Craniovascular traits in anthropology and evolution: from bones to vessels

Hana Píšová[1,2], Gizéh Rangel de Lázaro[3], Petr Velemínský[2] & Emiliano Bruner[4]

1) Katedra antropologie a genetiky člověka, Univerzita Karlova, Prague, Czech Republic
 e-mail: hana.pisova@natur.cuni.cz

2) Antropologické oddělení, Národní muzeum, Prague, Czech Republic

3) Area de Prehistoria, University Rovira i Virgili, Tarragona, Spain

4) Centro Nacional de Investigación sobre la Evolución Humana, Burgos, Spain

Summary – *Many aspects of human biology can be reconstructed from skeletal and fossil remains. The endocranial vasculature runs through cerebral, connective, and bone elements, where it is influenced by the functional and structural relationships among these different components of the endocranial system. The imprints and traces of these vessels can be used to analyze the craniovascular features of extinct species or historical samples. These traits can supply information about evolutionary adaptation, the mutual relationships between and within populations, and individual life history. In particular, bioarchaeology considers individual morphological variants as indicators of temporal and spatial relatedness and population structure, whereas paleoanthropology studies functional aspects to consider evolutionary changes and phylogenetic processes. Forensic science can investigate the cause of death associated with craniovascular pathologies by relying on morphological variations for individual identification. In this review, we consider the imprints of middle meningeal vessels, dural venous sinuses, emissary veins, and diploic veins. We summarize the most relevant morphological and functional information about craniovascular features and their applications in retrospective anthropological and medical fields, as well as describing the methodological issues associated with the sampling and quantitative evaluation of these elusive vascular remnants imprinted in the cranial bones.*

Keywords – *Bioarchaeology, Paleoanthropology, Middle meningeal artery, Diploic veins, Dural venous sinuses, Emissary foramina.*

Introduction

Anthropological and paleoanthropological human samples largely comprise bone remains and their fossilized anatomical elements. The information obtained from hard tissues is generally used to support morphological comparisons, which sometimes include functional biomechanical evidence. Nonetheless, bones may witness physiological processes associated with soft tissues, or more correctly, the traces that such tissues have left on their surfaces. An interesting case is represented by the imprints of the blood vessels, specifically arteries and veins, which comprise remnants of physiological functions related to blood flow, oxygenation, and thermoregulation. The endocranial cavity, which houses the brain and its associated structures, is a particularly rich source of this type of information. Due to the mutual functional and structural relationships between hard and soft tissues, many skeletal morphological features exhibit vascular patterns associated with the external surface of the brain as well as with the channels that bridge intra- and

extracranial blood networks. The traces of middle meningeal vessels, dural venous sinuses, emissary veins, and diploic channels are imprinted on the bone surface and within its thickness (Fig. 1). These traces can reveal alternative but equivalent functional systems, provide evidence for evolutionary adaptations, and be used as proxies for interspecific and intraspecific relationships.

In this review, we introduce and discuss the main endocranial vascular features used to obtain information about the dynamics of blood circulation based on the analysis of bone remains, which have applications in fields such as bioarchaeology, paleoanthropology, and forensic sciences. In bioarchaeology, cranial vascular features are used to assess the phenotypic distances between and within populations and groups. In paleoanthropology, these traits are employed to investigate functional aspects associated with encephalization and thermoregulation. In forensic science, the vascular networks can supply information about individual life history and recognition. Analysis of the endocranial vascular system is now being enhanced by the technical development of digital anatomy tools, which can facilitate quantitative approaches based on numerical modeling and computed statistics.

Endocranial morphology and functional craniology

Studies of the cranial morphology, particularly the braincase, have always been a key feature of anthropology because of its importance in biology and evolution, as well as its relationships with medicine. Cranial morphogenesis is influenced by genetic, biomechanical, and biochemical factors, which make it sensitive to environmental and physiological responses. The interactions between soft and hard tissues are central for generating a system of rules that underlie the phenotypic variability of a species and for channeling the observed morphological variation (Bruner, 2015). It has been hypothesized that the neurocranial dimension (size) is determined strictly by brain growth, whereas the

spatial distribution and geometry of the anatomical elements (shape) are driven by the redistribution of these forces via the endocranial connective tissues, particularly all of the meningeal layers and their inter-hemispheric extensions, i.e., the *falx cerebri* and *tentorium cerebelli* (Moss & Young, 1960). Thus, soft and hard tissues exert reciprocal ontogenetic and phylogenetic effects, and their morphogenesis represents a balanced structural network. The vascular imprints found on the bone surfaces are left by meningeal tissues, which envelop the blood vessels. Surgical practice suggests a good correspondence between vessels and traces. However, the presence and degree of expression of these traces also depends upon other physical variables (such as the meningeal thickness or endocranial pressure) (Dean, 1995; O'Loughlin, 1996). Therefore, there may be differences between the actual vascular morphology and its imprints on the bone surface, and thus the lack of a specific vascular imprint does not necessarily mean the absence of the associated vessels.

The final cranial phenotype is a result of polygenetic and pleiotropic relationships between genes and characters, the integration of genetic and morphological elements, and environmental influences. Multiple factors are involved in the expression of these cranial traits, so these traits are generally called "epigenetic" because they are sensitive to intrinsic and extrinsic influences. Unfortunately, the term "epigenetic" is used in different ways in various fields. Originally, the term *epigenesis* was used to describe an embryological theory based on the origination of organs from undifferentiated systems, as an opposite view to theories of preformism (Van Speybroeck *et al.*, 2002). In molecular biology, *epigenesis* refers to heritable environmental changes in the DNA structure (Bird, 2007). In this review, we use the terms *epigenetic* and *epigenetic traits* in a strictly morphogenetic sense. Epigenetic cranial features are also known as nonmetric, discrete, discontinuous, quasi-continuous, or minor skeletal variants (Saunders & Rainey, 2008), although "nonmetric traits" is the most frequently used term.
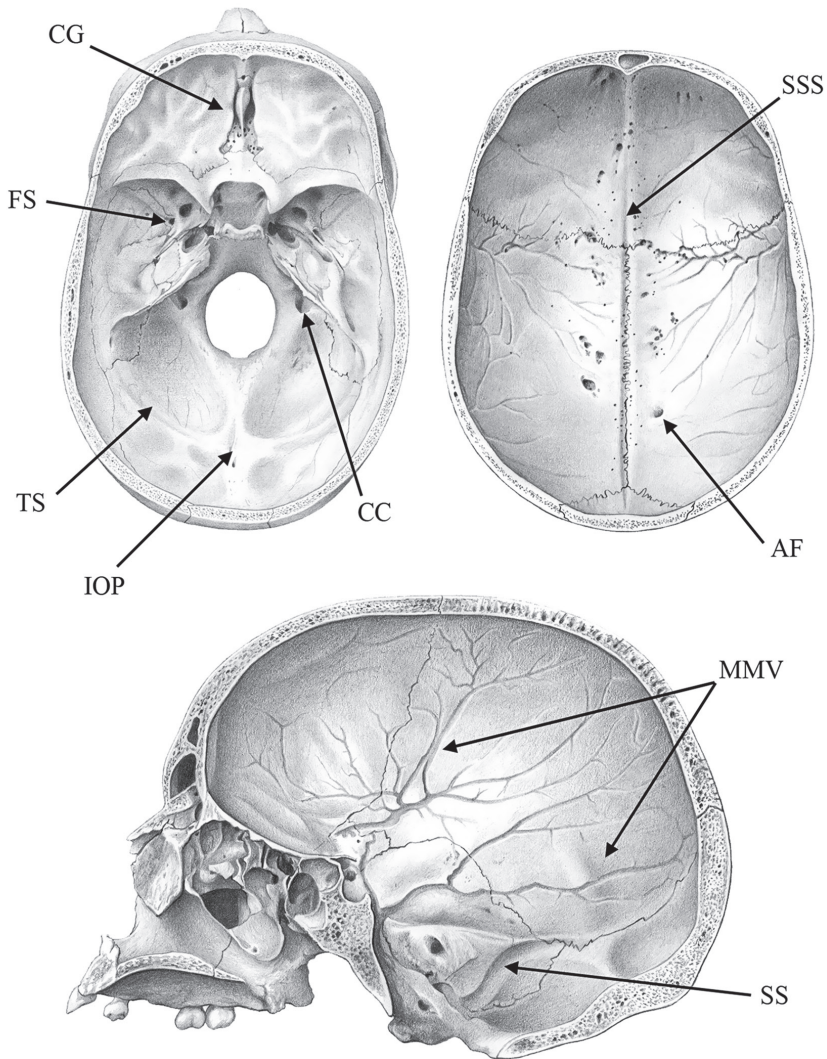
Fig. 1 - Endocranial morphological features. (AF arachnoid fovea, CC intracranial orifice of condylar canal, CG crista galli, IOP internal occipital protuberance, MMV middle meningeal vessels, FS foramen spinosum, SS sigmoid sinus, SSS superior sagittal sinus, TS transverse sinus).

