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Thin-Plate Spline Analysis of Allometry and Sexual Dimorphism in the Human Craniofacial Complex

Antonio Rosas* and Markus Bastir

Department of Paleobiology, Museo Nacional de Ciencias Naturales, 28006 Madrid, Spain

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ABSTRACT The relationship between allometry and sexual dimorphism in the human craniofacial complex was analyzed using geometric morphometric methods. Thin-plate splines (TPS) analysis has been applied to investigate the lateral profile of complete adult skulls of known sex. Twenty-nine three-dimensional (3D) craniofacial and mandibular landmark coordinates were recorded from a sample of 52 adult females and 52 adult males of known age and sex. No difference in the influence of size on shape was detected between sexes. Both size and sex had significant influences on shape. As expected, the influence of centroid size on shape (allometry) revealed a shift in the proportions of the neurocranium and the viscerocranium, with a marked allometric variation of the lower face. Adjusted for centroid size, males presented a relatively larger size of the nasopharyngeal space than females. A mean-male TPS transformation revealed a larger piriform aperture, achieved by an increase of the angulation of the nasal bones and a downward rotation of the anterior nasal floor. Male pharynx expansion was also reflected by larger choanae and a more posteriorly inclined basilar part of the occipital clivus. Male muscle attachment sites appeared more pronounced. In contrast, the mean-female TPS transformation was characterized by a relatively small nasal aperture. The occipital clivus inclined anteriorly, and muscle insertion areas became smoothed. Besides these variations, both maxillary and mandibular alveolar regions became prognathic. The sex-specific TPS deformation patterns are hypothesized to be associated with sexual differences in body composition and energetic requirements. Am J Phys Anthropol 117: 236–245, 2002.

Among the causes of variation in biological populations, sexual dimorphism is one of the most conspicuous (Hanken and Hall, 1993; Plavcan, 1994; Wood and Lynch, 1996). However, the integrated nature of the phenotype, in addition to the large morphological variability detected within populations, makes it difficult to identify the causes that control the expression of these features, in particular those directly or indirectly related to sex. Analysis of sexual dimorphism in primates has been approached from many different perspectives: the theoretical and methodological aspects derived from the quantification of sexual dimorphism in fossil and extant species (e.g., Plavcan, 1994; Marini et al., 1999; Rehg and Leigh, 1999), the relationship of sexual dimorphism to ecological and behavioral patterns (Clutton-Brock, 1985; Borgognini and Repetto, 1986), and the typological diagnosis of discrete characters in forensic anthropology and archeological demographic studies (Acsádi and Nemeskéri, 1970; Koski, 1996; Graw et al., 1999; Haun, 2000; Hill, 2000). From the evolutionary point of view, developmental processes leading to shape differences between sexes are often considered in terms of allometry and heterochrony (Leutenegger and Cheverud, 1985; Shea, 1988; Wood et al., 1991; Anemone and Swindler, 1999).

In spite of this corpus of knowledge, the identification of morphological features associated with sexual dimorphism still presents great difficulty (e.g., see Koski, 1996; Loth and Henneberg, 1996; Donelly et al., 1998; Graw et al., 1999; Haun, 2000; Hill, 2000). In paleoanthropological studies, variability patterns of fossil populations are mostly unknown, making it difficult to determine to what extent sexual dimorphism is responsible for the variation detected in fossil samples (Johanson and White, 1980; Trinkaus, 1980; Wolpoff, 1980; Heim, 1983; Frayer and Wolpoff, 1985; Liebermann et al., 1988; Rightmire, 1993). An important component of this uncertainty is the effect of size and sex on shape.

Size is a major factor influencing sex differences in the human craniofacial complex (Hall, 1982; Uytterschaut, 1986; Wood et al., 1991; Wood and Lynch, 1996). In particular, size modifies, to a certain de-

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*Correspondence to: Antonio Rosas, Department of Paleobiology, Museo Nacional de Ciencias Naturales, C/ José Gutierrez Abascal 2, 28006 Madrid, Spain. E-mail: arosas@mncn.csic.es

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gree, the differential development of bony superstructures, e.g., the presence of superciliary arches, a projecting glabella region, the eversion of the gonion region in the mandible, the prominence of the inion, the size and orientation of the mastoid processes, and aspects of robusticity (Acsádi and Nemeskéri, 1970). However, the difficulty of isolating size and shape has always been an unsolved problem in morphological approaches to sexual dimorphism. Traditional methods have difficulty isolating size and differentiating the shape variables which depend directly on size (allometry), from those (if any) which depend on sex. Thus, it is a goal of osteology to separate within the morphological complex of an organism (or any of its anatomical parts) features of shape associated with size from those exclusively linked to sex.

New methods of geometric morphometrics, based on the analysis of landmark configurations, allow further in-depth investigation of morphological processes (Bookstein, 1991; Rohlf et al., 1996; Zelditch et al., 1992). Among these new alternatives, one of the most important is the possibility of extracting size and successive analysis of morphology in a "size-free" shape space (Rohlf, 1996). The method of thin-plate splines (TPS) (Bookstein, 1991) permits a quantitative shape analysis by means of taking into account a new series of morphological variables, the so-called "principal warps." This methodology is opening a new and promising direction for morphological analysis in anthropology (Bookstein et al., 1999; Spoor et al., 1999) which allows the multivariate and integrated study of morphological configurations instead of linear measurements (Bookstein, 1991; Richtsmeier et al., 1992). Nevertheless, while there is literature about morphometric studies of sexual dimorphism in different primate species (e.g., O'Higgins and Dryden, 1993; Richtsmeier et al., 1993), detailed studies on human crania are scarce and are based on relatively small sample sizes (Wood and Lynch, 1996). Biologically integrated shape analysis, as provided by geometric morphometric shape analysis of the entire human skull on large cranial samples, is consequently greatly needed.

