

Endocranial traits. Prevalence and distribution in a recent human population

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SUMMARY

A recent human population from Italy was analysed for the prevalence and expression of endocranial characters, as well as for the presence of some ectocranial epigenetic traits. The purpose was to provide a supplementary database for the characterisation of some features used to compare the variability of extant and extinct human groups. Many differences between males and females are the result of allometric trajectories, with males shifted to a larger size. In contrast, other features may be unrelated to size and thus interpreted as real sexual characters. The cranial base angle is slightly but significantly related to size, particularly to the vertical skull development. The digital impressions are more expressed in males but there is no evidence of a correlation with size. Arachnoid granulations show no relationship with sex, age or size. The middle meningeal vessels are extremely variable but with a general dominance of the anterior branch providing the parietal supply, and with the left system slightly more developed than the right. The middle meningeal pattern is not related to the venous sinuses pattern. Some further aspects of the expression of these features are discussed, and data for the prevalence of epigenetic traits are reported.

Key words: Endocranium – Cranial morphology – Discrete traits – Cranial base angle

INTRODUCTION

Most of the skull bones involved in neurocranial anatomy develop under the pressure of cerebral and other soft tissue growth (Moss and Young,

1960). Brain expansion originates gaps at the sutures separating the bones, inducing the activation of osteoblasts and ectocranial bone deposition on the outer table, while at the endocranial surface the osteoclasts promote a shifting of the structures (Enlow, 1990). The morphological correspondence between the endocranial cavity and cerebral surface (including vessels or circumvolutions) renders endocranial traits sensitive to the structural balance of the whole system. Hence endocranial anatomy represents an interface that can be used to characterise cerebral and cranial biomechanics and development, following principles based on forces and tensions. The meningeal layers (falx cerebri, falx cerebelli and tentorium cerebelli) work as a complex of biomechanical supports that control the developmental dynamics (Moss and Young, 1960; Jeffrey and Spoor, 2002).

The knowledge of this complex relationship between the skull and brain is the functional basis of paleoneurology, namely the study of the central nervous system in extinct taxa by means of their endocranial casts (Falk, 1987).

The purpose of this paper is to provide an updated reference for the prevalence and characterisation of some endocranial features in humans, using a recent population from central Italy (Rome) as a case-study. Inferences about sexual dimorphism, allometry, and correlations between single traits will be also discussed.

Brief overview of endocranial features

A primary consequence of brain growth (both in ontogeny and phylogeny) is reorganisation of the general skull architecture. In primates, basiscranial flexion is related to brain enlargement, but this process seems not to be completely active as a source of human variability (Ross and

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Henneberg, 1995; Jeffery and Spoor, 2002; but see McCarthy, 2001).

Information about the vascular networks can be related to cerebral functions and requirements, such as the energy supply and thermoregulation. The human brain consumes 20–25% of the basal metabolic energy, compared with about 8% in non-human primates (Leonard and Robertson, 1992), and it has relatively high thermal loads. The inner thermal control is effected by regulation of the blood input and output. The major endocranial vessel is the middle meningeal artery, a branch of the maxillary artery, stemming from the external carotid artery. The anatomical origin of the meningeal traces is not yet completely clear and the principal vessel joins a couple of parameningeal veins draining the diploe, dura mater and periosteum. The boundaries and variability of these vessels have not been defined, and their reciprocal relationship has not been explained at all (Falk and Nicholls, 1992). Here, they will be referred to generally as Middle Meningeal Vessels (MMV). An anterior network of the meningeal system supplies the frontal areas joining the superior ophthalmic vessels, while the MMV represent a posterior complex running throughout the fronto-temporal surface and draining into the pterygoid venous plexus (Saban, 1995). The anterior ramus (bregmatic) may be homologous to the anterior orbital branch of non-human primates (Diamond, 1991, 1992; Falk and Nicholls, 1992; Falk, 1993). A middle ramus (obelic) runs mainly to the parietal areas, while a posterior (lambdatic) ramus runs backward toward the occipital poles.

Many efforts to formalise a classification model of the MMV have yielded different results and no agreement has been achieved on this issue (see Marcozzi, 1942; Grimaud-Hervé, 1997). The simplest classification is that of Adachi (1928). It concerns the origin of the middle branch which can derive from the anterior ramus (type I), the posterior ramus (type II), or from both of them (type III); the frequencies of these patterns in modern human populations are 45%, 52% and 3%, respectively (Falk, 1993). However, data reported in the literature are often quite variable, depending upon the characters used to describe the MMV (shape, surfaces, branching pattern or vessels origin) but also upon subjective interpretations that are unavoidable given such marked variability.

Regarding the venous sinuses, it must be stressed that the endocranial venous drainage in catarrhines, unlike in most other mammals, runs principally to the internal jugular veins (see Kimbel, 1984; Saban, 1995; Grimaud-Hervé, 1997). The superior sagittal sinus receives venous flows from the MMV, the diploe, the pericranium and the cerebral vascular complex, by means of

direct junctions, capillary nets and anastomoses. At the confluence of sinuses, the superior sagittal sinus joins the transverse-sigmoid systems and the straight sinus from the deeper cerebral volumes, and the blood flow is divided and organised toward the jugular fossae or alternative pathways. Different classifications of the morphological variability have never managed to provide consistent results concerning the quantification and prevalence of these traits (see Romagna-Manoia, 1911; Grimaud-Hervé, 1997); once again, problems arise from the extreme individuality of patterns, subjective interpretations and difficulties of dissection techniques. The most common pattern in recent human populations has the large blood volume from the superior sagittal sinus flowing into the right transverse system (but see Navsa and Kramer, 1998). However, flow into the left transverse sinus or doubled flow is common (Kuroiwa et al., 1995).

