. MARSH, S. KREIBORG, IEEE Trans. Med. Imaging, 19 (2000) 1053. — 18. MITTEROECKER, P., P. GUNZ, F. L. BOOKSTEIN, Semilandmarks in three dimensions. In: SLICE, D. E. (Ed.): Developments in primatology: Progress and prospects. (Kluwer Academic/Plenum Press, Dordrecht, 2003). — 19. BERNHARD, M., K. SCHAEFER, P. GUNZ, P. MITTEROECKER, H. PROSSINGER, F. L. BOOKSTEIN, H. SEIDLER, Am. J. Phys. Anthropol., 120 S36 (2003) 65. — 20. Gesetz vom 5. Dezember 1868, womit für die im Reichsrathe vertretenen Königreiche und Länder die Art und Weise der Erfüllung der Wehrpflicht geregelt wird. (Druck und Verlag der k.k. Hof- und Staatsdruckerei, Wien, 1868). — 21. Bundesgesetzblatt Nr. 368; Wehrgesetz. (Austrian code of law Nr. 368) (1975). — 22. BOOKSTEIN, F., K. SCHAEFER, H. PROSSINGER, H. SEIDLER, M. FIEDER, C. STRINGER, G. W. WEBER, J.-L. ARSUAGA, D. SLICE, F. J. ROHLF, W. RECHEIS, A. J. MARIAM, L. MARCUS, Anat. Rec. 257 (1999) 217. — 23. BOOKSTEIN, F. L., P. GUNZ, P. MITTEROECKER, H. PROSSINGER, K. SCHAEFER, H. SEIDLER, J. Hum. Evol., 44 (2003) 167. — 24. SLICE, D. E., F. L. BOOKSTEIN, L. F. MARCUS, F. J. ROHLF: A glossary for geometric morphometrics. ([http://life.bio.sunysb.edu/morph/bibliographies and glossary](http://life.bio.sunysb.edu/morph/bibliographies_and_glossary), 1998.) — 25. WEBER, G. W., K. SCHAEFER, H. PROSSINGER, P. GUNZ, P. MITTEROECKER, H. SEIDLER, J. Physiol. Anthropol., 20 (2001) 69.

E. Jonke

Kieferorthopädische Abteilung, Universitätsklinik für Zahn- Mund- und Kieferheilkunde, Währingerstrasse 25A, Vienna, Austria

KRANIOMETRIJSKA USPOREDBA LUBANJA RAZLIČITIH VREMENSKIH RAZDOBLJA – BRONČANO DOBA, 19. STOLJEĆE I DANAŠNJE VRIJEME

S A Ž E T A K

Cilj ove studije bio je procijeniti sekularni trend putem ortodontskih mjerenja lateralnih kranioograma. Korišteni su rendgenogrami triju populacija: 22 lubanje iz brončanog doba iz groblja blizu Hainburga (Austrija), lubanje 140 vojnika koji su služili u vojsci Habsburške monarhije koncem 19. stoljeća, te 154 današnjih vojnika Savezne Austrijske vojske. Korištenjem standardnih morfometrijskih analiza, nisu nađene statistički značajne razlike među uspoređivanim uzorcima. Primjenom geometrijske morfometrije u 2D koordinatama pentagona kojeg sačinjavaju kranio metrijske točke: sela, nasion, articulare, gonion i menton, pronađene su neke biološki interpretabilne razlike, pri čemu se mogla primijetiti samo razlika u veličini alometrije među populacijama 19. i 20. stoljeća. Autori zaključuju kako kranio metrijske točke trebaju biti direktno digitalizirane (i puno veći broj njih) te da standardne metode koje se koriste u kliničkoj ortodonciji nisu adekvatne za traženje odgovora na znanstvena pitanja kakva su ovdje postavljena.

Appendix: Glossary

Explanations below are mainly taken from references 24 and 25.