The aim of this line of research was the exploration of the physiological and structural causes of form and its laws of variation. In this paper, we apply geometric morphometric techniques to craniofacial variation, exploring visually the effects and interrelation of size and sex within a modern human population. Thin-plate spline-derived shape variables (partical warp scores) were analyzed quantitatively by analysis of covariance (MANCOVA) in order to delineate precisely the independent influence of size and sex on form.

MATERIALS AND METHODS

A human sample of 52 adult females and 52 adult males of known age and sex was studied (mean age of females, 33 years; mean age of males, 35 years; total age range in both subsets, 21–50 years). The material is housed at the osteological collection of the Anthropological Institute of Coimbra University, Portugal (Rocha, 1995). A set of 29 three-dimensional (3D) craniofacial and mandibular landmark coordinates was recorded (Table 1). The landmarks were digitized using a MicroScribe 3DX digitizer and InScribe software for personal computers. The corresponding software, i.e., Morpheus et al. (Slice, 1998), was used for superimposition, and the TPS series (Rohlf, 1997, 1998a,b) was used for further geometric morphometric analysis.

Before the two-dimensional (2D) TPS analysis could be performed, the 3D data had to be transformed into a 2D coordinate matrix. Thus, in the 3D coordinate data of each subset (52 females and 52 males), a generalized least square (GLS) Procrustes

TABLE 1. Description of digitized landmarks, according to Martin and Saller (1959), except where described further[1]

No.	Landmark	Description
1	Glabella	
2	Nasion	
3	Rhinion	
4	Anterior nasal spine	
5	A-point	Deepest point on the curvature of the alveolar clivus in the median sagittal plane
6	Prosthion	
7	Infradentale	
8	B-point	Deepest point at the mandibular symphysis curvature (between landmark 7 and landmark 9
9	Menton	
10	Gnathion	
11	Vomero-sphenoid junction	(Richtsmeier et al., 1993)
12	Basion	
13	Ophistion	
14	Inion	
15	Ophistocranion	
16	Lambda	
17	Bregma	
18	R. alveolar point	Right posterior limit of the maxillary alveolar arc at the pterygo-alveolar suture
19	R. optic canal point	Most superior, medial, and anterior points of the optic canal (superior border of the posterior face)
20	R. inf. basal border	Rosas (1995)
21	R. preangular incisure	
22	R. gonion	
23	R. ramus flexion	See Loth and Henneberg (1996)
24	R. condylion	
25	R. mastoid tip	Most distal point at the mastoid process
26	R. mental foramen	Anterior limit
27	R. lingula mandibulae	Antero-lateral base
28	R. foramen ovale	Postero-lateral corner
29	Posterior nasal spine	

[1] Landmarks that are not in the median sagittal plane were taken at the right side of the skull.

superposition was carried out (Rohlf and Slice, 1990). The aligned specimens were then rotated into the median sagittal plane. From the 3D coordinate matrix, the z-coordinates were eliminated, which led to a complete 2D data set in lateral view. During that step, the missing data were replaced by the mean values of the corresponding landmark coordinates of the female or male subset. Afterwards, these data were used in the following geometric morphometric analysis with the TPS software series (Rohlf, 1997, 1998a,b).

Formal description of thin-plate splines (TPS) and partial warp analysis can be found in Bookstein (1991). Further summaries and applications in anthropology can be looked up in Yaroch (1996) and Bookstein et al. (1999).

We present here only a short methodological summary. The application of TPS in morphological studies provides a highly effective means of visualization, while the derivations of partial warp scores therefrom are powerful tools for statistical shape analysis. TPS works with an interpolation function, the function "U" in Bookstein (1991, p. 27), that can be used to describe shape differences as a deformation. The fundamental principle of TPS is the comparison of two different shapes by distortion of the first one. It serves as a reference and is called the "tangent configuration," while the compared specimen is termed the "target configuration." The deformation requires bending energy, which leads to exactly reproducible deformation patterns that can be visualized as grids, introduced first by Thompson (1917) and analyzed further in terms of partial warp scores (Bookstein, 1991).

The first step is a generalized least squares (Procrustes) superimposition (Rohlf and Slice, 1990) of all specimens leading to a grand mean configuration, i.e., the consensus shape. All objects are superimposed using translation, scaling, and rotation, with the aim of reducing the distances between homologue landmarks. Once the centroid for each specimen is calculated (Bookstein, 1991) as an additional landmark that corresponds to the gravitational center of the object, i.e., the mean (GLS) or the median (GRF) of all x- and y-coordinates of the individual, objects are translated on it by subtracting the centroid coordinates from each landmark of the corresponding individual. Then they have to be scaled and rotated in order to continue reducing the distances between the homologue landmarks of the specimens. At this step of scaling, when all landmark configurations are set to the same unit size, a factor called "centroid size" can be extracted. It corresponds to the square root of the sum of the squared interlandmark distances (Bookstein, 1991). "In absence of allometry" it is the only size measurement that is "uncorrelated with shape variation" (Bookstein, 1991, p. 97). The x- and y-coordinates of larger objects have to be scaled by larger factors than the coordinates of smaller ones in order to get scaled to unit size. Hence, for each specimen, one size measurement is yielded.

In the next step, the TPS function "U" is used to transform this mean configuration into each specimen of the data sample, yielding finally a set of partial warp scores (PW-scores) that define each specimen exactly in shape space (Bookstein, 1996; Rohlf, 1998). Projected into a linear tangent space, the shape variables can then be used in further conventional statistical procedures.