Alternatively to the transverse-sigmoid systems, the occipital-marginal system can drain the main blood flow to the jugular fossa through the borders of the foramen magnum, representing a probable genetic-based marker (Falk and Conroy, 1983; Tobias and Falk, 1988; Kimbel, 1984). The prevalence of this trait in modern populations is about 6%, but in specific case-studies it reaches 45%. The presence of one of these two systems is not necessarily accompanied by the absence of the other. However, the absence of one of them necessarily requires the development of the other.

The speno-parietal sinus (Breschet's sinus) runs from parieto-sagittal arachnoid granulations to the cavernous sinuses, draining the dural, meningeal, diploic and anterior cerebral veins (Grimaud-Hervé, 1997). While an arterial groove enlarges downward, with branching and defined borders, the speno-parietal sinus gradually enlarges upward, with no arborisation and smoother boundaries. Anatomical confusion and morphological superimposition of this trait and the MMV make it difficult to detect the sinus, and many analyses have been biased by extreme variability (Saban, 1995). The speno-parietal sinus could be another genetic-based marker, although a relationship with structural constraints cannot be excluded.

Generally, the vascular systems are the result of a plastic interaction between function and morphology. Thus they fully correspond to the definition of "epigenetic" features, where the boundary between genetics and physiology cannot be completely resolved. Artificially deformed crania or synostotic skulls show responses to the morphological stress, revealing a large component of structural adaptability (O'Laughlin, 1996). For example, in deformed specimens the prevalence of an occipito-marginal system rises to

71%, or the internal jugular flow may be redirected to the vertebral plexus via the cranial base (Andeweg, 1996).

Nevertheless, it must be considered that endocranial marks are clearly correlated with cerebral surfaces, even though the association of characters is not complete. Large sinuses can leave only a weak trace on the endocranial surface (Mannu, 1911; Kimbel, 1984), depending upon the pressure and packing of the structures or upon the physical properties of the connective tissues. Therefore, caution must be taken when inferences about cerebral anatomy are based on endocranial traits, which mainly describe the variability of endocranial features and not of the corresponding cerebral structures. The advantage of this approach is its availability for many applications, most of all in epidemiological surveys, population biology, human paleontology and forensic sciences.

MATERIALS AND METHODS

The sample comes from the collections of the Museum of Anthropology "Giuseppe Sergi" at the

University "La Sapienza", Rome (Italy). The specimens, all adults, were collected and prepared at the beginning of the 20th century; at that time, they were sectioned transversely for visual inspection of the endocranial cavity (Fig. 1).

A total sample of 187 crania from this collection is considered here. Deformed or pathological specimens have been excluded. Sex was determined following Acsadi and Nemeskeri (1970; compare also Ferembach et al., 1979), while age at death estimations follow Lovejoy (1985), for dental wear, and Meindl and Lovejoy (1985), for ectocranial suture closure. The dental age is more precise but it is sensitive to environmental parameters. Thus it has been corrected by shifting the distribution according to the average indicated by sutural ages, which are less precise but theoretically more stable among different populations. Consequently, the sample consists of 87 females, 55 males and 45 indeterminate specimens. The average age is 41 ± 6 yrs for males, 39 ± 6 yrs for females and 41 ± 8 yrs for the indeterminate specimens, with an average pooled age of 40 ± 6 yrs (ranging from 32 to 64).

The endocranial features examined in this paper were characterised by discrete classes of



Figure 1.- Sectioned skulls showing the status of the sample used in this analysis.

expression for each trait. Anatomical structures are defined following Shapiro and Janzen (1960), Aiello and Dean (1990), and White (2000).

Digital impressions: expression of the circumvolitional grooves left on the orbital areas: light (hardly or not visible), clear (visible) or marked (extremely developed).

Arachnoid granulation presence: the frequency of parasagittal arachnoid granulations: absent (no granulations), present (few, scattered granulations) or frequent (many, widespread granulations).

Arachnoid granulation expression: low (hardly expressed), light (superficial), or deep (marked granulations).

Middle meningeal vessels pattern (left and right side): the branching model of the meningeal vessels: Adachi I, II and III.

Middle meningeal vessels dominance: greater expression (or equivalence) of the grooves of the right or left meningeal vessels.

Confluence of sinuses pattern: the sinusal pattern at the torcular herophili: doubled (trace of superior sinus running into both transverse sinuses), right or left (trace of superior sinus running into right or left transverse sinus), unclear (traces not well expressed).

Transverse-sigmoid dominance: greater expression (or equivalence) of the transverse-sigmoid system on the right or left side.

Transverse sinus expression: expression of transverse sinuses: light (hardly visible), clear (visible) or marked (deep).