The vascular traces on the skull represent ridges and crests formed by structural relationships between the bone and contacting tissues. In general, a physical pressure induces bone absorption through osteoclastic activity, whereas tension induces bone deposition through osteoblastic activity (Enlow, 1968). Hence, the imprints are strictly associated with the degree and distribution of the forces exerted by the soft tissues on hard tissues. An excess of ossification is called *hyperostosis* and defective ossification is called *hypostosis* (Ossenberg, 1970; Manzi & Vienna, 1997).

According to the principles of morphological integration, studying the relationships between the parts of an anatomical system is more
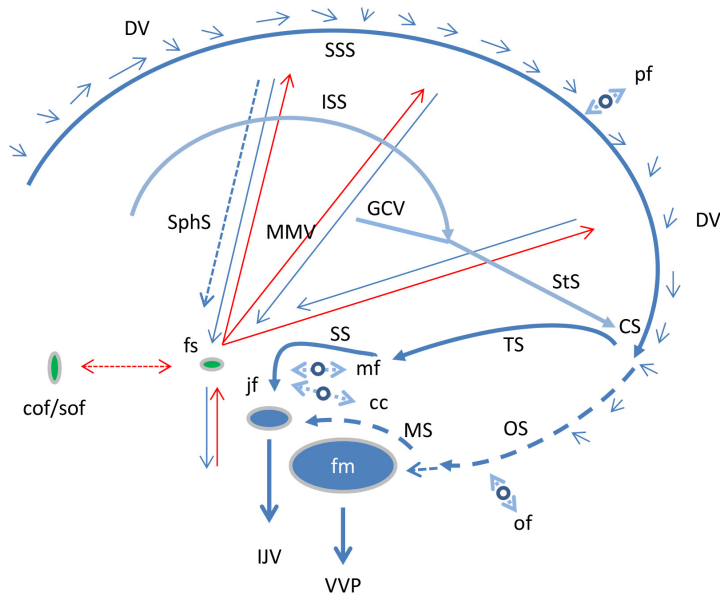
*Fig. 2 - Endocranial circulatory system diagram. Foramina: **cc** condylar canal, **fm** foramen magnum, **jf** jugular foramen, **mf** mastoid foramen, **cof** cranio-orbital foramen, **of** occipital foramen, **pf** parietal foramen, **fs** foramen spinosum, **sof** superior orbital fissure; Vessels and sinuses: **DV** diploic veins, **GCV** great cerebral vein, **IJV** internal jugular vein, **ISS** inferior sagittal sinus, **MMV** middle meningeal vessels, **MS** marginal sinus, **OS** occipital sinus, **SphS** sphenoparietal sinus, **SS** sigmoid sinus, **StS** straight sinus, **SSS** superior sagittal sinus, **TS** transverse sinus, **VVP** vertebral venous plexus, **CS** confluence of sinuses. Many of these vessels leave traces on the endocranial surface. The colour version of this figure is available at the JASs website.*

informative than studying single characteristics, which can even be misleading in some cases (e.g., Tobias & Symons, 1992; Cheverud, 1996). Current advances in multivariate statistics facilitate an integrated approach (Klingenberg, 2014). The expression of specific anatomical traits may be associated with the effects of the general morphogenetic background on the overall cranial geometry (Cheverud *et al.*, 1979; Konigsberg *et al.*, 1993). In this sense, epigenetic traits can be heritable via direct genetic effects (genes coding for traits) or indirect genetic influences (genes affect general developmental processes that induce the expression of the traits). In the latter case, the expression of a characteristic is not strictly genetic, but instead it should be interpreted as a secondary consequence of the general morphogenetic environment. It is likely that traits associated with early ontogenetic stages

(such as the emissary foramina) (Konigsberg *et al.*, 1993; Del Papa & Perez, 2007) are less influenced by the secondary effects expressed in later maturation processes, and thus they are more sensitive to direct genetic components. By contrast, other elements may be more sensitive to the biomechanical and structural effects induced by physical interactions between soft and hard tissues (Ossenberg, 1970). For example, the development of middle meningeal vascular patterns and the courses of the dural venous sinuses can be affected by cranial deformations induced by artificial cultural practices or by pathological and subpathological craniosynostosis (Dean, 1995; O'Loughlin, 1996). The vessels associated with the deformed surface are generally shallow and flat, whereas the vessels that run along the undistorted areas compensate for this change by being wider and deeper. In addition, morphological

asymmetries in the skull induce morphological asymmetries in the vessels, thereby further highlighting the importance of the environment for their final morphology.

However, the structural influences between bones and vessels are reciprocal. Thus, the craniovascular features can be affected by the cranial morphology and the vessels can similarly modify the local cranial morphogenetic processes. For example, the presence of a parietal foramen affects the complexity and integration of the attached sagittal suture segment. When foramina are present, the suture exhibits a lower degree of convolution and complexity (Mann *et al.*, 2009; Zollikofer & Weissman, 2011). Differences in the sutural morphology can be associated with the presence of sagittal fontanelles (lateral clefts) that accompany the parietal emissary vein during early ontogenesis, or simply with the fact that the presence of vessels creates a barrier to arrest ossification around the future foramen as well as redistributing the mechanical forces to organize the adjacent suture in a different manner (Gisel, 1964; Hauser & De Stefano, 1989; Scheuer & Black, 2000).

Although there are local interactions between bone and vessels, nonetheless these two systems display independence at a more general level, being sensitive to distinct physiological factors. A preliminary survey described no consistent correlation between the size of the meningeal and diploic vessels, or between the size of the vessels, cranial dimensions, and bone thickness (Eisová *et al.*, 2016). Also, gross morphological features associated with craniovascular anatomy do not show any patent correlation with the general skull form in normal adults (Bruner *et al.*, 2009).

Endocranial vascular traits: morphology and variations

Three main vascular systems can be traced based on cranial anatomy: the middle meningeal vessels, the venous sinuses of the dura mater (with associated emissary foramina), and the diploic veins. A fourth endocranial system is represented by the cerebral veins and arteries, which supply the inner brain volume. This system is not in contact with any bone surface so it does not leave any information in skeletal remains, as also the pericranial network outside the braincase (Saban, 1995). These vascular systems can be described separately but they represent a single functional unit (Fig. 2), and their variations and evolution must be a result of a shared functional context. In most cases, the terminology utilized is strictly directed at providing a common nomenclature but it is not based on homologous or independent features, which means that this terminology may reflect operational decisions, but not necessarily biological units. Thus, the division of the four systems can be considered a conventional issue. Furthermore, it must be noted that our basic knowledge of these anatomical elements was obtained from investigations in the 19th and early 20th centuries. Before the current advances in digital anatomy, basic anatomical research was necessarily performed on cadavers and histological preparations; therefore, these studies were limited by the conditions of the material (isolated from its functional and structural context) and small samples sizes. Due to these restrictions, there are currently some important biases in the anatomical nomenclature, including disagreements on the appropriate terminology or issues with the reliability of the observations. Given all of these limitations, the terms and definitions employed must be treated as general, and as preliminary in some cases.

Finally, as a cautionary note, it should be mentioned that working on traces is not the same as working on vessels, and this difference should always be kept in mind when using terms or statements. This review is dedicated to this topic but we may generally refer to vessels for brevity; however, it must be remembered that the actual observations and descriptions concern their traces on bone rather than the vascular elements themselves.

Middle meningeal vessels
The middle meningeal vessels originate from a single branch in the middle cranial fossa and they extend laterally to the braincase, mostly on the parietal and frontal bones (Figs. 1, 3, 4; see

Fig. 3 - Imprints of middle meningeal vessels of anatomically modern human with anterior branch dominance (Adachi I). The colour version of this figure is available at the JASs website.