Biological form is therefore decomposed into shape, measured by PW-scores, and size, i.e., centroid size. TpsREGR (Rohlf, 1998b) was used to calculate the PW-scores, the uniform components, and the centroid size. The scaling factor alpha was set 1, and the shape space was projected orthogonally onto tangent space (Bookstein, 1996; Rohlf, 1996).

Construction of morphospaces

TpsPLS software (Rohlf, 1998a) uses partial least-squares analysis (Bookstein, 1991; Rohlf and Corti, 2000) for the visualization of the relationship between shape and other independent variables. It computes covariation among the variables, between the variables and the partial warps, and among the partial warps (Rohlf, 1998c). The independent variables in this study are centroid size and the sex factor. A 2D morphospace in a size-sex gradient was constructed in order to analyze the influence of these factors (size, Fig. 1; sex, Fig. 2) on variability in a modern human sample (Fig. 3).

Analysis of covariance

Generally, the analysis of covariance (ANCOVA) is applied for comparison of different group mean values that are influenced by a common third continuous variable, i.e., the covariate. The total variance (the sum of squares) of the dependent variable is therefore influenced by two factors, the grouping variable, on the one hand, and the covariate, on the other. ANCOVA identifies this differential influence and partitions the total variance into the corresponding parts.

The analysis of covariance is performed in two steps. The first step looks at the correlation between the dependent variables and the covariate. This correlation must not be different between the groups, which is formally realized by testing for parallelism. Finally, the amount of explained variance of the covariate is determined.

During the second step, the rest of the variance is tested for group differences. This results in a second amount of explained variance, which is now attributed to the actual effect of the group factor. The compared group means can therefore be considered "adjusted" or "corrected" for the covariate. Even though the computations become increasingly complex, the logic and nature of the computations do not change when there is more than one dependent variable at a time (MANCOVA).

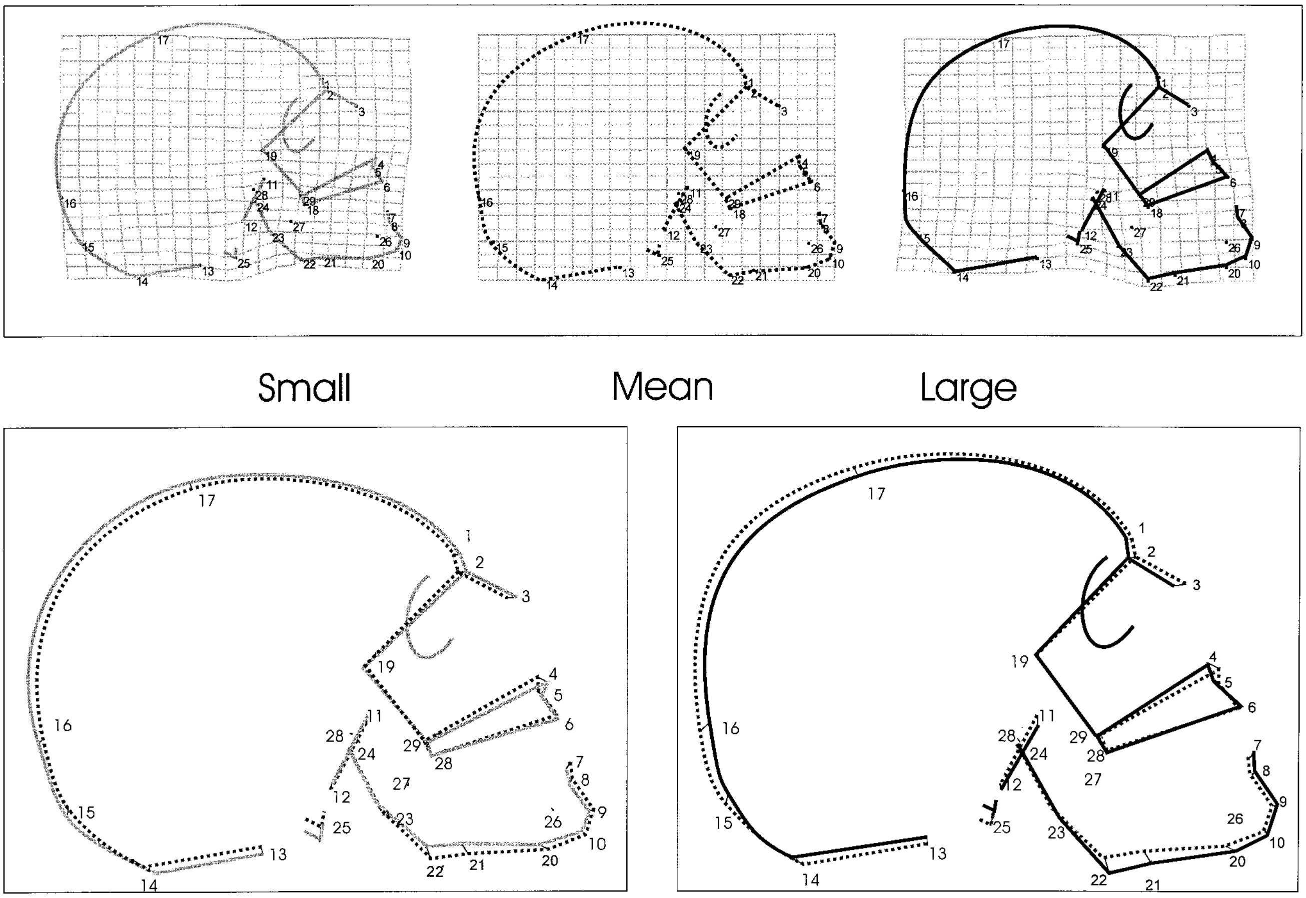

Fig. 1. Allometric shape changes. **Above:** Transformation grids are from mean centroid size (376.6) into a small individual (321.4) and into a large one (431.9), respectively. **Below:** Corresponding generalized least-square (GLS) superimpositions. With increasing centroid size, the subnasal clivus becomes enlarged and rotates counterclockwise; the increment of the mandibular ramus height leads to a more pronounced angulation at gonion; the antero-posterior dimensions of the splanchnocranium are reduced; the face is expanded supero-inferiorly; the face appears relatively larger than the neurocranium; and the braincase becomes more globular. (For definition of numbers, see Table 1.)