Occipital sinus (OS): presence/absence of an occipital sinus running along the lower tract of the internal occipital crest.

Marginal sinus (MS): presence/absence of a marginal sinus running along the border of the foramen magnum, on the left and right side.

Spheno-parietal sinus (SPS): presence/absence of a spheno-parietal sinus running close to the inner trace of the coronal suture from a lateral lacuna to the middle fossa, on the left and right side.

Foramen of Vesalius (VF): presence/absence of an additional foramen antero-medial to foramen ovale, on the left and right side.

Clinoid processes: (CP): presence/absence of anterior and posterior bone bridges at the sella turcica.

Condylar canal (CC): presence/absence of a posterior condylar canal behind the condyle, on the left and right side.

Mastoid foramen (MF): presence/absence of a canal at the mastoid process, on the left and right side.

In order to characterise the general size and shape of the specimens, some metric variables were included in the analysis.

Glabella-Opisthocranium (GO): total length of the vault, from the most forward point of the frontal bone to the most posterior of the occipital bone;

Eurion-Eurion (EE): maximum width of the skull;

Basion-Bregma (BB): height of the skull, from the most anterior point of the foramen magnum to the crossing point between the sagittal and coronal sutures.

Cranial Module (CM): used as a size index, calculated as the mean of the three previous diameters.

Cranial Base Angle (CBA): calculated using the lengths of the sides of the triangle formed by foramen caecum, sella, and basion.

Table thickness: thickness of the bone layers at the right and left parietal bosses (RT, LT) and at the frontal bone (FT), at the midsagittal maximum curvature point.

Some ectocranial characters were also considered in order to add information about the whole structure and to correlate internal and external features.

Pterion pattern: the bone pattern at the pterion area, with fronto-temporal junction (FT), spheno-occipital junction (SO), epipterice bone (EP), or unclear fused area (nd), on the left and right side.

Ossicle/s at lambda (OL): presence/absence of wormian bones at lambda (parieto-occipital midsagittal junction).

Lambdoid ossicle/s (LO): presence/absence of wormian bones along the lambdoid suture (parieto-occipital sutures), on the left and right side.

Ossicle/s at asterion (OA): presence/absence of wormian bones at asterion (temporo-occipito-parietal junction), on the left and right side.

The distributions of quantitative characters were tested by Analysis of Variance, the Tukey and Bonferroni post-hoc tests, Student t-test, and Pearson correlation coefficient ($p < 0.05$). The distributions of discrete characters were tested by the Chi-square test and Pearson exact test ($p < 0.05$).

RESULTS

Table 1 shows the mean, standard deviation, minimum and maximum values for metric variables in the male, female and indeterminate specimens. The three main diameters are significantly larger in males than females, with the indeterminate specimens in an intermediate position. Consequently, the Cranial Module shows males having larger skulls than females. The Cranial Module is more related to the BB height ($r = 0.81$) than to the other two diameters.

The cranial base is more flexed in males than females, with intermediate values for the indeterminate group. There is a modest but significant correlation between CBA and CM ($p = 0.001$; $r = -0.25$). Fig. 2 shows the values of CM plotted against CBA (outliers were not discarded from

