

# Landmark-Based Analysis of the Morphological Relationship Between Endocranial Shape and Traces of the Middle Meningeal Vessels

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## ABSTRACT

The morphogenesis and evolution of the cranium are the result of structural interactions among its components, leading to covariance between traits. Soft and hard tissues exert a reciprocal physical and physiological influence, leading to the final phenotype in terms of both ontogeny and evolution. The middle meningeal vessels, interfacing the brain and the braincase, provide an opportunity to study this network, even in extinct human species. Between and within-species variations of the vascular patterns may be mechanically influenced by the cranial morphology (structural hypothesis) or else by actual physiological responses and adaptations, mostly related to oxygen supply and/or thermoregulation (functional hypothesis). In this analysis, we tested the relationship between neurocranial shape and the general morphology of the traces of the middle meningeal vessels in a modern human population, by using landmark-based geometrical models. Although there are some neurocranial differences between groups with different vascular patterns, they are very small or not statistically significant. Only the depth of the imprints may be more influenced by the endocranial morphology. Even if the neurocranial differences among extinct hominids are definitely larger than those within the modern species, the present analysis suggests that it is unlikely that the differences in vascular patterns among the human species are related only to the effects of different neurocranial geometry. This is rather relevant when the marked development of the meningeal network in *Homo sapiens* is taken into account, compared with the patterns described for nonmodern human species. Anat Rec, 292:518–527, 2009. © 2009 Wiley-Liss, Inc.

**Key words: functional craniology; middle meningeal artery; endocranial anatomy; neurocranial morphogenesis; paleoneurology**

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Neurocranial morphology is the result of structural and functional relationships between hard tissues (the bones of the braincase) and soft tissues (the neural mass, the meninges and the vascular network). These components exchange information during and after morphogenesis via biochemical and biomechanical signaling. Accordingly, the final neurocranial morphology is the result of fine tuning between the genetic background, the physiological responses, and the actual anatomical environment. The latter factor influences the morphogenetic process by means of forces, strains, tensions, and pressures (Moss and Young, 1960). This functional matrix must be carefully considered when dealing with hypotheses concerning the evolution of the anatomical components or with the morphogenesis of the cranial elements (Bruner, 2007).

The patterns of morphological integration within the cranial system have been successfully investigated in the last decade (e.g., Zollikofer and Ponce de León, 2002; Bookstein et al., 2003; Bastir and Rosas, 2005), but the current knowledge of their dynamics is far from exhaustive. Unfortunately, many hypotheses cannot be thoroughly tested because of the limited samples available (even when dealing with modern human populations), scarce embryological information or difficulties in interpreting the complex ontogenetic networks of causes and consequences. Indeed, although the skull is the main topic of many anatomical studies, we cannot rely on robust statistical inferences to understand its evolution even in our own lineage (Pearson, 2008). Although this problem hampers knowledge of the dynamics associated with the general cranial architecture, endocranial morphology is even more neglected in terms of patterns of variation and morphogenetic relationships.

One of the best examples of the limited information available on such anatomical districts is the middle meningeal artery (Bruner and Sherkat, 2008). This vessel is a branch of the external carotid artery, generally entering the endocranial cavity through the *foramen spinosum* (see Falk and Nicholls, 1992). It is basically divided into two main branches (anterior and posterior), providing three principal derivations named according to their orientation toward main ectocranial osteometric points: bregmatic, obelic, and lambdatic. This vascular system is often mixed with an anterior network passing through the cranio-orbital foramen (meningo-orbital artery) and through the superior orbital fissure (sphenoidal artery) (Diamond, 1991). The exact embryological development of these vessels is uncertain, as is the homology of these structures with the corresponding vascular districts in the great apes (Falk, 1993). Nonetheless, it seems probable that there is a lack of embryological correspondence between humans and nonhuman primates in the vascularization of the endocranial wall, with different contributions of the internal and external carotids (Falk and Nicholls, 1992).

The traces left by these vessels on the endocranial wall have been of major interest in paleoneurology, allowing some inferences on the brain vascularization in fossil specimens (Saban, 1995). Differences between modern and nonmodern humans were soon detected and described, suggesting specialization in both the extant and extinct species (Marcozzi, 1942). For example, many less encephalised groups show a more developed posterior network, while modern humans and Neandertals

have a dominant anterior branch (Grimaud-Hervé and Saban, 1996; Grimaud-Hervé, 1997). However, the variation of these traits is poorly known, also because of the difficulties in classifying and scoring the complex and reticulated geometry of the vascular systems. The more the classification is detailed (generally referring to the number and pattern of the bifurcations), the more it is subjective. In contrast, simpler and more generalized morphological classes can supply more testable hypotheses, but they clearly provide more superficial information. One of the most accepted classification methods is that of Adachi, based on the origin of the middle (obelic) branch: from the anterior ramus (Type 1), from the posterior ramus (Type 2), or from both (Type 3) (Fig. 1). Nonetheless, even such a simple scoring method has yielded very different results, suggesting a marked populational variability or a bias associated with the method's reliability (see Grimaud-Hervé, 1997; Bruner et al., 2003a). It must also be considered that the traces on the endocranial walls cannot always be interpreted as arterial channels, possibly being the imprints of the parameningeal veins associated with the arterial network (see Falk, 1993).