Bruner & Sherkat, 2008). The imprints are probably left by both arteries and veins (Jones, 1912; Falk & Nicholls, 1992); therefore, although most authors refer to these traits as the middle meningeal *artery*, we prefer to use the more general term *vessels*. The middle meningeal vessels supply and drain blood from the cranial sidewalls, diploe, and dura mater. The middle meningeal artery originates from the maxillary branch of the external carotid artery and enters the endocranial cavity as a single trunk generally through the foramen spinosum, although different origins and passages have been described. In fact, the middle meningeal artery can also stem from the ophthalmic or stapedial artery, which branches from the internal carotid artery and enters the endocranial space through the orbits (Diamond, 1991). The foramen spinosum is usually absent in these cases. After entering the endocranial cavity, three major branches are typically recognized: anterior (bregmatic), middle (obelic), and posterior (lambdatic) (Rothman, 1937). The anterior branch of the middle meningeal artery generally anastomoses with the ophthalmic or lacrimal artery through the superior orbital fissure or the cranio-orbital foramen in the orbit (Diamond, 1991; Georgiou & Cassell, 1992; Lui & Rhoton, 2001).

The imprints of the middle meningeal vessels are already present in neonates on the parietal surface, but not necessarily in the middle cranial fossa (Lang, 1995). In earlier ontogenetic stages, the main branches can be already distinguished on the bone surfaces. The network complexity increases markedly in the first year of life and reaches the adult anatomical morphology by the age of 6–7 years (Saban, 1995). In modern humans, the enlargement of the parietal endocranial surface is associated with the first year of life (Neubauer *et al.*, 2009), and thus it is interesting to note that the main increase in vascular complexity occurs during the same period. In adults, generally at least five orders of branches can be recognized, with a mean lumen size of 1.4 mm (Eisová *et al.*, 2016).

The specific functions of the middle meningeal artery in the blood circulatory system are still unclear and it is generally eliminated during common surgical operations, without known

short-range functional impairments (Bruner & Sherkat, 2008). The middle meningeal artery is often associated with epidural hematomas after cranial fractures or internal damages. In adult individuals, it contains little or no blood flow at rest, thereby suggesting that it may be active only during specific ontogenetic stages, or in specific physiological conditions that are probably associated with heat load, such as physical exercise, alert, or pathological processes (Bruner *et al.*, 2011). Due to its large size and unclear functional effects, it has also been hypothesized to be involved in mechanical and hydrostatic protective functions.

The middle meningeal veins follow the pathways of the arteries, where they drain blood from the cranial sidewalls, meninges, superficial middle cerebral veins, diploic veins, and venous lacunae situated laterally to the superior sagittal sinus (Mancall *et al.*, 2001). The meningeal veins flow into the pterygoid venous plexus through the foramen spinosum, or they may join the sphenoparietal, cavernous, or transverse sinus through the petrosquamous sinus (Jinkins, 2002; San Millán Ruíz *et al.*, 2004). The dense interconnections of middle meningeal veins with diploic veins in the early ontogenetic stages become more limited after the development of the inner cranial table in the second year of life (Lang, 1995).

The traces of the middle meningeal vessels are always present, but their arrangement and degree of complexity is highly variable among individuals (Bruner *et al.*, 2003a). Among normal adults, the gross morphology of the traces is apparently not influenced by the general form of the braincase (Bruner *et al.*, 2009), although the effects of local factors (e.g., size and curvature of the parietal bone) have not been evaluated. Nonetheless, some morphological aspects of these traces can be influenced by extreme deformations of the neurocranium (O'Loughlin, 1996).

There are major differences among individuals in terms of the general branching pattern after considering the complexity and origins of the three main branches. There are several types of classification according to the origin and ramification of each specific branch, but the classification proposed by Adachi (1928) is applied most
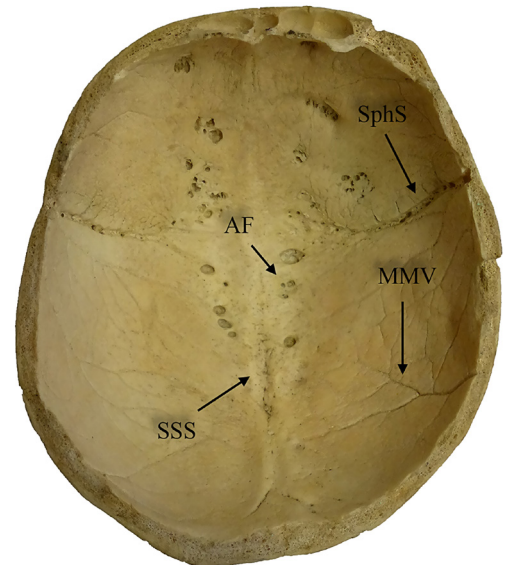
Fig. 4 - Calvarium of anatomically modern human with imprints of several endocranial vascular features. (AF arachnoid fovea, MMV middle meningeal vessels, SphS sphenoparietal sinus, SSS superior sagittal sinus). The colour version of this figure is available at the JASs website.

frequently in humans due to its reproducibility and simplicity. In this system, three categories are defined according to the origin of the middle (obelic) branch, which can originate from the anterior branch (Adachi I), posterior branch (Adachi II), or from both anterior and posterior branches (Adachi III) (Falk & Nicholls, 1992). The anterior branch frequently passes through a variable bony channel situated in the proximity of the pteric area (Derezinski, 1934). The main problems with vascular classification systems are the quantitative values employed; thus, if they are simple and objective, they tend to be scarcely informative because they are too general, whereas if they are complex and detailed, they are unreliable because they are too subjective. Therefore, appropriate methods for quantifying the spatial schemes of these vessels in modern human populations are still lacking. Fractal analysis has been used to quantify the degree of branching and space-filling properties of the middle meningeal vessels (Bruner *et al.*, 2005).
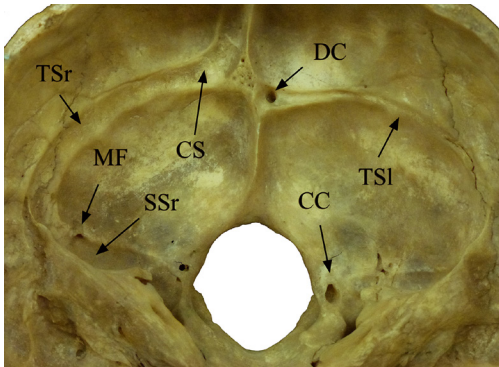
Fig. 5 - Endocranial surface of the occipital bone with imprints of the most common pattern for the confluence of sinuses, with right side dominance of the transverse sinus and other endocranially projected craniovascular traits. (TSr transverse sinus right, TSl transverse sinus left, CS area of the confluence of the sinuses with continuation of superior sagittal sinus into right transverse sinus, DC diploic channel running into left transverse sinus, SSr sigmoid sinus right, MF internal orifice of mastoid foramen, CC internal orifice of condylar canal). The colour version of this figure is available at the JASs website.

Dural venous drainage system

The dural venous sinuses (also called sinuses of the dura mater) comprise enlarged venous channels, which can expand to retain blood volumes, where they run through the dura mater connective layers between the brain and skull surface. They form an extensive and valveless network, which drains the blood from the brain, cranium, orbits, and meninges into the internal jugular veins, before leaving the endocranial cavity through the jugular foramina located at the posterior cranial fossa in front of the cerebellar hemispheres (Gray & Carter, 1858; Curé *et al.*, 1994).

The blood flow patterns are influenced by posture, where the drainage flows mainly through the venous sinuses in the supine position, but mainly through the internal vertebral venous plexus in an upright position (Epstein *et al.*, 1970). Both networks are largely interconnected via emissary veins (Breschet, 1832; Batson, 1940; San Millán Ruíz *et al.*, 2002). The dural venous sinuses are situated within the dura mater layers and most are anchored to the

endocranial surface. The pressure exerted by the blood retained in the sinuses induces osteoclastic activity to form imprints on the bone surface.

In general, two principal networks can be distinguished: the upper (posterior-superior) network drains the upper and posterior parts of the head (superior sagittal, inferior sagittal, straight, paired transverse sinuses, and occipital/marginal sinus), and the lower (anterior-inferior) network (paired cavernous, paired intercavernous, paired superior petrosal, paired inferior petrosal sinuses, and basilar plexus) receives blood from the orbits and from the frontal areas of head. The latter is located mainly at the cranial base where both venous networks merge into the internal jugular veins (Curé *et al.*, 1994). Other rarely and variably preserved sinuses are the paired sphenoparietal and petrosquamous sinuses.