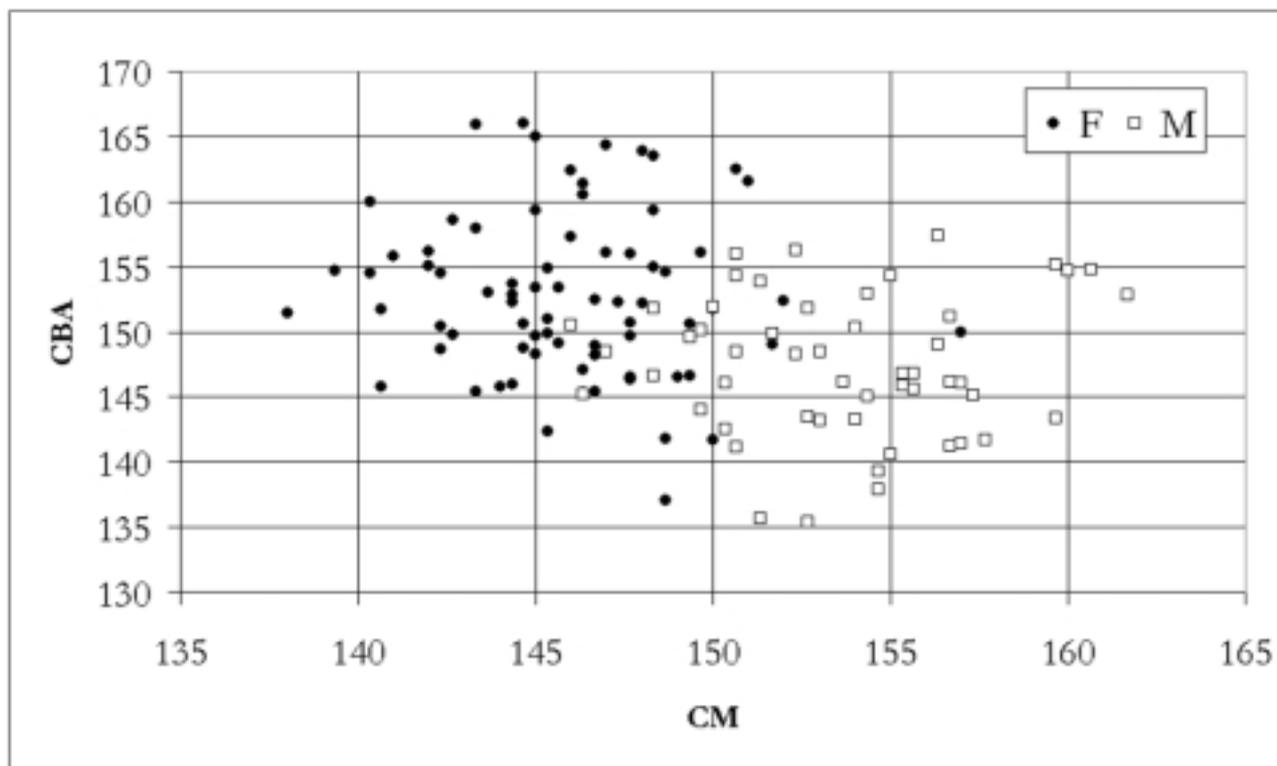


Figure 2.- Cranial Module plotted against Cranial Base Angle. Values are in mm. for CM and degrees for CBA. Outliers have not been excluded.

the analysis). Considering the main skull diameters, CBA is more dependent upon the BB height ($p=0.000$; $r=-0.35$). A discriminant analysis succeeded in separating the male and female skulls using the three principal diameters and CBA, showing that the BB height is the major discriminant variable.

There are no significant differences in bone thickness between the sexes or between the right and left parietal bosses. There is a slight correlation between the frontal and parietal thicknesses ($p=0.000$; $r=0.3$).

The distribution and prevalence of the discrete features are reported in Table 2 and Table 3.

Table 1.- Descriptive statistics of metric variables. Mean, standard deviation, minimum and maximum values are shown for the male, female and indeterminate (nd) specimens, and for the pooled sample. Values are in mm., except for CBA expressed in degrees. See the text for the abbreviations.

		GO*	EE*	BB*	RT	LT	FT	CM*	CBA*
<i>male</i>	Mean	183,5	142,5	134,7	5,8	6,2	7,2	152,7	148
	sd	5,3	6,3	5,8	1,5	1,4	1,6	7,2	5
	min	171,0	130,0	123,0	2,8	3,9	4,2	108,7	135
	max	194,0	160,0	156,0	8,7	10,5	11,2	161,7	157
<i>female</i>	Mean	175,2	135,6	126,5	6,0	6,3	7,6	145,8	153
	sd	5,6	4,9	5,0	1,5	1,5	1,7	3,3	8
	min	163,0	125,0	111,0	3,6	3,3	4,3	138,0	129
	max	190,0	153,0	138,0	11,8	10,0	11,4	157,0	180
<i>nd</i>	Mean	179,4	139,9	130,6	5,7	5,9	7,1	150,0	151
	sd	7,2	6,4	6,5	1,4	1,4	1,5	4,6	7
	min	164,0	125,0	116,0	3,4	2,8	4,6	142,0	136
	max	198,0	155,0	147,0	9,1	9,7	10,8	159,7	163
<i>TOT</i>	Mean	178,7	138,7	129,9	5,9	6,2	7,4	148,8	151
	sd	6,9	6,4	6,6	1,5	1,4	1,6	5,8	7
	min	163,0	125,0	111,0	2,8	2,8	4,2	108,7	129
	max	198,0	160,0	156,0	11,8	10,5	11,4	161,7	180

* differences between male and female are statistically significant.

When the differences between males and females are significant or even indicative, the frequencies are reported for both the pooled sample and each sex class. Otherwise, only pooled data are shown.

The sex differences in digital impressions are not significant, but indicative ($p=0.07$). There is a higher percentage of female specimens with only a light impression of the orbital circumvolutions, a condition rarely presented in the male phenotype. Therefore, males tend to show a stronger expression of this trait. No correlation was observed between digital expression and Cranial Module.

No particular distribution of arachnoid granulation presence was detected, nor is this variable correlated with CM. There is a moderate increase with age, but it is not significant. However, arachnoid granulation expression is more marked in males than in the other groups, with a higher percentage of deep traces. The pattern is not size-related.

The middle meningeal system is mainly characterised by a more developed anterior branch

accounting for the parietal vascularisation, although the other patterns are frequently represented. The correlation between the patterns on the two sides is highly significant ($p=0.000$), with the highest correspondence for Adachi type I and the lowest for Adachi type III (Fig. 3). A left dominance of the meningeal vessels is only slightly more frequent than a right dominance. The MMV pattern is not correlated with CM nor with sex.