Modern humans are characterized by a definite increase of the reticulation (number of vessels and anastomoses), mostly on the parietal surface by means of the obelic system (Saban, 1982, 1995). The degree of vascularization of these traces was recently quantified using a fractal analysis, providing numerical evidence of the differences recognisable on fossil endocasts (Bruner et al., 2005). Although some nonmodern specimens display a modern-like pattern (Bruner, 2009), the variation within the present and extinct species is definitely different. Secondly, the degree of vascular complexity is not related to the cranial capacity or to the antiquity of the species, taking into account that Neandertals and *Homo erectus* show a similar degree of reticulation.

Because of the tight morphogenetic relationship between endocranial soft and hard tissues, these variations may not necessarily be the results of physiological adaptations and differences. The brain tensors deriving from the meningeal layers, namely the *falx cerebri* and *tentorium cerebelli*, are one of the principal structural determinants of neurocranial morphogenesis (Moss and Young, 1960). Attached to five main endocranial areas in a pentagonal organization (*crista galli*, sphenoid wings, petrous pyramids), they redirect the growth forces associated with brain expansion, shaping the neurocranial morphology. The strain distribution associated with these tensors is thought to directly influence the pattern of growth and development, with dismorphologies (like craniosynostoses) possibly related to atypical spatial organization of the meningeal attachments (Moss, 1959). Although the meningeal vessels have a physiological role (blood flow), their channels are intimately associated with the meningeal sheets, suggesting probable structural constraints.

Hence, the vascular differences between human species results can be interpreted by both a functional and a structural hypothesis. The functional hypothesis states that the increase in the number of traces is associated with an increase in the number of vessels. "Functional" is referred here to the physiological role of the vascular system, associated with blood flow. Functions related to oxygen support or thermoregulation could have been

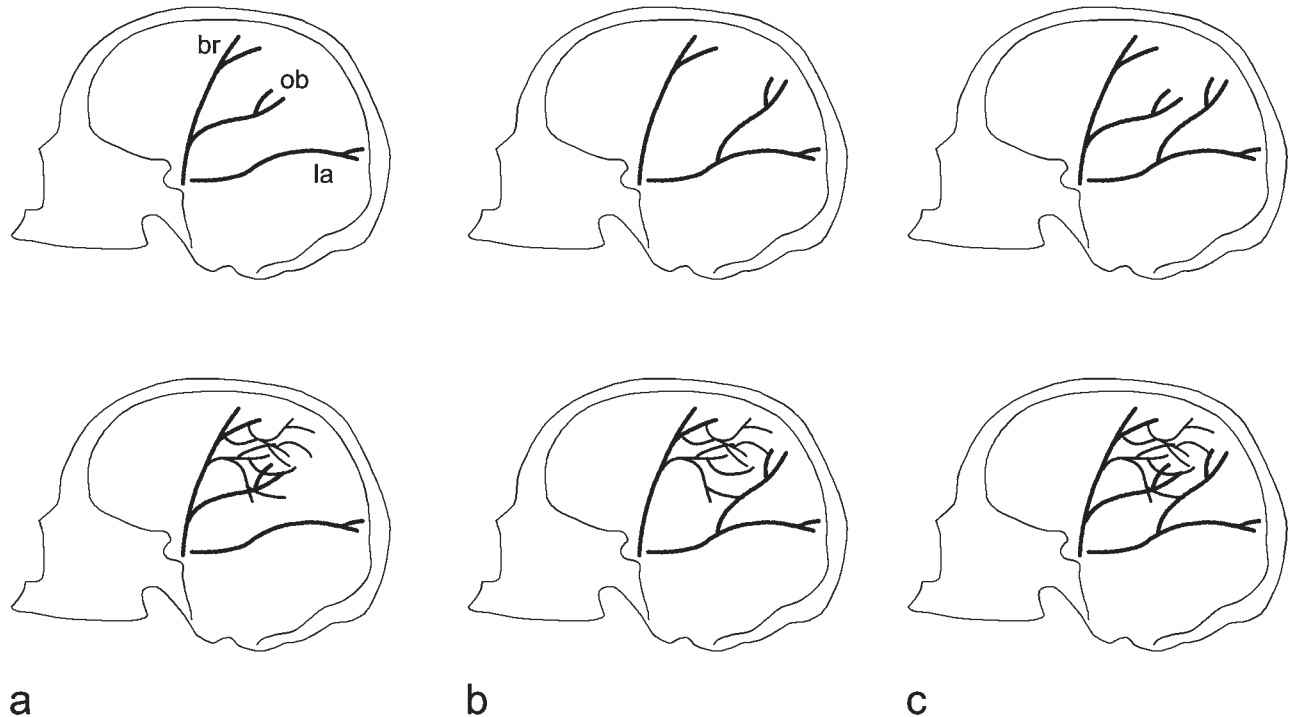


Fig. 1. Schematic drawings of the different types of vascular patterns according to the Adachi's classification, depending upon the relationships between the bregmatic (br), obelic (ob), and lambdatic (la) branches: Type I (a), Type II (b), and Type III (c). Although this classification is relatively objective and simple when compared with other

proposed methods, it is not always informative. The simple derivation of the middle branch may not reflect the actual contribution of the anterior versus posterior networks. Above: basic Adachi patterns. Below: the same patterns but with a dominance of the anterior network.

associated with the endocranial changes in modern humans. In contrast, the structural hypothesis states that the increase in the number of traces is associated with some change in the biomechanical relationships among the cerebral cortex, meninges and neurocranial bones, leading to a larger number of imprints left on the endocranial wall without changes in the actual number of vessels. Interestingly, in modern humans such differences are mainly located on the parietal surface, and the parietal lobe is supposed to have undergone important cortical adjustments in the evolution of modern humans (Bruner et al., 2003b; Bruner, 2004, 2008, 2009). Undoubtedly, we must also take into consideration a possible influence of both factors.