Applied to sexual dimorphism, and according to the hypothesis, some morphological differences between males and females are related to differences in size, which affects females and males in the same way. Other differences could be related strictly to the sex factor. When MANCOVA is applied to all shape variables, the total variance can thus be partitioned into those components of variance related to size, common to males and females (allometry), and into others related specifically to males, on the one hand, and to females, on the other. TpsREGR (Rohlf, 1998b) is used to visualize shape changes related to each of the above-mentioned steps of analysis of covariance.

Size and shape relationship: allometry

Centroid size is taken as the continuous predictor variable, a covariate, of the PW-scores. The variance of the PW-scores explained by the covariate reflects allometry. TpsREGR software permits the visualization of PW-scores of this part of explained variance. Their transformation pattern can be seen as a gradient along the x-axis in Figure 3.

Sex and shape relationship: sexual dimorphism

The remaining (residual) part of the variance is further analyzed and explained by the group factor “sex,” as well as by a final general error term. When the group factor is represented by dummy variables, the software displays shape changes (PW-warp scores) that are correlated with sexual differences, but that are now adjusted for the covariate, i.e., centroid size (y-axis in Fig. 3).

RESULTS

A GLS Procrustes mean configuration (Rohlf and Slice, 1990) of the whole data set was calculated. A TPS transformation of this mean shape into each specimen yielded a linear combination of partial warp scores for each individual that was used for subsequent statistical analysis. In order to analyze the independent influence of size and sex on human craniofacial shape variability, a MANCOVA of the partial warps scores was performed (StatSoft99). Taking into account size adjustments, the influence