At the confluence of sinuses, the sagittal sinus trace usually runs into the right transverse sinus. However, the percentage of cases with an unclear pattern is extremely high. The number of specimens in which the sagittal sinus runs into the left TS system is not high enough to test for significant differences, but males show a larger percentage of this pattern (15%) than females (5%). In contrast, differences in the TS system development are significant, with males showing a greater prevalence of left system dominance than females, the percentage being comparable

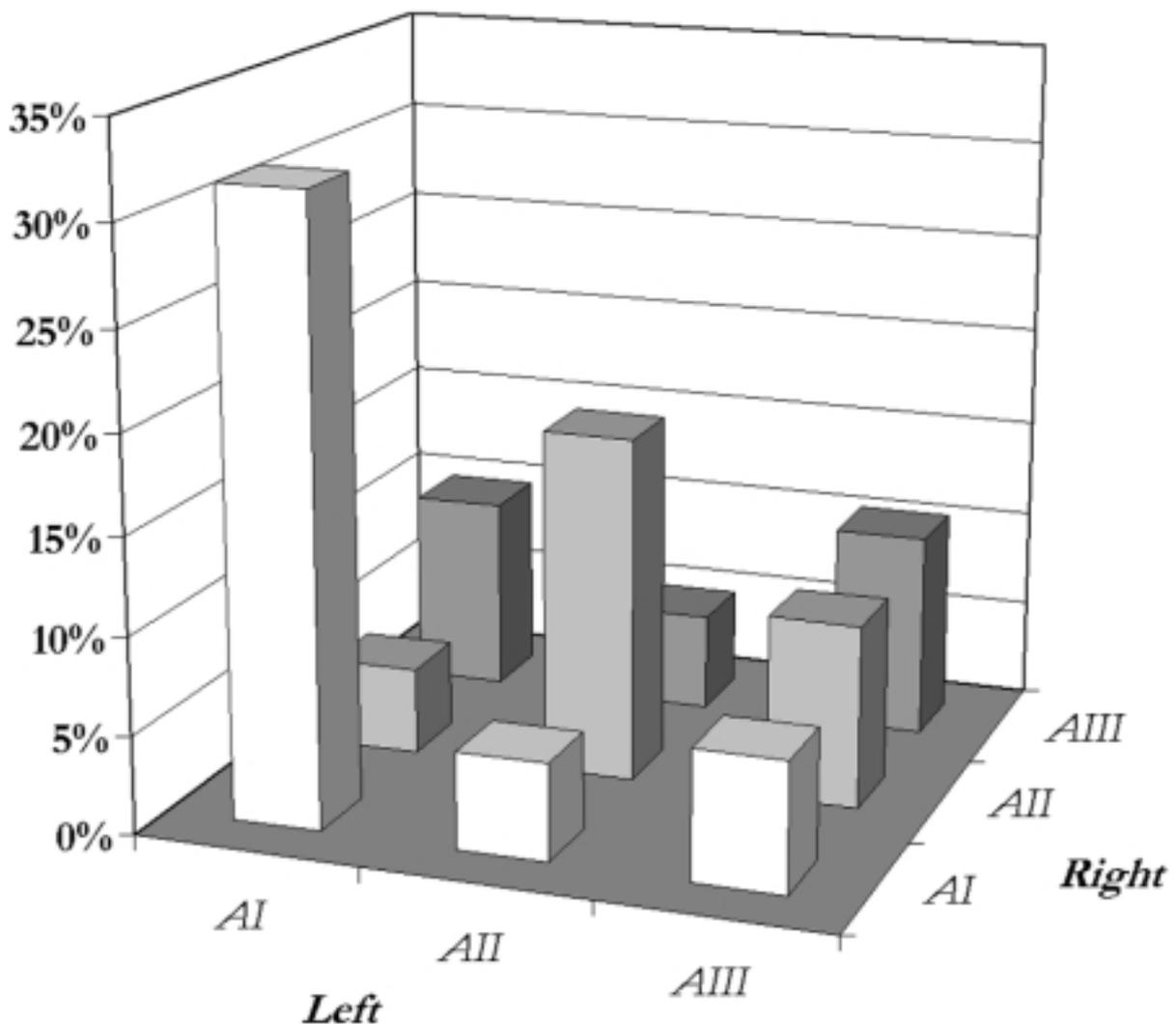


Figure 3.- Percentage of individuals presenting specific pairs of MMV patterns on the two sides. Types are referred to Adachi I (AI), Adachi II (AII) and Adachi III (AIII).

with that of right system dominance ($p=0.001$). Consequently, skulls with a more developed left TS system present a larger cranial size. There is no clear relationship between the pattern at the confluence of sinuses and the MMV dominance. The transverse sinus expression shows no particular distribution.

An occipital sinus trace was detected in 7% of the specimens. In the absence of an occipital sinus, a single marginal sinus occurs in 2% of specimens, while there are never paired marginal sinuses. In the presence of an occipital sinus, the prevalence of a single marginal sinus rises to 46% and that of paired marginal sinuses to 8%.

Marginal sinus traces on the right of the occipital foramen were detected in 3.8% of cases and on the left in 2.2%. The occipital sinus was found without a marginal sinus in 3.3% of specimens, with the right marginal in 2.2%, with the left marginal in 1.1% and with both marginal traces in 0.5% (1 case).