One way to discriminate between these two hypotheses is to test if and to what extent the shape of the endocranium influences the morphology of the traces or the degree of their expression. Because of the close relationship between morphogenesis of the brain and that of the braincase (Richtsmeier et al., 2006), it can be expected that some degree of covariation occurs between the neurocranial and vascular systems. This is quite important when the neurocranial architecture is very different between modern and nonmodern morphotypes (Ponce de León and Zollikofer, 2001; Lieberman et al., 2002; Bruner et al., 2004; Bastir et al., 2008). Following a null hypothesis of no influence of endocranial shape on the traces of the arterial pattern, we used geometric models to investigate the relationship between the endocranial morphology and the vascular pattern in a modern human population.

## MATERIALS AND METHODS

### Sample

The total sample included 186 adult skulls sectioned in the fronto-occipital transversal plane. The individuals represent a modern European population (Italy, 19th–20th century), with estimated age ranging between 32 and 64 years (see Bruner et al., 2003a and Bruner and Ripani, 2008 for further information on the sample). According to sexual determination, the sample is composed by 47% females, 24% males, and 29% indeterminate specimens. Sexual variation was not considered in the present article, as there is no evidence of sexual dimorphism in basic middle meningeal patterns (Bruner et al., 2003a). The individuals were divided into classes according to four criteria: (1) obelic derivation; (2) general dominance; (3) degree of reticulation; (4) depth of the imprints. The influence of these factors was tested independently, comparing the morphological endocranial differences between different patterns. The scoring procedure was based on visual inspection, generally following a classic criterion of seriation: after examination of the whole sample, the individuals showing the smaller or larger expression for a given traits were separated from the rest of the specimens, which in contrast were assumed to represent the standard (i.e., more frequent) morphology. Clearly, this approach is largely subjective and depends on the personal experience of the anatomist. Nonetheless, it delineates classes of gross morphology which can be used in statistical comparisons.

For each individual the two hemispheres were scored independently, and for each analysis the comparisons were performed using only those specimens showing the same pattern on both sides. If the morphology influences the arterial outline, it is supposed that individuals with the same pattern on both sides are well representative of a given cranial morphotype. Hence, by scoring the more extreme morphologies within the observed variation and comparing only the symmetric individuals, the subjectivity of the scoring procedure is further reduced, and any signal is potentially strengthened. This approach did not support a robust analysis of the combination between different vascular characters, because of the small number of cases in the combined classes (extreme morphology for different traits in both hemispheres).

*Obelic derivation* reflects the Adachi typology, depending on the anterior, posterior or double origin of the middle branch. This is the less subjective classification, being associated with a more discrete criterion of separation among classes. The morphological comparison between neurocranial shapes was computed between the individuals with bilateral anterior and bilateral posterior obelic derivation. *General dominance* refers to the relative contribution of the anterior and posterior branches, independently of the obelic origin (see Fig. 1). Features like the size of the imprints and the degree of vascularization were used to deduce the importance of the anterior and posterior derivations. In modern humans, the complexity of the middle meningeal vessels is generally associated with a double origin of the obelic branch. Nonetheless, one of the two principal branches is often dominant, even if the obelic branch has a double contribution. With modern humans, the recognition of a general dominance may be more informative than the origin of the middle branch alone. The dominance was scored as anterior, equivalent or posterior, depending upon the general volumetric distribution and branching complexity of the three districts. The hemisphere was scored as equivalent (i.e., intermediate) dominance also when the middle branch is dominant and its origin approaches the *foramen spinosum* (that is, neither anterior nor posterior derivation), or when the anterior and posterior systems show a similar contribution to the vascularization. The morphological comparison was computed between the individuals with bilateral anterior and bilateral posterior general dominance. *Reticulation* is related to the degree of complexity of the vascular network, influenced by the number of anastomoses and bifurcations. The specimens were scored as normal (generally characterized by many connections and a well distributed vascular system) or scarcely reticulated (showing a very linear and simple network). *Depth of the imprints* refers to the general depth of the traces in the bone wall. Traces were scored as normal (hemispheres with imprints well shaped on the endocranial wall) or as weak (hemispheres with very faint or even null meningeal marks).

### Geometric Model and Comparisons

A bilateral configuration of 25 three-dimensional landmarks was used as a geometric model of the neurocranial morphology (Fig. 2). The configuration included

both ectocranial and endocranial landmarks: *foramen caecum*, anterior and posterior limits of the *planum sphenoidale*, sella, endobasion, endopisthion, internal occipital protuberance, *foramen rotundum*, *foramen spinosum*, Broca's cap, posterior border of the anterior fossa, pyramidal apex, pyramidal base, bregma, lambda, pterion, asterion (see Bruner and Ripani, 2008 for further details). The coordinates were sampled using a Microscribe 3DX. The geometric differences between groups were then compared using both the Procrustes superimposition and the Euclidean distance matrix analysis.