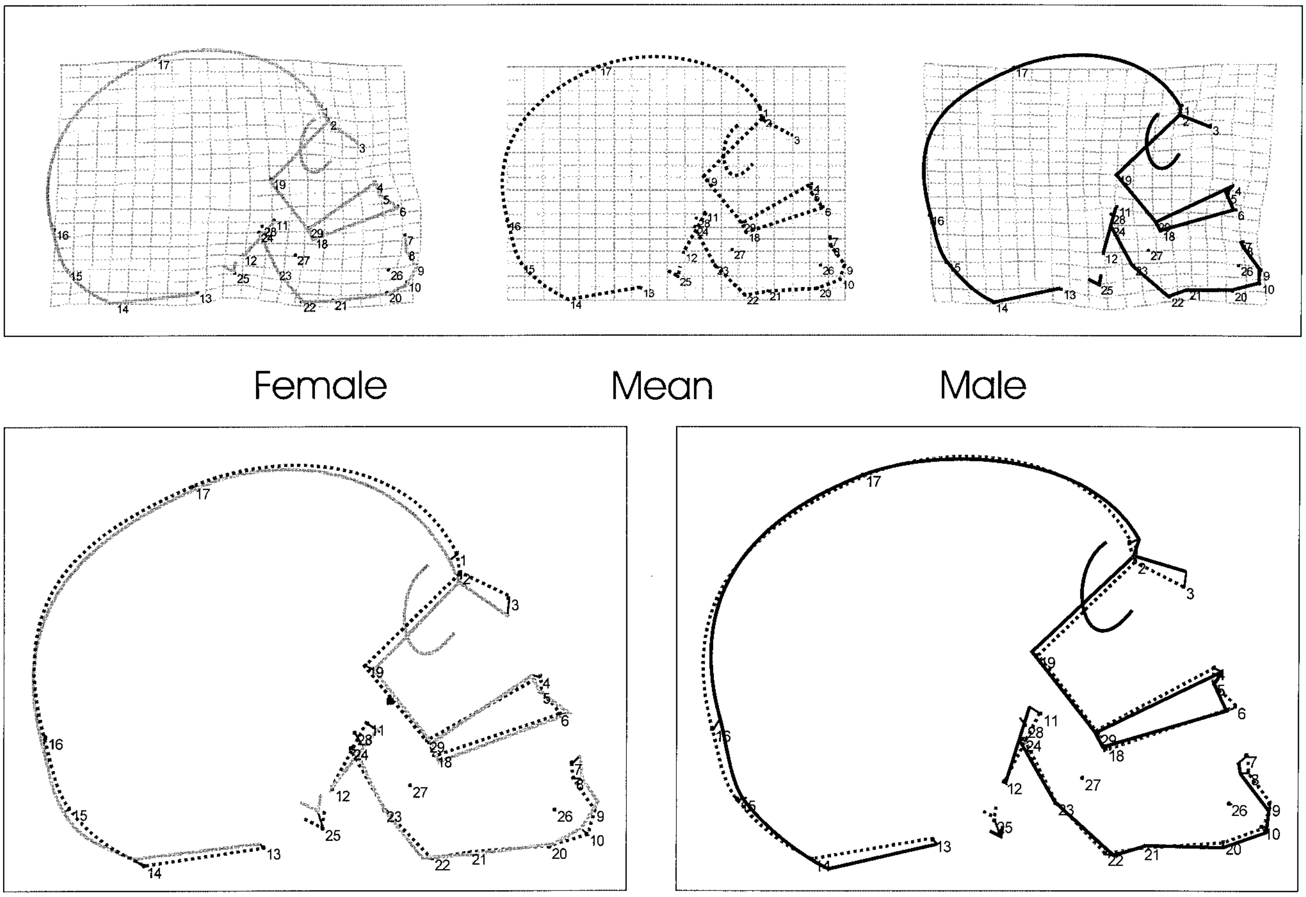

Fig. 2. Sex-specific shape changes. **Above:** Transformation grids (fivefold magnified) from the mean into a female and into a male, respectively. **Below:** Corresponding GLS superimpositions. In males, the nasoglabellar profile becomes curved and projecting, and the subnasal profile rotates clockwise. The nasal roof is elevated, and the nasal floor shifts downwards. The outer table of the occipital clivus rotates counterclockwise. The chin is lowered, and the gonial region gets strongly curved. At the occipital bone in males, the squamous proportion dominates over the nuchal area, and the whole basi- and neurocranium is deformed globularly.

of size on shape as well as the difference between male and female mean shapes was tested.

No difference in the influence of size on shape was detected in females and males (F = 0.9195; df = 54, 47; $P = 0.619$). There was no difference between the allometric pattern of the male and female subsamples. Therefore, only the main effects (size and sex) were used in the MANCOVA generalized linear model (Dobson, 1990). It was confirmed that both size (F = 2.8807; df = 54, 48; $P = 0.0001$) and sex (F = 1.9013; df = 54, 48; $P = 0.0125$) had significant influences on shape. Analysis of the corresponding sums of squares (Sokal and Rohlf, 1998) showed that the factor size explained 53.7%, and the factor sex 37.3%, of the total variance. Since size yielded significant influence on shape variation, the male and female means were also tested for statistical differences. Student's t-test showed that the male centroid size mean (386.4) was significantly larger than the mean of the female subset (366.5; t-value = 8.912; df = 102; $P = 0.000$).

TpsREGR (Rohlf, 1998b) facilitated the visualization of how the specific independent variables, centroid size and sex, were able to deform a given mean shape.

Allometry

The influence of centroid size on shape is shown in the TPS grids in Figure 1. The transformation pattern reveals a shift in the proportions of the neurocranium and the viscerocranium, with a marked allometric variation of the lower face. This is accompanied by a vertical increase of the maxillary alveolar process and mandibular ramus. As a result, the alveolar region becomes prognathic. At the same time, a downward location of the occipital clivus is observed as size increases. Landmarks of the occipital squama are displaced upwards in the profile of the neurocranium, while landmarks at the glabella region become relocated backwards (Fig. 1).

Sex

The magnified pattern of the sex-specific deformation of the mean configuration into a male individual shows, as the most eye-catching feature, an increase

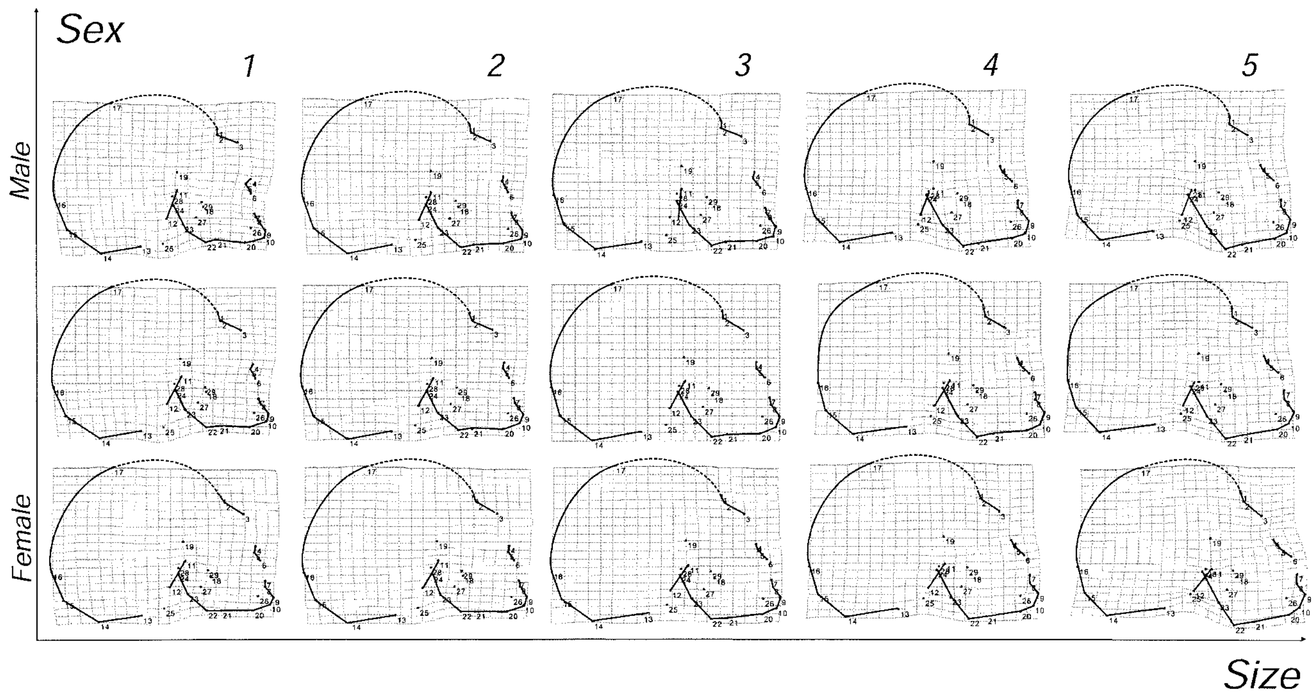

Fig. 3. Two-dimensional morphospace of allometry and sex. Centroid size increases along the abscissa. Female, mean and male shape trajectories are located along the ordinate. In the female and male gradients the individuals 2–4 are real specimens of the sample (minimum, mean and maximum centroid size). The specimens 1 and 5, and those of the middle section are theoretical shapes of extremely decreased or increased centroid size.