The upper venous sinuses leave more traces on the endocranial surface than the lower ones, and thus their morphology and variations are generally better described in the osteological literature. The largest element of this upper system is the superior sagittal sinus (Figs. 1, 4), which runs below the metopic and sagittal sutures from the *crista galli* to the internal occipital protuberance, where it then runs into the confluence of sinuses (*torcular Herophili*) and meets the transverse sinuses. The confluence of sinuses is asymmetrical in terms of both size and the connections of the crossing vessels, and its morphology is highly variable. The superior sagittal sinus flows preferentially to the right transverse sinus (aka the lateral sinus). The lateral sinus that receives the blood from the sagittal sinus is generally larger than the contralateral one (Fig. 5). The lateral sinuses, which run laterally between the cerebral and cerebellar hemispheres, turn into the sigmoid sinuses at the jugular fossae. The second sagittal sinus, i.e., the inferior one, runs at the base of the *falx cerebri* and it does not contact the bone. It runs into the straight sinus, which reaches the confluence of sinuses and often runs into the smaller transverse sinus (Curé *et al.*, 1994).

There is great variation in the patterns of the confluence, which is also complicated by the irregular presence of occipital/marginal sinuses (Kaplan *et al.*, 1972; Dora & Zileli,

1980; Kimbel, 1984; Singh *et al.*, 2004; Kopuz *et al.*, 2010). The occipital sinus is attached to the *falx cerebelli* at the internal occipital crest and it may run into marginal sinuses that surround the foramen magnum (Fig. 6). In some cases, the enlarged occipital/marginal sinuses functionally replace one or both of the transverse sinuses. During the early ontogenetic stages, the occipital sinus is relatively large and frequent. It has been suggested that the switch from the occipital/marginal system to the transverse/sigmoid system is triggered by a change in posture due to the establishment of an upright condition, where the major blood outflow is taken over by the vertebral plexus and the occipital sinus becomes functionally redundant, thereby reducing or disappearing (Widjaja & Griffiths, 2004; Kopuz *et al.*, 2010). It has also been proposed that the occipital/marginal network can drain blood either to the internal jugular veins or to the internal vertebral plexus (Falk, 1986). Small occipital sinuses are highly prevalent in human modern populations (60%–90%) whereas enlarged forms are more rare (6%–43%) (Matiegka, 1923; Dora & Zileli, 1980; Kimbel, 1984).

The presence of occipital/marginal sinuses influences the size and morphology of the transverse sinuses. Both the transverse/sigmoid and occipital/marginal networks are equivalent and complementary in terms of their drainage pathways; hence, they can coexist or even replace each other. A higher incidence of occipital/marginal sinuses has been reported in cranially deformed individuals, thereby suggesting structural factors, functional compensation, and the high plasticity of the dural venous sinuses organization (Dean, 1995; O'Loughlin, 1996).

The presence of other endocranial venous sinuses is inconsistent among adult humans. The sphenoparietal sinus (Fig. 4) is variable and problematically defined, where it represents a conventional term rather than an anatomically evidenced pathway. This sinus may comprise a combination of two separate vascular elements (San Millán Ruíz *et al.*, 2004). For simplicity, it is recognized anatomically as a pathway situated under the lesser sphenoid wing, which bridges
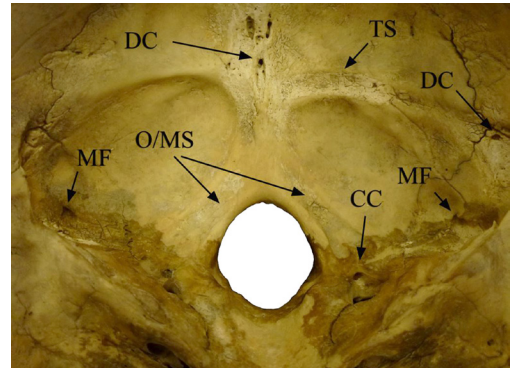
Fig. 6 - Endocranial surface of the occipital bone with rare presence of occipital/marginal sinus. (DC *diploic channels running into sinuses at variable positions,* **TS** *transverse sinus,* **MF** *internal orifices of mastoid foramina,* **CC** *internal orifice of condylar canal,* **O/MS** *occipital/marginal sinuses). The colour version of this figure is available at the JASs website.*

the anterior middle meningeal vein and the cavernous sinus, with variable contributions from other cerebral and dural veins. In paleoanthropology, based on fossil evidence, the sphenoparietal sinuses are considered to be imprints of enlarged anterior middle meningeal veins behind the coronal suture (Saban, 1995; Grimaud-Hervé, 2004).

The dural venous sinuses are frequently accompanied by arachnoid foveae (Fig. 4). The arachnoid foveae are small convexities of variable size, which are situated in close proximity to the venous sinuses, middle meningeal vessels, and diploic veins. The arachnoid foveae are imprints of the arachnoid granulations (Pacchionian bodies) formed by small portions of the arachnoid layer pressing onto the endocranial surface after prolapse of the dura mater (Schuenke *et al.*, 2010). The arachnoid granulations establish direct communications with the sinuses and filter the cerebrospinal fluid into the vascular system (Bradley, 1970; Grzybowski *et al.*, 2007). They are generally found along and laterally to the superior sagittal sinus. The arachnoid granulation can be located inside the lateral lacunae, which are lateral expansions of the venous sinuses that generally protrude from the superior sagittal sinus in the upper parietal area.
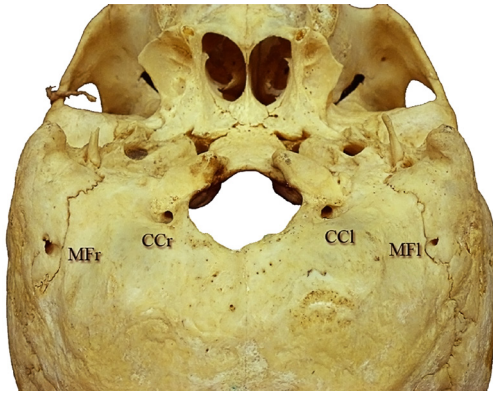
*Fig. 7 - Presence of large emissary foramina and channels at the nuchal area (**MFr** mastoid foramen right, **MFl** mastoid foramen left, **CCr** condylar canal right, **CCl** condylar canal left). The colour version of this figure is available at the JASs website.*

Emissary foramina

The dural venous sinus network is highly connected with other vascular systems, i.e., the middle meningeal vessels, the cerebral veins, and the diploic veins (Breschet, 1832; Schuenke *et al.*, 2010). More importantly, the dural venous sinuses are constantly bridged with the vertebral venous plexus, where these connections are based on valveless emissary veins distributed in different cranial bones, which interconnect the intracranial and extracranial venous systems (Epstein *et al.*, 1970; Eckenhoff, 1971; San Millán Ruíz *et al.*, 2002; Gisolf *et al.*, 2004). The prevalence and expression of emissary veins are highly variable among individuals and populations. The largest and more frequent emissary veins are the parietal, mastoid, occipital, and posterior condylar veins associated with visible foramina or channels (Boyd, 1930; 1934). Interestingly, during the early ontogenetic stages, the emissary foramina have valves that are absent in adults (Gisel, 1964).

The condylar canals transmit the largest emissary veins, where these canals are situated behind the occipital condyles (Figs. 6, 7, 8) and they are present bilaterally in 15%–70% of individuals and unilaterally in up to 95% (Boyd, 1930; Berry & Berry, 1967; Ginsberg, 1994; Berge &

Bergmann, 2001). The condylar canals contain veins that connect the sigmoid sinuses and suboccipital venous plexus, as well as possibly containing the occipital artery (Kiyosue *et al.*, 2007). The mastoid foramen (lying behind the mastoid processes) is present bilaterally in 34%–92% of individuals (Figs. 7, 8) and it is frequently formed of multiple passages (Boyd, 1930; Berry & Berry, 1967; Berge & Bergmann, 2001). The emissary mastoid veins connect the sigmoid sinuses with occipital veins and possibly with the posterior auricular veins. The mastoid foramina may also contain a small occipital artery, which can pass through a separate canal without entering the endocranial cavity (Choudhry *et al.*, 1996; Fig. 8). These pathways may be confused with multiple mastoid foramina. Extracranially, the mastoid emissary vein can form extensive confluences with occipital veins (Louis *et al.*, 2009). The parietal foramina are located laterally to the sagittal suture (Fig. 9) where they approach lambda and their bilateral incidence is 20%–62% (Boyd, 1930; Berry & Berry, 1967; Hauser & De Stefano, 1989). Their veins connect the superior sagittal sinus with the veins of the scalp and their arteries unite the middle meningeal artery with scalp arteries (Yoshioka *et al.*, 2006). The occipital foramen is a rare (2%) and unpaired route located on the occipital bone, which is usually close to the margin of the foramen magnum (Boyd, 1930; Fig. 10). This passage allows an emissary vein to connect the marginal sinus with the occipital veins.