The prevalence of a sphenoparietal sinus shows some differences between males and females, which need to be discussed in detail. When the presence of probable sphenoparietal traces is considered, right prevalence is 14.3% for females and 30.8% for males ($p=0.06$), while left prevalence is 21.4% and 32.7%, respectively ($p=0.34$). This difference becomes significant when only clearly identifiable right sphenoparietal sinus traces are considered, with a prevalence of 5.3% for females and 16.3% for males. The difference in left sphenoparietal sinus traces is not significant but still marked, with values of 12.0% and 20.5%, respectively. A crossed analysis shows a matched probability of the two sides presenting a sphenoparietal sinus. In particular, the presence of a sinus on one side increases the prevalence of enlarged marks on the other side. No correlation with size was found.

There are no sex differences in the clinoid processes, although the posterior processes are slightly more frequent in females. Posterior processes are only found in association with fully developed anterior processes. The mastoid foramen tends to be more prevalent in males, 66% and 60% for the right and left sides, than in females, 56% and 45%, respectively ($p=0.08$ and $p=0.06$ for right and left prevalence between sexes). Moreover, this foramen is generally more marked in males. No particular distributions were found for the condylar and Vesalian foramina, nor for the presence of lambdatic and lambdoid supernumerary ossicles. The sex difference in wormian bones at asterion is not significant, although they are more frequent in males.

Table 4 shows the distribution of the pterion patterns. Epipteric bones are more frequent in females, although the difference is not significant because of the small number of specimens ($p=0.20$ and $p=0.15$ for the right and left sides).

Table 2.- Distribution of the sample in the classes described for each character. Percentages of female (F), indeterminate (N) and male (M) specimens are reported when significant or indicative. Otherwise, only the pooled data are presented.

Digital Impressions	<i>light</i>	<i>clear</i>	<i>marked</i>
F	13,1	46,4	40,5
N	8,9	48,9	42,2
M	1,9	56,6	41,5
pooled	8,8	50,0	41,2
Arachnoidal Granulations Presence	<i>absent</i>	<i>present</i>	<i>frequent</i>
pooled	22,7	64,6	12,7
Arachnoidal Granulations Expression	<i>low</i>	<i>light</i>	<i>deep</i>
F	20,2	63,1	16,7
N	28,9	55,5	15,6
M	23,1	42,3	34,6
pooled	23,2	55,2	21,5
Middle Meningeal Vessels	<i>type I</i>	<i>type II</i>	<i>type III</i>
right	42,9	31,3	25,8
left	45,9	27,6	26,5
mean	44,4	29,5	26,2
Middle Meningeal Vessels Dominance	<i>right</i>	<i>equal</i>	<i>left</i>
pooled	37,4	21,2	41,3
Confluence of Sinuses	<i>doubled</i>	<i>right</i>	<i>left</i>
pooled	15,4	46,2	7,1
Transverse-Sigmoid System	<i>right</i>	<i>equal</i>	<i>left</i>
F	67,1	18,8	14,1
N	60,0	15,6	24,4
M	41,5	17,0	41,5
pooled	57,9	17,5	24,6
Transverse Sinus Expression	<i>light</i>	<i>clear</i>	<i>marked</i>
pooled	43,4	40,7	15,9

Table 3.- Prevalence (%) of discrete endocranial and ectocranial traits (see text for abbreviations). Data for the left and right sides are reported along with the average value of both.

OS		7,1
MS	<i>right</i>	3,8
	<i>left</i>	2,2
SPS	<i>right</i>	20,5
	<i>left</i>	24,3
	<i>mean</i>	22,4
VF	<i>right</i>	20,7
	<i>left</i>	21,3
	<i>mean</i>	21
CP	<i>anterior</i>	30,1
	<i>posterior</i>	7,7
CC	<i>right</i>	63,9
	<i>left</i>	59
	<i>mean</i>	61,5
MF	<i>right</i>	56,8
	<i>left</i>	50,8
	<i>mean</i>	53,8
OL		16,9
LO	<i>right</i>	27,3
	<i>left</i>	23,5
	<i>mean</i>	25,4
OA	<i>right</i>	14,2
	<i>left</i>	13,7
	<i>mean</i>	14,0

Table 4. Percentage of individuals showing each pterion pattern (see text for abbreviations). Data for the left and right sides are reported along with the average value of both. The epipterion bone prevalence is reported for both males and females.

PTERION	EP	FT	SO	nd
<i>right</i>	9,3	1,1	77,0	12,6
<i>left</i>	10,4	1,6	74,9	13,1
<i>mean</i>	9,9	1,4	76,0	12,9

	M	F
<i>right</i>	5,7	14,1
<i>left</i>	5,7	15,3
<i>mean</i>	5,7	14,7

Mastoid foramen, pterion pattern and ossicle/s at asterion are significantly correlated with Cranial Module. A significant correspondence between left and right sides was found for the condylar, mastoid and Vesalian foramina, and the pterion and lambdoid patterns. The frequency of ossicle/s at asterion is too low to test for correspondence.

DISCUSSION

The primary aim of this paper was to provide an updated database for the prevalence and distribution of endocranial traits, for which information is scattered and heterogeneous. For those features known to present great variability, this study represents an additional source of information.