of the piriform aperture (Fig. 2). Morphologically, it is achieved by increased angulation of the nasal bones with respect to the pronounced glabella, and a downward rotation of the anterior nasal floor. On the other hand, the mean-female transformation is characterized by a nasal aperture that becomes more closed and a flattening at the glabella region. In addition, both the maxillary and mandibular alveolar regions become prognathic.

Sexual dimorphism is clearly expressed in the mandible, and several of its anatomical regions become affected in the transformations. The symphysis is retracted and the chin is more prominent in males. On the contrary, the whole symphysis acquires a more upward and forward location in females, giving rise to a more rounded chin and a smoother anterior profile. The mandibular basal border and the posterior border of the ramus are also considerably affected by the TPS transformation (Fig. 2). In males, the gonion relocates anteriorly, and the preangular notch is much more accentuated than in females. The position of the condyle is also anteriorly relocated in males and, together with the above-mentioned forward movement of the gonion, alters the curvature of the posterior border of the ramus. Reverse landmark displacements are found in the mean-female transformation. As a result, the basal border of the mandible appears smoother and the gonial region more flattened.

The occipital bone, at its neuro- and basicranial components, is strongly affected by the sex factor. The basilar part of the occipital clivus in males is rotated almost upright due to a postero-superior translocation of the vomero-sphenoid junction. As a result, the posterior face is anteroposteriorly expanded. Likewise, the mastoids as well as the inion project more downward in males. The region of lambda, at the same time, follows an upward and forward trajectory. When these displacements are considered together, it can be seen that the occipital squama appears more globular in males than in the mean configuration.

These analyses allow derivation of a number of morphological features useful for sex diagnosis in the skull: subnasal prognathism, nasoglabellar profile, projection of the mastoids, orientation of the occipital clivus, and the differential relationship of the relative proportions of the occipital squama and nuchal area of the occipital bone. Three features can be extracted for sexual diagnosis in the mandible: curvature of the anterior symphysis, development of the preangular notch, and flexion of the ramus. Once the effect of size is removed, this remaining set of features is specifically and directly related to the sex factor.

DISCUSSION

Allometry

Our results clearly confirm that the most general aspect of static allometry in *H. sapiens* relates to a shift of proportions between the neurocranium and the face, with positive allometry of the latter (Huxley, 1863; Aiello and Dean, 1991). This is the reason