It is important to mention that the emissary veins appear to play a minor role in the overall venous drainage dynamics, at least in normal thermal conditions. However, during hyperthermia, the blood circulation can change its direction through the emissary veins to flow from the skin into the cranium, which probably cools the endocranial cavity (Cabanac & Brinnel, 1985). The functional importance of the emissary veins is related to the efficiency of the jugular veins, and the dimensions of the mastoid foramina and condylar canals are associated with the dimensions of the jugular foramina (Solter & Paljan, 1973). The size of each foramen is highly variable, but

their summed areas are inversely correlated with the area of the jugular foramina, possibly as a remnant of early ontogenetic changes that reflect the disproportional development of the relatively large transverse sinus and small sigmoid sinus leading into the internal jugular vein, which is compensated for by the mastoid emissary vein helping to drain the insufficiently developed sigmoid sinus (Solter & Paljan, 1973; Schelling, 1978; Qureshi, 2014).

Diploic venous channels

The diploic channels are pathways left by diploic veins within the cancellous bone between the compact internal and external cranial tables of the braincase. The calvarial diploe contains several large valveless diploic veins, which are interconnected via a widespread network of microscopic channels that run through the cancellous bone (Fig. 11).

The diploic channels were discovered at the beginning of the 19th century, but relatively little work was done until the 20th century because of the difficulty accessing them using traditional dissection methods. Breschet (1829) distinguished four main diploic vessels: one frontal, two parietal, and one occipital. Similar to other vascular systems, different nomenclatures were established but the high variability of the diploic network hindered any integrated classification (Testut, 1893; Lindblom, 1936; Warwick & Wiliams, 1973; Hershkovitz *et al.,* 1999; García-González *et al.,* 2009; Rangel de Lázaro *et al.,* 2016). Due to their variability, diploic veins have been referred to as the "fingerprint" of the skull (Hershkovitz *et al.,* 1999) given their diversity in terms of the number, size, and disposition of the vessels, which range from absent or modest networks to reticulated and complex systems with several anastomoses, usually with symmetrical trends (Zenker & Kubic, 1996; Hershkovitz *et al.,* 1999; Skrzat *et al.,* 2004; García-González *et al.,* 2009; Tsutsumi *et al.,* 2013; Rangel de Lázaro *et al.,* 2016).

Physical and digital methods have been used to study the diploic veins and their channels, i.e., corrosion casts, cadaveric head dissection (Testut, 1893; Jefferson & Stewart, 1928; Zenker & Kubic,
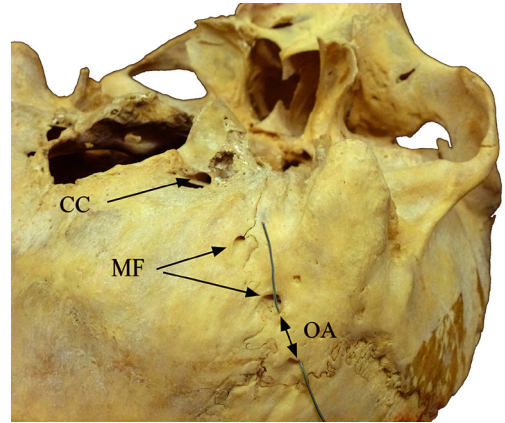
Fig. 8 - *Posterior view of the skull, showing details of the left mastoid area. Presence of emissary foramina and other vascular pathways. (CC condylar canal, MF double entrance of the mastoid emissary foramina, OA pathway for occipital artery). The colour version of this figure is available at the JASs website.*

1996; García-González *et al.,* 2009), and biomedical visualization based on radiological techniques such as X-rays, angiography, computed tomography (CT) (Hershkovitz *et al.,* 1999; Skrzat *et al.,* 2004; Patel, 2009; Rangel de Lázaro *et al.,* 2016; Eisová *et al.,* 2016), magnetic resonance imaging (Hatipoglu *et al.,* 2008; Jivraj *et al.,* 2009; Tsutsumi *et al.,* 2013), and experimental studies (Toriumi *et al.,* 2011). The physical study of diploic channels can be difficult and destructive, where it requires long preparation procedures that usually destroy the original specimens. By contrast, digital approaches and imaging methods are more precise, fast, and non-invasive tools. Using radiographs, Hershkovitz *et al.* (1999) described the remarkable diversity of the distribution and morphology of the diploic channels, particularly those developed in the parietal area.

More recently, the patterns of variation in the diploic channels of adult humans have been described following semi-automatic segmentation of tomographic data, thereby defining their dimensions, distributions, and connections with other vascular systems (Louis *et al.,* 2009; Patel, 2009; Rangel de Lázaro *et al.,* 2016). According to published information, the diploic channels are
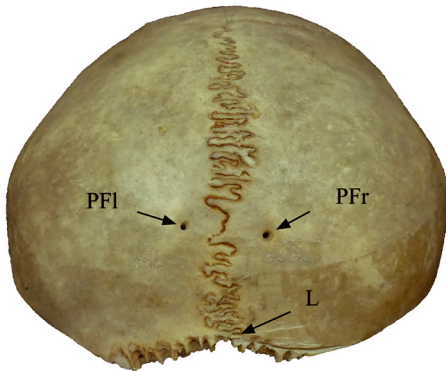
*Fig. 9 - Posterior view of the calvaria, showing the presence of paired parietal foramen. (**PFl** parietal foramen left, **PFr** parietal foramen right, **L** lambda). The colour version of this figure is available at the JASs website.*

mainly developed in the parietal areas, followed by the frontal and occipital ones. The degree of development is symmetric between sides and among particular vault areas, and there are connections with the middle meningeal artery (mostly at the pteric area) and with the emissary veins (mostly in the occipital area). The diploic system is frequently connected with the sphenoparietal and superior sagittal sinus in the parietal and frontal regions, and with the transverse/sigmoid sinuses and confluence of sinuses in the parieto-occipital areas. Due to their bridging role between endocranial and ectocranial spaces, the diploic vessels are particularly interesting in medicine and human biology, where they may represent a passage for infections and to allow the hematogenous spread of metastases (Kunz & Iliadis, 2007; Patel, 2009). It has been hypothesized that the diploic veins can avoid clot formation in extradural hematomas by creating fistulous communication with a broken meningeal artery (Ericson *et al.,* 1979). Like in the emissary veins, the absence of valves and the multiple connections with other systems allows the blood to flow in both directions according to thermal responses. These mechanisms are essential in pathological conditions such as pyrexia, stroke, or migraine. However, the evidence for an inverse blood supply in the diploic vascular system is still inconclusive (Toriumi *et al.,* 2011).

Three different histological phases of cranial growth can be identified in the vault bones (García Gil *et al.*, 2016). In children, vault bones are primarily composed of avascular lamellar bone. In contrast, the adolescent bones show a larger extension of mineralized regions (highly remodeled areas), with a reduced diploe. In adults, the vault bones are highly vascularized and the diploe is largely expanded. The sealing of the cranial bone surfaces minimizes the bone porosity while increases bone expansion (during childhood) and thickness (during youth). In this case, the sealing process could play a main role controlling head thermoregulation until the brain finishes its maturation. Ontogenetically, the presence of diploic vessels has been described in fetuses aged 7–9 months (Hershkovitz *et al.*, 1999). The function, distribution, and intensity of the network as well as its relationship with the cranial bones during the early ontogenetic stages remain unclear. In the first years of life, the fontanelles close progressively, while the diploic channels are scarcely developed and the cancellous bone is thin and uniform (Li *et al.*, 2011; Tsutsumi *et al.*, 2013). Hatipoglu *et al.* (2008) noted that the thickness of the diploic bone increases slowly before the age of 20. These age-related changes influence the morphology of the diploe space and the diploic vessels undergo a relevant expansion during the childhood (Hershkovitz *et al.*, 1999; Hatipoglu *et al.*, 2008). With age, the bone density of the external layer increases and the internal layer becomes narrower due to diminution of the calcium concentration (Skrzat *et al.*, 2004). It has also been suggested that after middle age, the progressive loss of the diploic bone can lead to an enlarged marrow cavity and replacement of the red marrow by yellow marrow, which is rich in fat components (Kohan *et al.*, 1989; Schellinger *et al.*, 2001; Gurevitch *et al.*, 2007; Li *et al.*, 2011). However, there are few reports of the normal cranial bone marrow distribution (Hajek *et al.*, 1987; Okada *et al.*, 1989; Ricci *et al.*, 1990; Moon *et al.*, 2007) and the possible consequences of these changes in relation to the diploic channels are still poorly understood. In adults, three orders of branches can be commonly recognized, with a mean lumen size of 1.5 mm (Eisová *et al.*, 2016).