The Procrustes superimposition translates all the specimens to a common centroid, scales the configuration to unitary centroid size, and rotates the coordinate systems to minimize the sum of the squared differences between the corresponding landmarks using a least-square approach (Bookstein, 1991; Zelditch et al., 2004). Therefore, the residuals between the superimposed specimens were reduced to the minimum differences after the removal of the position, orientation and size from each configuration. After superimposition, the mean shapes were computed for each group, and the difference in their variations was tested using a permutation approach (the sum of squares explained by each group was compared to the value for random permutations of group membership; 1000 permutations,  $P < 0.05$ ). Mean shapes and permutation tests were computed using MorphoJ (Slice, 2000). The analyses were also performed using symmetrized configurations, discriminant analysis and cross-validations, by using MorphoJ 1.0 (Klingenberg, 2008).

As superimpositions can introduce bias when the distribution of the differences is not random (Richtsmeier et al., 2002) and some localized differences can be lost when performing shape normalization, the raw coordinates were also compared by Euclidean Distance Matrix Analysis (see Lele and Richtsmeier, 2001). In this approach, all the corresponding interlandmark distances of the two groups were compared as ratios and the distribution of the resulting matrix was compared with an expected value of 1 for all ratios (assuming no form differences). This approach provides a general indication of the size differences (as the mean or the median value of the ratio distribution) and identifies the interlandmark distances exceeding the isometric figure (being shorter or larger). One method relies on identification of the metrics exceeding N-times the standard deviation (e.g. Bruner and Ripani, 2008). Here we computed confidence intervals for each interlandmark distance and identified the diameters that exclude isometry (Lele and Richtsmeier, 2001). Because of the large number of comparisons and the possibility of spurious results, symmetric responses were assumed to be more informative than asymmetric results. In this analysis, the lateral ectocranial landmarks (pterion and asterion) were not considered, because they are not very informative on account of their absolute proximity to the endocranial landmarks (lateral anterior fossa and base of the petrous pyramids). EDMA was computed with WinEdma (Cole, 2002).

There were no differences among groups in the centroid size (Mann-Whitney test) and no significant differences in the left-right meningeal patterns (chi-square test). Hence, these factors were not considered in the