Sex was determined to distinguish between two basic phenotypes. From this perspective, what really matters in this study is not whether an individual was effectively male or female, but if it shows a male or a female cranial morphology. Hence, we use the terms “male” and “female” not to express an actual sexual state, but rather a fully expressed morphotype. Sexual dimorphism is the result of allometric and heterochronic trajectories (Shea, 1992), which are well characterised in primates (e.g. Leutenegger and Cheverud, 1982; Corner and Richtsmeier, 1991; Leigh and Shea, 1996, Bruner and Manzi, 2001). In humans, sexual dimorphism of cranial allometric patterns is well recognised as a major component of the variability of both ectocranial (Rosas and Bastir, 2002) and endocranial structures (Bruner and Manzi, nd), although a non-allometric component may provide an important contribution. In primates, males show a peramorphic component with respect to females, with longer ontogenetic trajectories; these are based upon the rate or timing of growth and are related to the hormonal

environment (Shea, 1992). Therefore, males and females share a common ontogenetic model, with the latter growing more slowly or for a shorter time. All those features determined by size-related constraints will be expressed only as a function of the final adult size.

Therefore, even indeterminate crania are useful, since they can be ascribed to a well defined phenotype, intermediate between a complete male or female characterisation. They may represent large females or small males, but what is really important is their intermediate position along the ontogenetic, sexually dimorphic scaling of the human cranium.

The metric variables confirm that males have larger cranial diameters than females. Among the three main diameters, the BB height seems to be the major size determinant, suggesting that the vertical direction of growth is the preferential or, at least, the most variable axis of development in modern human crania. Clearly, every size-related feature will also be sexually dimorphic, and every sex-related character will show a different size distribution. It must be stressed, however, that correlation does not necessarily mean causality; it may be the result of a common biological pattern or, conversely, the evidence of independent occurrences.

CBA is related to size, particularly to the skull height. It can be hypothesised that while the skull becomes higher, the whole structure is involved in this vertical stretching and not only the vault. Therefore, this process leads to a vertical separation of the anterior and posterior fossae. The cranial base links these two functional areas and becomes more angled as a consequence of this adjustment. Flexion of the cranial base is one of the principal changes accompanying increased brain size in primates, and thus it has been interpreted as a major evolutionary determinant (Gould, 1977; Ross and Ravosa, 1993). However, further studies of the relationship between brain size and CBA in humans failed to prove an intraspecific allometric pattern, suggesting that the modern human skull base may be less flexed than would be predicted by models based on non-human primates (Ross and Henneberg, 1995; Jeffery and Spoor, 2002). Nevertheless, the landmarks used in these approaches are not easy to define, and the results are often related to constraints in sampling techniques or analytical methods. For these reasons, the relationship between the cranial base angle and brain size in humans has not received an unequivocal interpretation (McCarthy, 2001). In the present study, we found a weak but significant correlation between flexion of the cranial base and the Cranial Module (used as a size index), led mainly by the vertical development of the skull. If size is related to basicranial flexion, males will show

a more flexed cranial base, while females will display a more platybasic skull.

A larger cranium does not correspond to thicker bone tables. Bone thickness is a hotly debated character which has been used to compare extinct and extant human populations, even in a phylogenetic context. Nevertheless, experimental data have demonstrated that this trait is extremely sensitive to physiological (individual) responses (Lieberman, 1996). Moreover, the variability of bone thickness within a single specimen is a source of further interpretative bias, and should be correctly formalised (see Zollikofer and Ponce de León, 2000).

The stronger expression of digital impressions in males than females (when confirmed) cannot be interpreted as the result of their larger cranial capacity. The anterior fossa grows by displacement, inducing an adjustment and rotation of the upper face, orbits and nasomaxillary complex (Enlow, 1990). At the end of the ontogenetic trajectory, some constraints could limit these rotational movements and force the orbital roof into contact with the brain (upward) and with upper facial structures such as the orbits (downward). On the basis of the common allometric relationship between volume and surface, it can be hypothesised that with higher volumes the contact between bone layers and cerebral structure would be tighter and the cerebral pressure might produce a deeper trace on the endocranial surface. Nevertheless, the data do not validate this model, and other interpretations will be required if a sex difference is confirmed.

The distribution of arachnoid granulations agrees with previous works showing a prevalence of 70-78% and a lack of significant correlation with sex, age or size (Koshikawa et al., 2000). In addition, males show more marked traces. Arachnoid granulations are produced by a local collapse of the dural layers, with a subsequent increase of cerebral pressure against the inner table. Therefore, if an allometric relationship continues to be excluded, differences in brain pressure or tissue structure might be taken into account.

Meningeal vessels are extremely plastic in their functional and physiological responses (Dean O'Loughlin, 1996), and many classifications demonstrate the heterogeneity of patterns and interpretations (see Grimaud-Hervé, 1997). Our results suggest a distribution in which the anterior branch is more frequently involved in parietal vascularisation, even though all the patterns are well represented, and the prevalence of left system dominance is only slightly higher than its counterpart. The correspondence between right and left MMV systems emphasizes a strong dominance of the anterior branch with respect to the posterior. The MMV patterns are

probably related to physical forces (minimum energy paths) and physiological constraints (energy requirements) of the brain surface, and not to direct genetic influences. Therefore, parietal vascularisation covered by both the anterior and posterior branches (Adachi type III) represents an intermediate phenotype more sensitive to cerebral asymmetries.