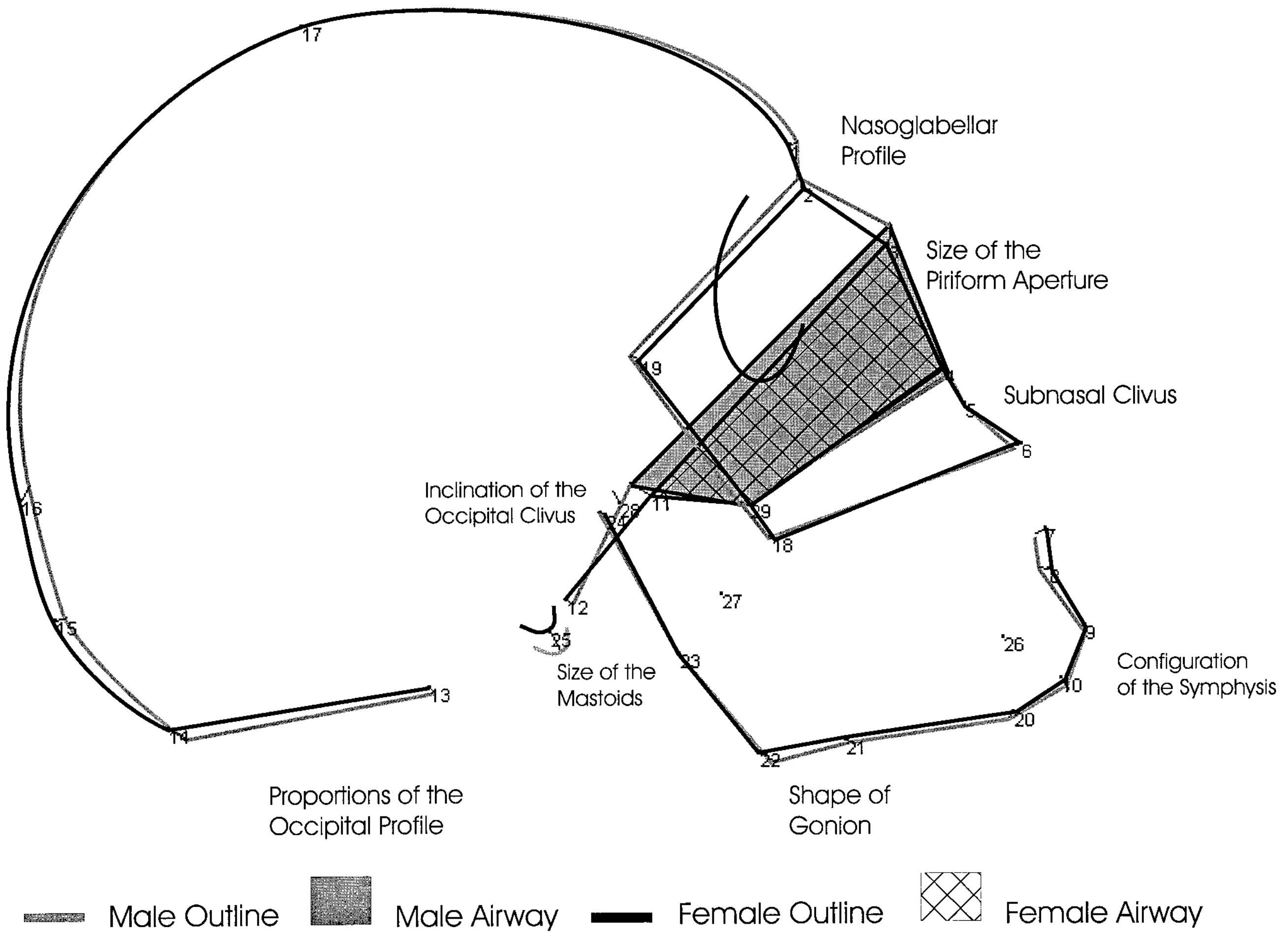

Fig. 4. GLS superimposition of increased male and female craniofacial profiles with equal centroid size (431). A structural (and not allometric) difference of the entire nasopharynx accounts for the increased airway dimensions in males. Also, the sites of muscular insertions (inion, mastoids, and gonion) show a sharper profile in masculine individuals.

why, in the allometrically increased version of the human skull (Figs. 1, 3), the neurocranium appears "smaller" than its original mean configuration, while the face appears proportionally larger.

Apart from the changes in relative size of the anatomical regions constituting the head, there are a number of changes in the orientation of these regions along the allometric series. One of the best-documented of these changes in orientation is the rotational movement of the mandible. During growth, the mandible rotates forward and upward (Moss and Salentijn, 1971; Björk and Skieller, 1972; Moore and Lavelle, 1974; Enlow and Hans, 1996). Positive facial growth allometry results in a forward rotation of the middle and lower parts of the face. A similar result is found in the static allometry and can be easily appreciated in Figure 3 by examining the nasal floor and basal border of the mandible. Even though this hypothesis was not considered in this study, a number of authors have claimed that allometric variation is produced by ontogenetic scaling: males and females share a common ontogenetic trajectory (Leigh and Cheverud, 1991). In addition, the positive allometry of the face co-occurs with various sorts of morphological phenomena, leading to a spatial reorganization of the craniofacial system. Variation in size, for instance, modifies the inclination of the occipital clivus, glabella and the occipital squama areas which also undergo changes in their relative positions.

Sexual dimorphism

Regarding the sex influence on shape, a clear effect was identified in this analysis. Figure 4 shows a female and a male outline of the same centroid size superimposed. For a similar centroid size of the whole skull, males present a relatively larger size of the naso- as well as oropharyngeal space. It can be demonstrated that the male nasal cavity is increased anteriorly (piriform aperture) and posteriorly (choanae). Also, the upper roof of the nasal cavity is expanded, and seems to follow, to a certain degree, the postero-inferior displacement of occipital landmarks. Two different lines of questions can be posed. On the one hand, one may question the possible factors that could explain an enlarged pharyngeal space. On the other hand, one can explore the morphological consequences of an enlarged pharyngeal space.

Starting with the first, analysis of human body composition shows a different pattern in the distribution of body fat, muscle mass, and bony tissue between males and females (Malina, 1978, 1996). Increased male body mass (mainly all muscle mass) and increased basal metabolic rates require an increased energy supply (Henry and Rees, 1991), which must be associated with an elevated oxygen input. Sexual differences in body size are reflected spirometrically, since for the same size and age in males, the pulmonary capacity is about 15% larger than in females (Silbernagl and Despopoulos, 1991). Owing to augmented energy requirements, male airway dimensions have to be increased, an argument that was already stated earlier (Enlow and Hans, 1996), in order to show the interaction between nasal characteristics and sexual differences in relative body and lung size. It seems that these physiological requirements can also be detected in this study by looking at the hard tissues. Figure 4 shows that not only the difference of discrete morphological characters can be seen, but also how the male shape of the whole pharyngeal region provides a larger volume of air intake than does the female shape.

Breathing by the nose, the increased nasal cavity corresponds to physiological needs, although it must be mentioned that in the living, the soft tissue of the nostrils would also play an important role. However, although not a subject of the present study, our supposition is corroborated by other researchers who stated that males tend to have "larger and more flaring nostrils" (Enlow and Hans, 1996, p. 130). On the other hand, breathing by the mouth, the enlarged oropharyngeal dimensions provide an increased air supply, as set by metabolic necessity.

In this context, all sexually diagnostic characters, as generally known and reported many times (e.g., Martin and Saller, 1959; Acsádi and Nemeskéri, 1970), and as related to the male muscle insertions, leave a more pronounced relief. Examples of these characteristics are found in the nuchal musculature at the inion, the sternocleidomastoid muscles at the mastoid processes, and the masseteric and pterygoid insertions at the mandibular angle. These, as do many others, seem to support the systemic evidence for the difference in the male muscle-energetic system.

According to this hypothesis, the physiologically increased requirement of air intake in males, which relates fundamentally to the enlargement of the naso- and oropharyngeal cavity, gives rise to sex-specific morphological consequences in the craniofacial complex.