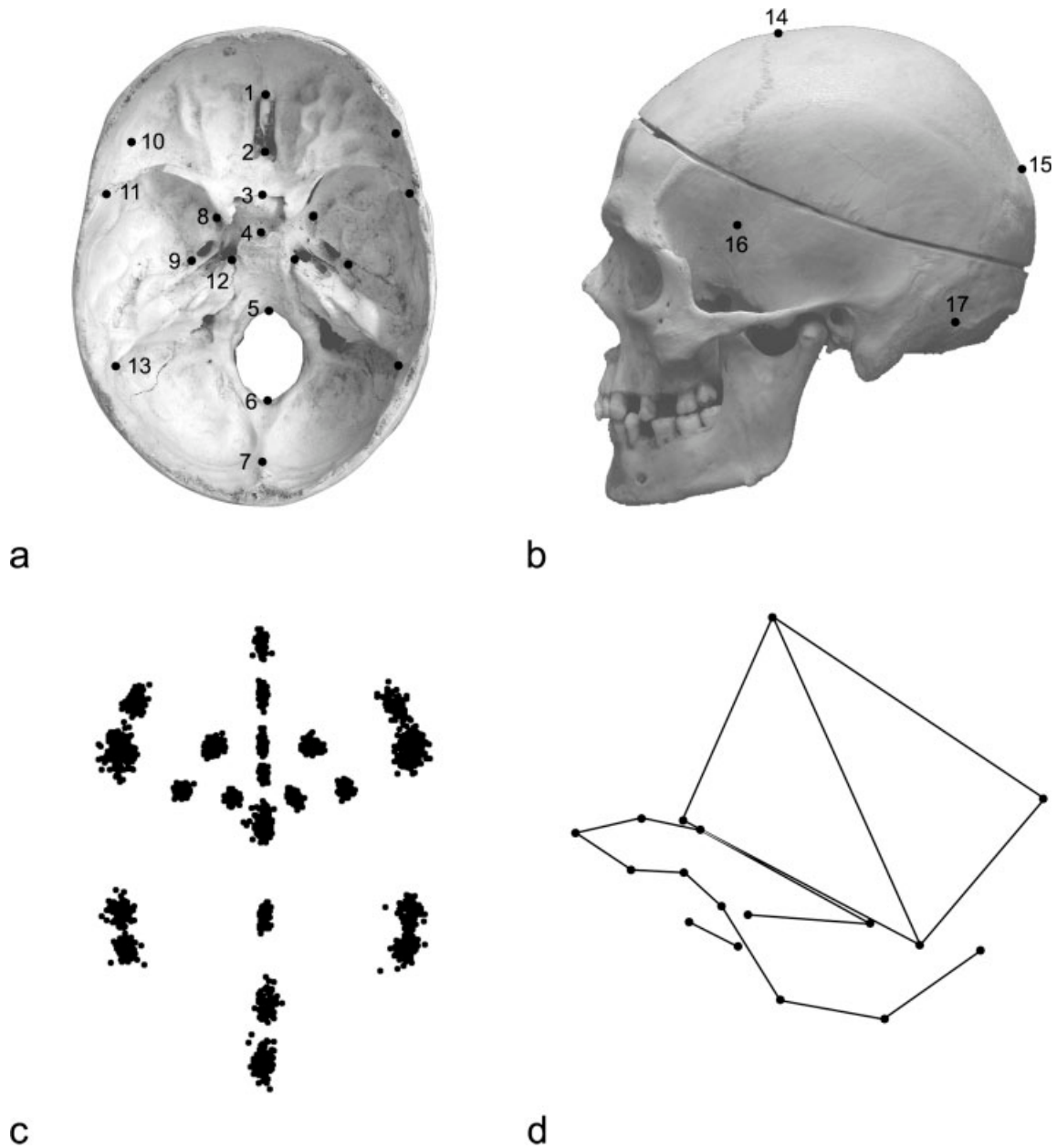


Fig. 2. The bilateral 3D configuration used in this analysis includes 25 endocranial (a) and ectocranial (b) landmarks: (1) *foramen caecum*; (2) *planum sphenoidum*, anterior; (3) *planum sphenoidum*, posterior; (4) sella; (5) endobasion; (6) endopisthion; (7) internal occipital protuberance; (8) *foramen rotundum*; (9) *foramen spinosum*; (10) Broca's

cap; (11) posterior border of the anterior fossa; (12) pyramidal apex; (13) pyramidal base; (14) bregma; (15) lambda; (16) pterion; (17) asterion. All the specimens were superimposed using the Procrustes approach (c: upper view) and using a wireframe to delineate the endocranial base and the vault (d: left lateral view).

analysis. Basic statistics were computed with PAST 1.81 (Hammer et al., 2001).

## RESULTS

### Obelic Derivation

The comparison included 23 individuals with bilateral anterior derivation of the obelic ramus and 12 individu-

als with bilateral posterior derivation of the obelic ramus. The permutation test on the superimposed configurations and on the form difference matrix failed to support differences between these two groups ( $P = 0.83$  and  $P = 0.71$ , respectively). Only two diameters exclude isometry from the range of the confidence intervals, by no more than 1%, and only for one side (Fig. 3a). Superimposition on the endocranial landmarks alone did not reveal any significant differences ( $P = 0.75$ ).

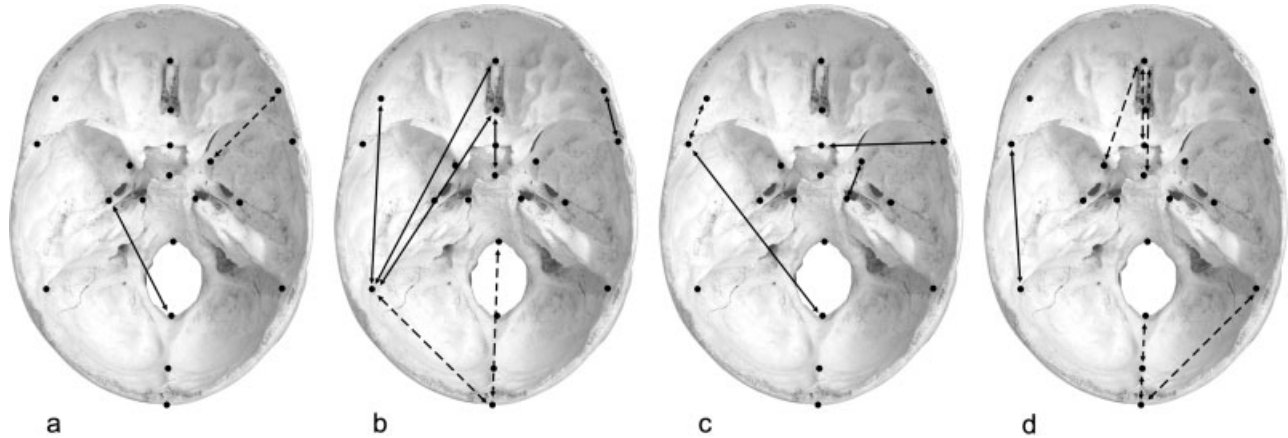


Fig. 3. Euclidean Distance Matrix Analysis: the diameters with values lower (dashed lines) or higher (solid lines) than the ratio of one (meaning no changes) after computation of 95% confidence intervals are shown for the groups with posterior obelic derivation (a), anterior dominance (b), linear vascular traces (c) and weak vascular imprints (d).

### General Dominance

Considering the whole sample, there is a dominant anterior system in 39.6% of the hemispheres and a dominant posterior system in 31.8% of the hemispheres. An intermediate or double dominance of the anterior and posterior network was scored in 28.6% of the cases. No significant differences were found between the groups with bilateral anterior dominance ( $N = 34$ ) and bilateral posterior dominance ( $N = 25$ ) when the Procrustes approach on the whole configuration ( $P = 0.72$ ), the endocranial landmarks alone ( $P = 0.45$ ) or the form difference matrix ( $P = 0.30$ ) were used. Nonetheless, the distribution of the interlandmark distances suggests longer anterior and middle fossae and a shorter posterior fossa in the group with anterior vascular dominance (Fig. 3b). However, the range of the confidence intervals exceeds isometry by no more than 1% and the pattern is definitely asymmetric.