Craniovascular traits in anthropology and evolution

In bioarchaeology and paleoanthropology, the endocranial vascular morphology is employed to address different scopes. The difficulties accessing the endocranial cavity of an intact cranium and the fact that the morphology represents only partial information about the vascular system have hindered the development of exhaustive hypotheses and analyses of their anatomical variations. Furthermore, their irregular shape, variability, and inconstant presence and prevalence in different human populations have prevented appropriate quantification and robust numerical treatments. Thus, much information is based on subjective and descriptive approaches, and only a limited number of traits were investigated prior to recent advances in digital anatomy. Interestingly, in some cases, more information is available for fossils than for modern human populations. Clearly, any evolutionary inference based on these traits is necessarily speculative if we lack information about their variation and functions in living humans. This is even more crucial when we consider that some of these craniovascular traits may have medical importance.

Craniovascular traits and bioarchaeology

Bioarchaeology can be defined as the contextual study of human populations across time and space based on their skeletal remains. The study of biodistances, which is one of the principal topics of bioarchaeology, aims to quantify morphological affinities or differences to compute indirect measures of biological relationships in terms of heritability, kinship, and phenetic/genetic closeness (Buikstra & Ubelaker, 1994; Larsen, 1997; Slavec, 2004). Non-metric traits are assumed to be influenced by direct genetic or indirect morphogenetic factors (Grüneberg, 1963). The presence/absence of a specific trait or its degree of expression is generally considered when scoring phenotypes, which is used as a proxy for biological relatedness. Their variation may be continuous, but thresholds and ranges are used to define categories with increasing degrees of expression (Hauser & De Stefano,

Fig. 10 - Detail of the foramen magnum. The wire passes through occipital foramen close to the posterior edge of the foramen magnum. The colour version of this figure is available at the JASs website.

1989). Specific similarity/dissimilarity distances and indexes are calculated from these datasets, which are generally based on multiple characteristics, and clustering algorithms are used to compute hierarchical and non-hierarchical group-wise and specimen-wise comparisons (Irish, 2010). These models are sensitive to different theoretical and methodological criteria, including the biological interpretation of the traits themselves, the choice of the distance metrics, and the choice of different clustering algorithms. These phenotypic distances can supply information about population history, microevolutionary processes, and specific aspects of social structure and organization (Buikstra *et al.*, 1990; Velemínský & Dobisíková, 2005; Stojanowski & Schillaci, 2006; Weiss, 2009). It should be noted that due to various operational limitations, these results should only be used to support or contrast hypotheses based on multiple forms of evidence and not as conclusive outputs.
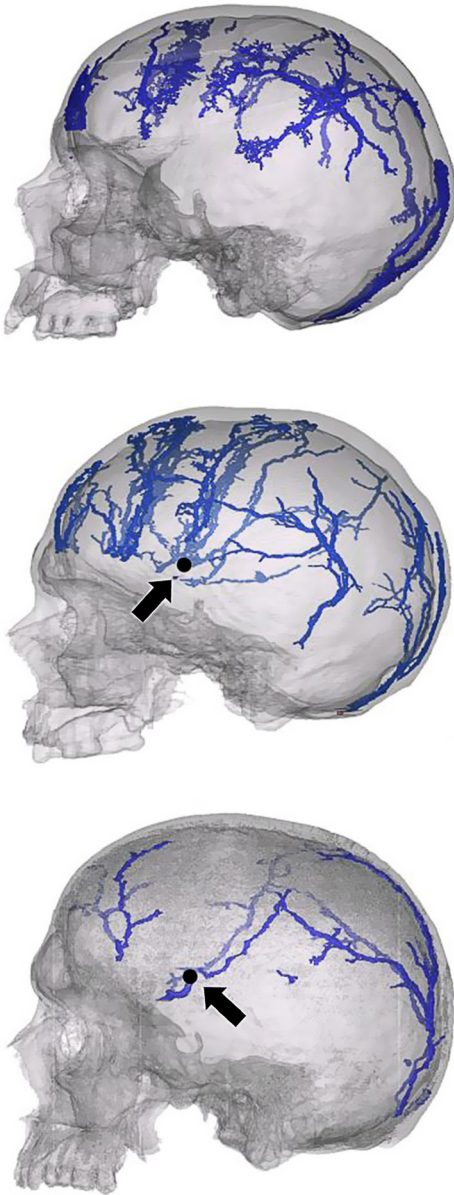
Fig. 11 - Three-dimensional reconstruction of diploic vein channels (blue) with variable degree of expression spanning from complex (above) to simple networks (below). The communications of diploic channels and middle meningeal vessels are frequent at the pteric area (black spots and arrows). The colour version of this figure is available at the JASs website.

However, among the various endocranial vascular traits, only foramina have been used frequently in bioarchaeology because most of the others cannot be scored appropriately according to quantitative criteria (e.g., Berry & Berry, 1967; Berry, 1974; Ossenberg, 1976; Ardito, 1977; Trinkaus, 1978; Conner, 1990; Sciulli, 1990; Brasili *et al.*, 1999; Sutter & Mertz, 2004; Česnys & Tutkuviene, 2007; Godde, 2010; Nikita *et al.*, 2012). In general, vascular traces are described based on their presence, general appearance, and branching patterns, but all of these variables are used infrequently in a statistical context. Thus, they are not considered to be generally applicable due to differences in etymology, scoring methods, and subsequent statistical assessment (Saunders & Rainey, 2008).

The specific traits used frequently in bioarchaeology include the foramen spinosum, mastoid foramen, parietal foramen, occipital foramen, condylar canal, and foramen of Vesalius (Hauser & De Stefano, 1989; Buikstra & Ubelaker, 1994). However, other endocranial vascular traits should be evaluated to test their suitability as biological indicators (Hauser & De Stefano, 1989). For example, enlarged occipital/marginal sinuses have been found at high frequencies in the Gravettian Upper Paleolithic Předmostí population from the Czech Republic (Matiegka, 1923). The incidence was 42% in a sample of 12 individuals, whereas the prevalence is about 2%–28% in recent populations (Ayanzen *et al.*, 2000; Kobayashi *et al.*, 2006; Das *et al.*, 2008). This high prevalence was interpreted in terms of close kinship among the individuals. The groove left behind the coronal suture by the middle meningeal veins (the sphenoparietal sinus according to some anthropologists) has been described as a characteristic feature in some populations (Jones, 1912). The diploic veins and their patterns were also proposed to support heritability and individual relationships, but the results are not conclusive (Hershkovitz *et al.*, 1999).

It should be noted that the traits are a means to an end in biodistance studies and not the actual targets of the study itself. Their

main biological importance is related to heritability and not their specific functions. Hence, these characteristics have not been investigated in detail in these fields, at least in terms of their functional aspects. Compensatory mechanisms have been described that balance vascular development during early ontogenesis with structural consequences (e.g., Solter & Paljan, 1973; Qureshi, 2014), but adequate knowledge of the possible integration among these traits is essential to evaluate their actual effectiveness as markers. Until their exact functions, morphogenetic mechanisms, and structural correlations with other features are known, any use of these features as population-based characteristics will be biased by our incomplete knowledge of their biological meaning.

Some comparative studies of non-human primates have been used to further evaluate the heritability of groups of traits. A study of genetically related macaque samples showed that some foramina traits exhibited lower heritability compared with hyperostotic features (Cheverud & Buikstra, 1982), which might support the functional importance of cranial vascular traits, possibly with minor effects of genetic and environmental factors. However, these traits exhibited relevant population differences, and thus caution is necessary when specific samples are used to generalize their degree of expression. Moreover, the results of analyses of sexual and allometric factors are not conclusive. In general, the nonmetric features do not have any discriminant value when used to evaluate sex differences (Berry & Berry, 1967; Carpenter, 1976). Thus, sex-related differences in the craniovascular traits used in biodistance studies are actually variable (see Hauser & De Stefano, 1989). According to an extensive study based on primate sample, it was concluded that sex differences have random effects and most of these features are not affected by body size (Bonis *et al.*, 2001). The relationships among craniovascular features and age are also limited by the fact that the vascular system develops during early ontogenesis and it remains stable throughout the life of an individual in adults (Lang & Brückner, 1981).