The expansion of the nasopharyngeal cavity pushes the surrounding systems, resulting in a series of morphological consequences in the features that constitute these anatomical regions. Thus, the upward displacement of nasal bones, on the one hand, and the downward displacement of the nasal floor and the mandibular basal border, on the other, may be attributed to this effect. The net effect is a clockwise rotation of the lower face in male individuals (Fig. 2). In addition, a retraction of the upper border of the posterior face and a retraction of the basilar part of the outer table of the occipital clivus are also observed, which provides a backward displacement and a spatial expansion of the oropharyngeal soft-tissue attachment. Altogether, these architectonic reorganizations probably contribute to the above-mentioned expansion of the nasal and pharyngeal spaces.

To sum up, regarding sexual dimorphism, two opposing effects take part in the morphological variation of a modern human sample. On the one hand, allometry produces a counterclockwise rotation of the middle and lower parts of face. On the other hand, the sex-specific factor, described as an increment of the naso- and oropharyngeal cavity, produces, among other effects, a clockwise rotation of the lower face. How do both factors interact?

Interaction of allometry and sex

Once the sex-specific differences are identified and isolated, we are prepared to examine how allometry acts on shape and potentially modifies the expression of sexual dimorphism; in other words, the effect of allometry is extremely important because it may confound sex determination. The influence of size and sex on shape can be understood in a size-sex morphospace (Fig. 3). The interaction of these factors may be summarized in a constant principle: in both sexes, size increases the relative proportions of the face as compared to the neurocranium. Similarly, in all size classes, the effect of sex on shape increases the nasopharyngeal space and musculo-skeletal insertions. Despite the apparent simplicity of this principle, interesting synergic effects can be appreciated.

Naso-glabellar region. Two components can be distinguished in the variation of the naso-glabellar region: 1) increment of the frontal sinus, and 2) upward displacement of the rhinion. Allometry accentuates the relief of glabella, whereas an upward displacement of nasal bones occurs in males. Therefore, in large males both factors sum up in parallel, accentuating the sex condition of the features.

Piriform aperture and subnasal region. As previously noted, the sex effect produces a proportionally larger height of the piriform aperture. By contrast, the allometric effect tends to decrease the relative size of this aperture as a secondary result of the counterclockwise rotation of the middle and lower face; in the process, the subnasal clivus is elongated in a postero-superior direction. If we concentrate on the allometric increment of the mandible in the series, it can be seen that the subnasal region behaves allometrically, together with the lower face. As a consequence, the piriform aperture becomes relatively reduced. The morphology of the subnasal region suffers deformation as a result of the antagonistic effects of size and sex: males of a given size show a subnasal profile similar to that of slightly smaller females.

Symphysis. The profile of the symphysis is more marked in the female mandible, and the menton area is directed upwards. In addition, allometry of the mandible tends to project the basal symphysis forward and upward. In this way, the relief of the male symphysis is accentuated along the allometric series, while the combining effect of both factors results in a masking of female features as size increases.

Gonion and basal border. The mandibular angle displays sexual dimorphism, by an accentuation in males due to an antero-inferior displacement of the gonion, which shortens the length of the gonial region, and a very slight upward movement of the preangular notch under the sex factor. The allometric shape change is characterized by a downward displacement of the gonion and a downward and forward shift of the preangular notch. The combination of the effects of sex and size leads to a relative straightening of the inferior basal border in larger males, and an increased curving in large females because of the strong allometric downward component of the preangular notch. This structure seems to be related to the expansion of the nasopharyngeal cavity associated with the already-mentioned clockwise rotation. The converse effect of allometry in the mandible, with the counterclockwise rotation, tends to mask the (masculine) sex effect. However, since in larger individuals of both sexes the inferior border get straightened by allometry, the criterion of the length of the gonial region (short in males, longer in females, as defined by the antero-posterior location of the preangular incisure) gets masked.

Occipital clivus. An antagonistic effect is also detected in the orientation of the occipital clivus. Inclination of the occipital clivus varies in females and males. In the latter, the clivus adopts a much more vertical orientation. Thus, the visual prolongation of the clivus intersects the female outline at the level of the nasal bones, clearly below the glabella. On the contrary, virtual prolongation of the clivus in males crosses the frontal bone, above the glabella. However, allometry tends to displace the clivus downward and forward in the same direction as the mandibular ramus. Because of this, the clivus in large males is oriented in such a way that its virtual prolongation determines an intermediate position, more or less at the level of the nasion, thus precluding determination of sex on the basis of this criterion alone.

Mastoid process. A clear opposing effect in the mastoids is observed. While the mastoids are larger in males, allometry tends to reduce the relative projection of the mastoid process. Thus, the mastoids are reduced with respect to the level of the foramen magnum in large males. In contrast, in large females the mastoids are located at the level of the foramen magnum.

Occipital curvature. The position of the inion is affected by the sex factor, giving rise to a proportionally larger nuchal area in the females. The allometric effect amplifies the forward trend of lambda and stabilizes the position of the inion. This leads to an increase of globularity of the braincase in large males, with a larger squamous part. In females, the posterior trend of the inion explains the oval shape of large female braincases, characterized by enlarged nuchal areas.

To sum up, in sex diagnosis it is necessary to consider not only the features associated with sex, but also the influence of allometry on the expression of these features. Further knowledge of patterns of allometry will certainly clarify these extremes. Geometric morphometric methods allow a deeper insight into craniofacial sexual dimorphism in the human species. In particular, by completely removing size, it is possible to eliminate the deceiving effect of size in sexual dimorphism. Analyses of data used in this study have clarified some aspects of the relationship between size and sex in modern humans. They raise, nevertheless, a number of questions that should be addressed in future investigations. For example, how does the relationship between body composition and craniofacial morphology work in other human groups, extant primates, and fossil hominids? An exploration of well-documented samples in other species using this method is the next step in this line of research.

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