### Reticulation

A very simple pattern of vascular imprints was scored in 24.6% of the hemispheres. There are no differences between the specimens with a bilateral simple pattern ( $N = 22$ ) and those with bilateral normal reticulation ( $N = 87$ ) after superimposition of the whole configuration ( $P = 0.40$ ), of the endocranial configuration ( $P = 0.44$ ) or according to the form difference matrix ( $P = 0.08$ ). The differences between the  $P$ -values for the shape versus form analysis suggest a certain importance of the size differences. Actually, the comparison of the centroid size distribution in the other analyses (by using ANOVA, Mann-Whitney test, or permutations) gives  $P$ -values ranging between 0.65 and 0.95, whereas in this specific comparison the  $P$ -value approaches 0.30. Nonetheless, because these differences do not reach a significant  $P$ -level, they will not be further discussed. An analysis of the single interlandmark distances indicates enlargement of the anterior fossa in the specimens with simpler vascular networks, although the pattern is asymmetric and the range of the confidence intervals exceeds isometry by no more than 1% (Fig. 3c).

### Depth of the Imprints

The vascular imprints were scored as weak (or absent) in 32% of the hemispheres. The final sample included 32 individuals with bilateral weak traces and 69 individuals with bilateral normal depth. In this case, the differences between the two groups were significant when the superimposition of the whole configuration ( $P = 0.029$ ) or just the endocranial landmarks ( $P = 0.013$ ) were used. A similar result was obtained by discriminant analysis of the first eight principal components of the shape variation for the whole sample, using a bilateral or unilateral left configuration ( $P = 0.037$  and  $0.044$ , respectively). Eight components, explaining 53% and 60% of the total variance in the two approaches, were used to maintain a balance between variables and sample size. Although the discrimination is significant, the determination coefficient is rather low ( $r^2 = 0.16$  in both cases). Nonetheless, the pattern is symmetric, at least because it is largely related to the midsagittal plane. The differences were the same when the pairwise comparisons between the mean shapes or the discriminant vector were visualized (see below). The specimens with faint or null traces are characterized by a slight flattening of the middle and posterior fossae (mostly in the occipital area), posterior rotation of the parietal bones, widening and shortening of the anterior fossa, and lengthening of the middle fossa. Interestingly, the analysis of the form difference matrix did not show significant differences ( $P = 0.41$ ), even though many single diameters display nonisometric shortening (Fig. 3d). In particular, the anterior and posterior fossae undergo absolute shortening (ranging between 2% and 11% less than the normal figure). The analysis of the single diameters also showed lengthening of the middle fossa, asymmetrically by enlargement of the middle fossa itself or reduction of the posterior one.

The main statistics for each analysis is reported in Table 1.

### Symmetrized Data and Discrimination Analysis

The superimpositions computed on symmetrized configurations confirmed all the previous results (Fig. 4).

Skulls with vascular posterior dominance have enlarged posterior volumes and a flatter posterior fossa. The specimens with scarcely reticulated patterns show cranial base flattening and endocranial widening. Those with weak traces display a flatter neurocranium (mostly in the posterior fossa) and relative lengthening of the middle fossa. Nonetheless, permutation tests performed on the Procrustes and Mahalanobis distances failed to show statistical significance in most of the analyses, and cross-validations were unable to efficiently separate the classes. The only exception is the analysis of the depth of the traces, for which both metrics are significant ( $P = 0.03$  and  $0.001$ , respectively). However, cross-validation

correctly recognized only 63% of the weak-traces endocrania and 74% of the normal-traces endocrania.

## DISCUSSION

Neurocranial anatomy is the final result of the integration of genetic programs, physiological responses, and biomechanical relationships. This network must be considered at the phylogenetic and ontogenetic levels. In both the evolutionary and morphogenetic contexts, some changes are directly related to the physiological roles of tissues and organs (like metabolism or neural transmission), while others are more associated with the spatial organization of the anatomical elements and the system of forces, strains, tensions, and pressures exerted by the physical components. This separation between functional (physiological) and structural (biomechanical) variations is not so discrete and must be understood more as a conceptual than a real biological difference. Many structural changes involve functional adjustments, and functional responses may produce structural reorganizations. Nonetheless, it is important to recognize the final phenotype as the result of two different frameworks, which must be carefully considered when interpreting phylogenetic changes or morphogenetic processes.

The imprints of the meningeal vessels in the endocranial wall are available for palaeoneurological analyses. The fossil record shows probable species-specific patterns of the meningeal traces within the human genus. The Asian *Homo erectus* endocasts often show a larger contribution of the posterior network compared with the

**TABLE 1. Statistics for each comparison**

	N	GPS1	GPS2	FDM	ILD
Obelic derivation	35	0.83	0.75	0.71	2 (1%)
General dominance	59	0.72	0.45	0.30	7 (3%)
Reticulation	109	0.40	0.44	0.08	4 (2%)
Depth	101	0.03	0.01	0.41	7 (3%)

N, total sample; GPS1,  $P$ -values after generalized procrustes superimposition for the whole configuration; GPS2,  $P$ -values after generalized procrustes superimposition for the endocranial configuration; FDM,  $P$ -values between form matrices; ILD, absolute and relative number of interlandmark distances excluding isometry according to the 95% confidence intervals.