Enlarged parietal foramina (*foramina parietalia permagna*) exceeding 5 mm in the diameter have received special attention in anatomy and anthropology (Boyd, 1930; Hauser & De Stefano, 1989; Wu *et al.*, 2013). These foramina arise as an ossification defect. In fact, normal and enlarged parietal foramina are not homologous features due to their distinctive and heterochronic development (Currarino, 1976; Piagkou *et al.*, 2013). The etiology of enlarged foramina is unclear, but genetic factors might have important roles (Kutilek, *et al.*, 1997; Wuyts *et al.*, 2000; Mavrogiannis *et al.*, 2006). In particular, the enlarged form can serve as a more reliable kinship marker than common parietal foramen. Their presence may be associated with vascular and cranial structural modifications and malformations, which usually do not affect the physiology of the organism and they might remain undiscovered throughout the entire course of life of an individual (Stallworthy, 1932; Reddy *et al.*, 2000; Piagkou *et al.*, 2013). Interestingly, a rich network of vessels has been observed running from the parietal foramina toward the middle meningeal imprints (Symmers, 1895; Boyd, 1930; Stallworthy, 1932; Piagkou *et al.*, 2013). In addition to their unclear origin and functional aspects, the larger parietal foramen has been described as a shunt for sinus pericranii, which represent an unusual form of communication between the extra- and intracranial venous drainage system (Brook *et al.*, 2009).

In some cases, the preservation of the middle meningeal vessels has been described in mummified brain tissue (Kim *et al.*, 2008; Isidro *et al.*, 2015). Cranial trepanation may affect the craniovascular elements (Kurin, 2013). Interestingly, in some rare cases, trepanation can also be confused with enlarged parietal foramina (Rathbun & Mallin, 1979).

Craniovascular traits and paleoanthropology

In paleoanthropology, vascular traits are used to address both functional and phylogenetic issues because of their assumed adaptive meanings (e.g., Falk, 1986). However, their morphological variation must also consider the

functional matrix of the skull and the structural relationships among the endocranial components (Moss & Young, 1960; Bruner, 2015). Paleoneurology deals with the morphological study of the endocranial anatomy in extinct species, where anatomical surveys are often based on analyses of endocasts to reveal vascular traces, sulcal patterns, and the general proportions of the brain (Holloway *et al.*, 2004).

The homology of the origin of middle meningeal artery among hominids and hominoids has not yet been established (Diamond, 1991, 1992; Falk, 1993). In some apes and in rare cases also humans the middle meningeal artery ramifies from the internal carotid artery instead of the external carotid artery and enters the endocranial space through the orbit. Hence, it is possible that the "internally" and "externally" derived network represent independent and parallel functional elements in humans, apes and possibly hominids.

Due to clear phylogenetic variations in the middle meningeal vessel imprints in the endocranial surface, the traces of the middle meningeal artery have been considered since the earliest paleoneurological studies (see Bruner & Sherkat, 2008). Differences among hominids have been described according to the types of branching patterns, dominances of the branches, their orientations, the origins of the vessels, the presence of anastomoses, and the degree of reticulation in the networks (Grimaud-Hervé, 1997). Saban (1980; 1983) described differences among australopithecines, *Homo habilis*, *Homo erectus*, Neanderthals, and anatomically modern humans, hypothesizing an increase in the complexity of the network from primitive to derived species (Saban, 1995). Gracile australopithecines even lack traces of the middle/obelic branch in the middle meningeal vessels. The middle meningeal vessels are particularly developed on the parietal surface, most notably in modern humans. In general, the parietal areas are characterized by a high degree of vascularization in anatomically modern humans. Interestingly, the parietal cortex is also a meeting point for the anterior, middle, and posterior cerebral arteries (Haines, 2004).

The only attempt to quantify the degree of complexity in this network was based on fractal geometry and a box-counting method (Bruner *et al.*, 2005). The results did not support Saban's hypothesis that the complexity of the vessels is associated with cranial capacity, or even that there has been a gradual increase from the earliest to more recent species. The only confirmed differences were between modern humans (higher complexity of the network) and the rest of the extinct human species (lower complexity of the network). At least among modern adult humans, there is no evidence suggesting that the cranial form can influence the morphology of the vascular traces (Bruner *et al.*, 2009). Other physical factors such as endocranial pressure or meningeal thickness could theoretically influence the capacity of the vessels to leave imprints. Thus, given current information and the good correspondence between vessels and traces, the increase in the complexity of traces in modern humans may be interpreted as an increase in the complexity of their vessels. A similar difference between modern and non-modern humans has been described for the diploic channels, which are more developed in the former, particularly in the parietal bones (Rangel de Lázaro *et al.*, 2016).

The development of the meningeal vessels occurs mainly in the first year of life (Saban, 1995), which is exactly when the endocranial morphology in *Homo sapiens* undergoes a species-specific stage of parietal bulging (Neubauer *et al.*, 2009; 2010; Gunz *et al.*, 2012). Given that only our species exhibits an expanded parietal surface (Bruner, 2004; Bruner *et al.*, 2014a, 2016) and complex parietal vascularization (Bruner *et al.*, 2005; Rangel de Lázaro *et al.*, 2016), then correlations among these factors and processes are likely.

A second difference in the middle meningeal vessel traces among hominids concerns the relative proportions of the anterior and posterior branches (Grimaud-Hervé, 2004; Saban, 1995). Many archaic specimens (generally included in the *Homo erectus* hypodigm) exhibit posterior dominance of the network, where the posterior branch is more reticulated than the anterior. By contrast, most Neanderthals and modern

humans exhibit anterior dominance of the middle meningeal branches. The functional implications of these differences cannot be excluded, but they are likely to be a secondary structural consequence of different braincase arrangements. In fact, *Homo erectus* is characterized by marked platycephaly and antero-posterior elongation with bulging and projecting occipital lobes, so it is expected that the vascular network is more distributed between the anterior and posterior areas.

The dural venous sinuses have frequently received attention in paleoanthropology. Despite their marked variability at the confluence of the sinuses, Neanderthals exhibit more asymmetric and separated imprints of the transverse sinuses, which deviate from the midline (Rosas *et al.*, 2008; Peña-Melián *et al.*, 2011). In terms of absolute size and their relative proportions, Neanderthals have the widest brain among hominids (Bruner & Holloway, 2010); therefore, it can be hypothesized that this marked lateral growth may influence the observed separation of the sinuses. It remains to be evaluated whether a minor degree of continuity between endocranial sides might influence the capacity for integration and exchange among the different vascular districts, and particularly their capacity to respond to thermal stress (Bruner *et al.*, 2014a).

Another sinus that is discussed frequently in paleoneurology is the sphenoparietal sinus, although its definition and consistency should be reconsidered according to current anatomical evidence (San Millán Ruíz *et al.*, 2004). Traditionally, the sphenoparietal sinus was considered to be a structure located under the lesser sphenoid wing, where it leaves no apparent trace. In paleoanthropology, the sphenoparietal sinus actually refers to the great anterior meningeal vein (Diamond, 1992), which leaves a deep and wide sulcus close behind the coronal suture, where it connects large sagittal lacunae in the upper vault with the cavernous sinuses on the cranial base. This element is often independent of the sphenoparietal sinus *sensu stricto*. The incidence of the latter sinus is 14% in anatomically modern humans whereas it is almost always present

in Neanderthals (Grimaud-Hervé, 2004). Due to the physical overlapping with the anterior branch of the middle meningeal vessels, their respective traces may sometimes be confused. In general, the traces of the arteries have sharp edges and their diameter decreases from the endocranial base to the vault. By contrast, these sinuses have smooth edges and their diameter increases toward the vault. In addition, the petrosquamous sinuses, which connect the transverse/sigmoid sinus with middle meningeal veins and that usually disappear during the early ontogenetic stages (Butler, 1957), have been described in some extinct humans (Grimaud-Hervé, 2004). Higher incidence of the petrosquamous sinus was described in Neanderthals compared to anatomically modern humans (Rosas *et al.*, 2014).

The different vascular arrangements of the venous sinuses are also hypothesized to be associated with functional adaptations and selection associated with body posture and bipedal evolution in australopithecines (Falk, 1986). *Australopithecus afarensis* and the robust clade of the australopithecines shared a direct drainage pathway from the superior sagittal sinus to the enlarged occipital/marginal sinus, which drains blood to the vertebral venous plexus. By contrast, most gracile australopithecines species had a distinct drainage system characterized, as generally found in humans, by the absence of an enlarged occipital/marginal sinus and a higher frequency of emissary veins (parietal and mastoid). As mentioned earlier, this arrangement drains blood into the vertebral venous plexus in an upright position, whereas the blood is drained by the transverse/sigmoid sinuses into internal jugular veins in a supine position. In addition to functional hypotheses related to encephalization, bipedal posture, and thermoregulation, these traits may also suggest a phylogenetic relationship between robust australopithecines and *A. afarensis*.