Although data from different sources are quite heterogeneous, the confluence of sinuses pattern in the present study confirms the predominance of a right TS system receiving most of the sagittal sinus flow, the low frequency of the opposite scheme and the large number of unclassified cases (Table 5). Both the pattern at the torcular herophili and the TS system asymmetry indicate a higher percentage of males with left dominance. The relationship between the right and left TS systems is determined mainly by the asymmetric development of the occipital lobes (Kimbel, 1984). Usually, the left occipital lobe is more developed than the right, leading to greater growth of the right transverse sinus which is less limited by cerebral pressure. If this mechanism can be used to explain the TS patterns, then differences in brain asymmetry could account for sex differences in TS balance. Moreover, there is no evidence of a correspondence between the sinus and MMV patterns, and the processes involved in the characterisation of these structures may be independent. In structural stresses such as artificial deformations or craniosynostosis, the meningeal vessels and sinuses are known to exhibit different, even opposite, physiological responses (Dean O'Loughlin, 1996).

The prevalence of the occipital sinus (7%) is in agreement with that found in most populations studied (Kimbel, 1984). Whether the trait is related to genetic factors or structural constraints, this value was expected for a generalised mixed sample. The low prevalence does not allow a valid statistical test of correspondence between the occipital and marginal sinuses (in particular for asymmetric patterns), but the raw data stress

Table 5.- Percentage of individuals showing a specific pattern at the confluence of sinuses: superior sagittal sinus running into the right transverse-sigmoid system (TSr), into the left transverse-sigmoid system (TSl), doubled (DD) or not described by the previous patterns (nd). Data are pooled from Romagna-Manoia (1911).

	TSr	TSl	DD	nd
<i>Sperino 1884</i>	52	15	7	
<i>Rudinger 1888</i>	70	27	3	
<i>Le Double 1903</i>	68	14		11
<i>Romagna-Manoia 1911</i>	40	17		36
this work	46	7	15	31

the marked dependence of the latter upon the former. This relation is not obvious because we are not dealing with the sinuses themselves but with their endocranial traces, which do not exactly represent the original soft tissues (Kimbel, 1984).

Our results for the sphenoparietal sinus provide prevalence values for a character whose distribution in modern populations has still not been investigated sufficiently. The correspondence between the right and left sides may reflect common structural or genetic processes for the expression of the two cerebral hemispheres. More interesting is the possibly higher prevalence in males, especially on the right side, since evidence of a size-related pattern is lacking. It has been hypothesised that this trait can be considered a genetic marker, with a high prevalence in extinct hominines such as the Neandertals (Saban, 1995; Grimaud-Hervé, 1997). However, structural influences cannot be excluded, and the functional role has still to be investigated.

Regarding the “epigenetic” or “non-metric” traits, the literature is full of exhaustive reviews (compare Hauser and De Stefano, 1989) and the analysis of discrete characters is beyond the scope of this paper. Nevertheless, we should mention the role of these features as potential markers of ontogenetic stresses on cranial structures, with some important consequences for modern variation and human evolution (Manzi and Vienna, 1997; Manzi et al., 1996, 1999, 2000).

The prevalence of the clinoid processes is comparable with the high values reported in the literature, but a higher frequency in males is not confirmed (Hauser and De Stefano, 1989). Moreover, posterior bridging is rare and usually only associated with the anterior processes. The mastoid foramen presence suggests a higher frequency in males, while the foramen of Vesalius, the condylar canals, the lambdatic and lambdoid ossicles do not show sex differences. Supernumerary ossicles at asterion tend to be more frequent in males. The pterion pattern variability confirms the results of previous studies, with low frequencies of the fronto-temporal junction (1.4%) and a tendency to a higher prevalence of pteric bones in females.

All the discrete characters analysed here show a significant correspondence between sides, with higher values for pterion morphology. Therefore, the presence of a character on one side increases the probability of finding it on the other side, without asymmetric tendencies. Despite a possible bias in the analysis related to the generally low prevalence of these features, such paired traits could be explained by a common genetic substrate and/or by a common physical/physiological environment. It is extremely difficult to separate these two

sources of variability and to test whether differences are the result of direct genetic influences or consequences of similar responses to general geometric rules, such as those involved in allometry or minimum energy paths of growth or asymmetry. All the features showing some sex difference are clearly related to size. What is difficult to assess is the nature of this relationship. Size could be the direct cause of their expression, or instead they both may be independent gender-related features.

Sexual dimorphism in humans and non-human primates is largely dependent upon size variations. Allometry and heterochrony are sources of variability based on common ontogenetic trajectories, in which the hormonal system exerts a major regulatory control. Yet the borderline between causes and effects can be difficult to recognise, and inferences must be based upon an integrative approach using anatomical, morphological and physiological data. Some endocranial features are easy interpretable as allometric patterns, while others show sexual dimorphism without a marked relationship with size. Many of these traits present a very low prevalence, and a large sample size is required to describe such morphological variability. Dependence upon the genetic background and ecological environment make these features even less characterisable and variable. A further bias is represented by the nature of the traits, i.e. often difficult to formalise and score. All these conditions have resulted in heterogeneous and controversial information about these characters. Therefore, our knowledge of them can be improved and developed only by the creation of a large database and the description of new samples.

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