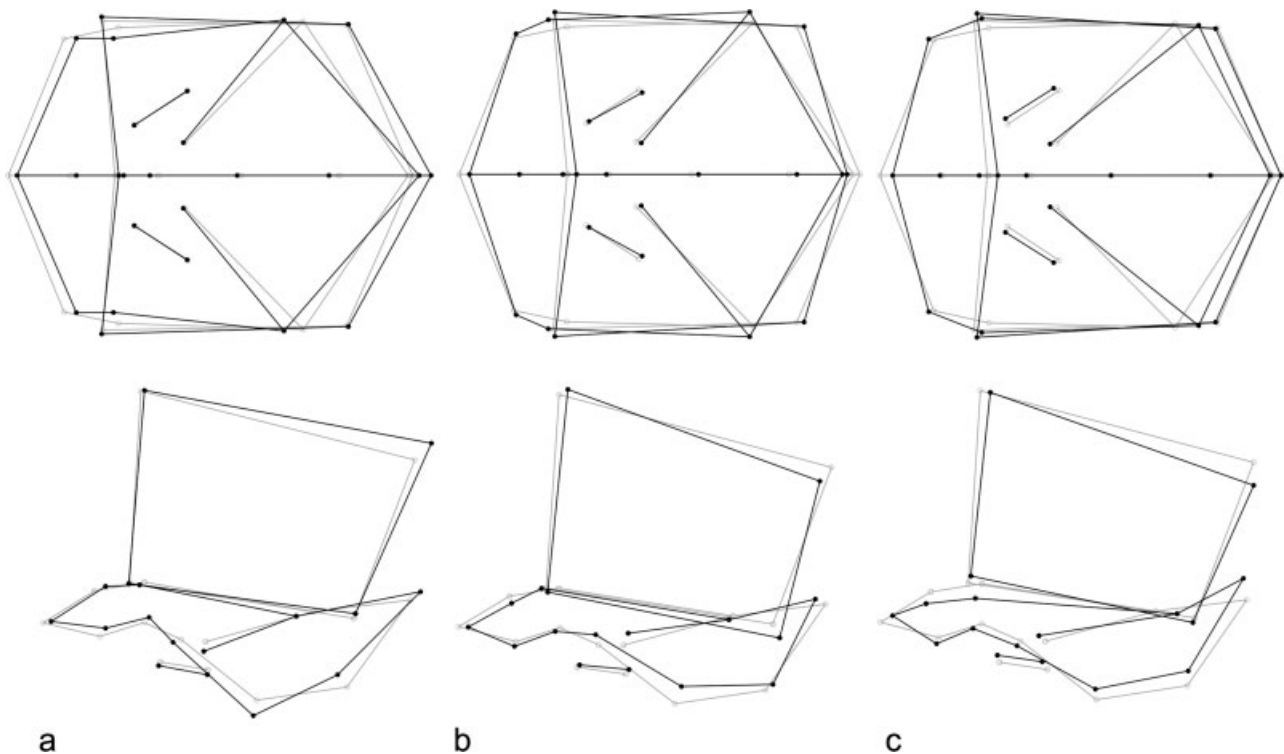


Fig. 4. Procrustes superimposition: the mean shapes are shown (bold wireframes) for the groups with posterior vascular dominance (a), linear vascular traces (b), and weak vascular imprints (c).

other species (Grimaud-Hervé, 1997), and *Homo sapiens* shows a definite increase of the vascular reticulation with respect to nonmodern taxa (Bruner et al., 2005). However, the pattern of the vascular traces is sensitive to the neurocranial geometry, being influenced by changes in endocranial structure associated with artificial or pathological deformation of the braincase (O'Loughlin, 1996). Modern humans have a very specific neurocranial form, with rounded and globular braincase mostly related to the bulging of the frontal and parietal bones, flattening of the occipital bone and flexion of the cranial base (Lieberman et al., 2002; Bruner et al., 2004). In contrast, Asian *Homo erectus* specimens are characterized by platycephaly and projecting occipital lobes (Anton, 2002; Bruner, 2004; Baab, 2008). Hence, the vascular differences described between human species may be simply the consequence of different cranial architecture, without any functional meaning.

According to the data presented here, however, if the neurocranial shape influences the morphology of the vascular traces, this contribution must be very limited. Taking into account the adult variation in modern humans, the endocranial diameters associated with changes in the morphology of the imprint of the middle meningeal vessels are very few (1%–3%). Mostly, their distribution is often asymmetric, and their confidence intervals generally exclude isometry for no more than 1%. Even if these results do not exclude completely a possible relationship between neurocranial morphology and the patterns of the meningeal imprints, we must admit that a clear association between their variations is not likely.

The bilateral dominance of the posterior network is associated with a certain reduction of the anterior and middle fossae, enlargement of the posterior areas and flattening of the cerebellar fossa, but the signal is quite asymmetric (more evident on the left side) and the differences are very small. Thus, a more developed posterior network is also associated with relatively enlarged parietal, occipital and cerebellar areas. This makes sense in terms of both function and structure (more spatial availability or more physiological demand in the posterior regions), but the differences are not robustly supported in terms of statistical significance. The derivation of the obelic ramus seems even less informative than the general antero-posterior dominance.