Superimposition (Procrustes) methods superimpose a sequence of specimens so that corresponding landmarks match as closely as possible according to an optimality criterion. In this process, size, position and orientation are partialled out and differences in shape are recorded as residuals from the reference shape. The residuals can also be graphed as displacement vectors at each landmark. In numerous software packages there are least squares and resistant-fit methods available.

Procrustes residuals: The set of vectors connecting the landmarks of a specimen to corresponding landmarks in the consensus configuration after a Procrustes fit. The sum of squared lengths of these vectors is approximately the squared Procrustes distance between the specimen and the consensus in Kendall's shape space.

Shape coordinates: In the past, any system of distance-ratios and perpendicular projections permitting the exact reconstruction of a system of landmarks by a rigid truss. Now, more generally, coordinates with respect to any basis for the tangent space to Kendall's shape space in the vicinity of a mean form: see Procrustes residuals.

Centroid Size: One of the fundamental differences between geometric and traditional morphometrics is the way the size of objects is computed. In traditional methods this is done by using either one of the original variables or by computing

some multivariate estimate (e.g., PC1, Size Factor). Such estimates are allometric size estimates. They are correlated with random measurement error (noise) around original shape variables. In contrast, the size estimate used in Geometric Approach (Centroid Size) is computed using interlandmark distances. Centroid Size is the square root of the sum of squared distances of a set of landmarks from their centroid, or, equivalently, the square root of the sum of the variances of the landmarks about that centroid in x - and y -directions. Centroid Size is used in geometric morphometrics because it is approximately uncorrelated with every shape variable when landmarks are distributed around mean positions by independent noise of the same small variance at every landmark and in every direction. Centroid Size is the size measure used to scale a configuration of landmarks so they can be plotted as a point in Kendall's shape space.

Centroid Size can be used in conjunction with shape variables (shape coordinates, residuals from procrustes analysis). It can be used to 1) measure size differences among specimens or groups, and 2) evaluate allometric patterns.

Relative warp analysis is a modification of principal component analysis for shape coordinate data. A relative warp is an eigenvector of the matrix of variances and covariances of the Procrustes shape coordinates. When principal components are computed using covariances in this

way, sums of squared differences of scores preserve the underlying original geometry of Procrustes distance.

Thin Plate splines compare the shape differences between two landmark configurations. Bookstein (1991)¹¹ proposed the thin-plate spline interpolation formalism to visualize the differences in the positions of the landmarks by modeling the deformations taking place between the landmarks; i.e., in all regions without landmark points. Imagine a combination of landmarks printed on a thin plate and compare it with a second combination of landmarks, supposing that the differences in coordinates are taken as vertical displacements of this plate perpendicular to itself, one Cartesian coordinate at a time. The energy necessary to deform the plate at each landmark is the so-called bending energy. And, as the bending energy is highest for the most local deformations, its minimization in all the non-landmark areas models their position. Interpolants modeling such plate deformations are called thin plate spline functions.

They are, first, a convenient solution to the problem of interpolation by constructing continuous deformation grids for data in the form of two landmark configurations (which could be the consensus configurations of the two populations under discussion) and, second, the basis for sophisticated analyses of shape difference like Relative Warps Analysis of these two configurations.

Eigenvalues: The eigenvalues λ_i of a matrix \mathbf{A} are solutions to the *eigenvalue equation* $\mathbf{A}\bar{e}_i = \lambda_i\bar{e}_i$. In other words, one looks at those vectors \bar{e}_i that do not change direction (but possibly length) when mapped by the matrix \mathbf{A} . If all eigenvalues are different, the eigenvalue spectrum is said to be non-degenerate. For a square, nonsingular $n \times n$ matrix, there are n eigenvectors and n eigenvalues, albeit with degeneracy possible. Of particular interest in geometric morphometrics are the eigenvalues and eigenvectors of the covariance matrix Σ . Even if all the entries in a matrix are real, some eigenvalues can be complex.