Skulls with a very simple vascular system (linear networks, without or with few anastomoses) may have a relatively wider and shorter endocranium, with flatter cranial base and flatter posterior vault. A wider and flatter endocranial organization may relax the meningeal tensions at the lateral walls, leaving the smaller channels entirely within the connective tissue, with only the main vessels contacting the endocranial surface. Again, the overall differences are not significant and the pattern of the specific diameters is not uniform.

The differences in the endocrania with very weak or null traces are a bit more robust, albeit of small magnitude. These skulls show flattening of the posterior neurocranial areas (both vault and base), widening of the anterior fossa and lengthening of the middle one. The depth of the traces basically depends on two factors: the pressure of the soft tissues on the hard ones and the thickness of the meningeal layers. More pressure or thinner layers probably produce deeper imprints. None-

theless, it remains to be established how such a cranial shape is related to one or the other factor. Overall cranial size (assumed to be proportional to brain size) does not influence the depth of the vascular traces.

All this information enriches the debate in functional craniology, as it shows that a certain percentage of the vascular morphology could be related to the neurocranial architecture. Actually, many factors involved in vascular morphogenesis are shared with the growth and development of the neural tissues (Eichmann et al., 2005), and neurons themselves act and react like structural biomechanical elements (Van Essen, 1997; Hilgetag and Barbas, 2005; Toro and Burnod, 2005). Nonetheless, the main result of the present study is the scarce influence of these factors. That is, it is unlikely that the marked differences in the vascular traces among the human species are due only to differences in cranial shape.

Of course, this statement must be properly weighted. Firstly, the scoring method used in this analysis is necessarily subjective, and more detailed quantification in future studies is needed to strengthen these results. Secondly, the forces acting in morphogenesis are not necessarily the same as those acting during evolution. As a matter of fact, morphogenesis is more constrained by the sequence of maturation, whereas selective pressures may induce more independent adaptations producing departures from the ontogenetic pathways when necessary. Most of all, however, the variation within the human genus is definitely larger than the variation within the modern species. Hence, the small differences associated with the low variation within *Homo sapiens* may contrast with much more conspicuous differences within the human genus, associated with the greater variation. In any case, in *Homo erectus* a more developed posterior network is associated with a low vault and posterior endocranial elongation (Grimaud-Hervé, 1997; Bruner, 2004), a pattern different from the one described here for the specimens with bilateral posterior dominance. On the other hand, a general increase of the reticulation can be associated with cranial base flexion, lengthening of the middle fossa, endocranial widening and upper rotation of the parietal profile (see Fig. 4b). Interestingly, these vascular and cranial traits have all been described in the evolution of modern humans (Lieberman et al., 2002; Bruner, 2004; Bruner et al., 2005, 2008).

As final cautionary note we must observe that even if these results do not support a marked association between the overall adult neurocranial shape and vascular patterns, we cannot exclude the possibility of more subtle biomechanical influences. In terms of space, it may be hypothesized structural influences more confined to small areas, mainly in regions which are not covered by the present analysis. The geometrical differences described in modern humans for the parietal surface may in fact induce some local structural changes associated with connective thickness or endocranial pressures, restricted only to the interested area and without strong relationships with the general neurocranial organization. This issue can be considered only analysing in a detailed quantitative manner the arterial patterns (for example using fractal analysis; Bruner et al., 2005) and the parietal surface (for example using sliding landmarks; Gunz et al., 2004). In terms of time, possible structural influences may be related to the morphogenetic dynamics more than to the final neurocranial

shape *per se*. The endocranial shape and size changes are dissociated during ontogeny, with modularized patterns changing along the morphogenetic trajectory (Bastir et al., 2006; Bastir and Rosas, 2009). This complex framework, associated with the limited morphological integration of the endocranial districts (Bruner and Ripani, 2008), may hide possible structural influences when only the final neurocranial phenotype is taken into account. This second possibility can be investigated only through longitudinal and transversal studies, including the embryological stages.

Considering the overall neurocranial shape, we must recognize that the possible geometric signal associated with the gross morphology of the traces of the middle meningeal vessels, whenever confirmed, is definitely very low. Accordingly, we can conclude that the present data do not support the hypothesis that the morphology of the vascular meningeal imprints is consistently influenced by the neurocranial spatial organization. At least, we can state that it is unlikely that the differences among the human species are related only to the effects of cranial geometry.

If the hypothesis of a relationship between skull shape and meningeal traces loses strength, we must pay attention to the functional (physiological) alternatives, mostly taking into account the definite increase in the number of channels in *Homo sapiens* (Bruner et al., 2005). In terms of blood flow, this may mean oxygen consumption and thermoregulation. This vascular system has a scarce direct contact with the neural substrate, and as a matter of fact there are no recognized functional consequences in adult patients who undergo neurosurgical resection of the whole middle meningeal artery (Bruner and Sherkat, 2008). The first observation may support a thermoregulatory function (heat exchange) more than a biochemical one (oxygen exchange). The second observation may suggest a larger importance in the earliest life stages, mostly considering that a large part of the neurocranial growth and development (with consequent high energy loadings) is complete after the first 2 years in modern humans. Actually, both craniosynostoses and cultural practices of cranial deformation (associated with changes in the orientation of the meningeal vessels; O'Loughlin, 1996) involve processes generally taking place from the intrauterine period to the first 2 years of life.

Taking into account the data available at present for the middle meningeal vessels and the related morphological investment in terms of phylogeny and ontogeny, it seems probable that we are currently missing some relevant information on these vascular networks.

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