Craniovascular traits and forensic sciences

Endocranial vascular features can be used in forensic contexts for identifying specific cranial parts and individual recognition. The pathological conditions associated with craniovascular

Fig. 12 - Ectocranial and endocranial view of the right lateral side of the skull with a fracture of right parietal bone, with interruption of the middle meningeal vessel imprints and calcification. The colour version of this figure is available at the JASs website.

morphology can reveal aspects of individual life history, types of injury, and even clarify the possible causes of death. In addition, specific traits could serve as complementary features to support estimates of the age at death.

Identification. Due to their complex morphology and individual variability, the endocranial and diploic vascular patterns represent individual-specific traits in a similar manner to fingerprints (Hershkovitz *et al.*, 1999). Given the existence of previous records (generally radiographic or tomographic data), the combination of only a few features can conclusively identify an individual. The diploic vessels have a large idiosyncratic component and because they are preserved within the bone thickness, they are resistant to destruction or alterations due to taphonomic and post-depositional processes. However, despite their individual specificity, the

use of these traits is rare in forensic fields. The patterns of the vascular traces can be also used to associate bone fragments from mixed samples or unknown origin, like when assembling a puzzle (Nagesh *et al.*, 2005).

Pathology and cause of death. Vascular features can reveal cranial fractures or mechanical disruptions involving bleeding and extradural/epidural, subdural, or subarachnoid hemorrhages. Hemorrhages are caused by the rupture of blood vessels with consequent hematoma (blood accumulation) in the brain, or between the brain and cranial bones. The middle meningeal artery is the most common source of epidural bleeding (Vij, 2005; Zasler *et al.*, 2006) because they are located in close proximity to the weakest cranial surface (around the pteric area) and they extend further into the parietal and squamosal bones (Ma *et al.*, 2012). The anterior and posterior meningeal arteries, the emissary veins, the dural venous sinuses, and the diploic veins are affected less commonly by hemorrhages. Epidural hemorrhages can leave some indirect evidence on cranial bones, such as cranial fractures, interrupted vascular imprints, local disappearance of the traces, and even osseous calcifications in the case of chronic hematoma (Nagane *et al.*, 1994; Teegen & Schulzt, 1994; Likovský & Drda, 2003; Vlček *et al.*, 2006; Fig. 12). Epidural bleeding can be suggested by cranial fractures, but a lack of fractures does not exclude the presence of hemorrhage. Subadult skulls are more elastic, so epidural bleeding is not necessarily accompanied by fractures (Vij, 2005). In newborns, the presence of parietal foramina can be mistaken for fractures (Chasler, 1967) and the presence of enlarged parietal foramina leads to a fragile calvarium, which increases the danger of breakages in rare cases (Landon *et al.*, 2012).

Age estimation. Arachnoid granulations and foveae have been reported to be age dependent (Le Gros Clark, 1920). The arachnoid granulations are already present during the early ontogenetic stages, but they are not impressed on the endocranial surface. The absence of imprints at a young age and their occurrence at a later age can be explained by postural changes from supine

to upright positions. Increasing pressure in the venous sinuses can push the arachnoid bodies onto the wall and induce their expansion (Adeeb *et al.*, 2013). Some studies suggest that the foveae become deeper and their number increases with advanced age. However, in adults, little or no correlation has been confirmed between foveal number and volume with age, thereby suggesting that the use of this trait is not reliable for age estimation and it should be used as a secondary marker (Grossman & Potts, 1974; Koshikawa *et al.*, 2000; Duray & Martel, 2006).

Vascular system and thermoregulation

The endocranial vascular system has many different functions in addition to oxygenation. For example, it is rarely considered that the brain itself has no "form" and its morphology is strictly dependent upon biomechanical forces, including the tensions exerted by the bone adjacent to connective tissues and the pressure provided by the blood flow, thereby acting as a "hydrostatic skeleton." One of the most important functions of the cerebral blood is thermoregulation based on the management of the input and output of the blood volume, and the subsequent balance between heat production and heat dissipation (see Bruner *et al.*, 2012). Modern humans have a brain that is approximately three times larger than a primate with a similar body size (Neubauer, 2014). The human brain uses 20%–25% of the total body energy compared with a maximum amount of 10% in other primates and 5% in other mammals (Leonard *et al.*, 2007). Neurons are extremely sensitive to heat variation and it is not clear whether our brain has a specific cooling mechanism (e.g., see Brengelman, 1993; Cabanac, 1993). Brain thermoregulation depends on many anatomical elements and physiological processes, as well as various behavioral and pathological factors (Sukstanskii & Yablonskiy, 2006; Bertolizio *et al.*, 2011; Rango *et al.*, 2012), which have specific relevance for clinical applications (Zenker & Kubik, 1996; Zhu *et al.*, 2006).

Clearly, the physiological processes that underlie brain thermoregulation cannot be investigated directly in extinct species. However, quantitative models can be designed to test correlations between anatomy and functions (Nelson & Nunneley, 1998; Collins *et al.*, 2004). Among other factors, heat dissipation also depends upon the geometry of an object, mainly as a consequence of the spatial relationships between its volume, responsible for heat production, and its surface, which dissipates heat. Size is clearly a major issue that affects heat distribution, particularly given that the volume increases at a higher rate (at a power of three) than the surface area (at a power of two). Therefore, according to this geometric rule, an isometric increase in a body or structure will lead to increased thermal accumulation. Different patterns of heat distribution can be achieved by changes of shape, thereby changing the relationships between the volume and surface of an object. Beyond the overall thermal load of the whole brain, changes in brain shape can alter heat loads of specific areas. This is particularly relevant in neuroanatomy given the complexity of the cerebral morphology and its sensitivity to heat stress. These patterns can be modeled and quantified in numerical simulations to determine the distribution of the heat loads on the endocranial surface as well as to quantify their global and local values (Bruner *et al.*, 2012; Fig. 13).

In addition to important differences in size, changes in the brain form and proportions have been described for distinct hominid species (Bruner *et al.*, 2003b). As mentioned earlier, the increases in the relative and absolute size of the brain in *Homo sapiens* are associated with marked bulging of the parietal areas (Bruner, 2004; Gunz *et al.*, 2010; Bruner *et al.*, 2011). According to a model of the temperature distribution based on endocranial geometry, it can be concluded that modern humans and Neanderthals exhibit different patterns of heat dissipation (Bruner *et al.*, 2014a). In particular, the upper parietal area of Neanderthals is very flat and closer to the brain geometrical core, representing an important surface for dissipation. By contrast, in modern humans, this area is enclosed in the deeper brain
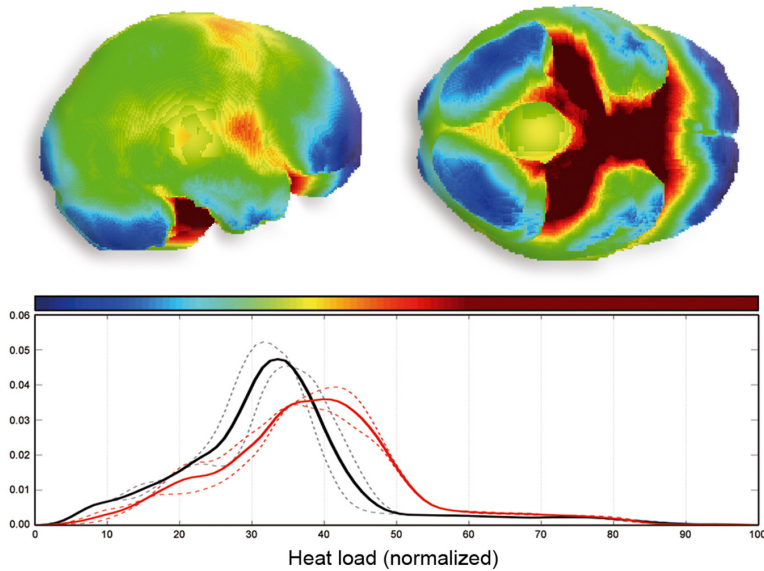
Fig. 13 - In addition to physiological mechanisms, geometry is a factor that influences the distribution of heat, which can be investigated in the context of paleoneurology. Simulations performed according to specific criteria and principles (such as the heat equation) can quantify the distribution of the heat load on the surface or throughout the volume of an object. Top: simulation based on modern human endocasts showing areas of dissipation (blue) and the accumulation (red) of heat as a function of spatial position. The basal areas are associated with a high level of heat, and they are actually highly vascularized. These patterns can be quantified and analyzed statistically. Bottom: heat distribution curves based on modern humans (black) and chimpanzees (red) after size normalization, showing different heat distributions due to differences in brain shape. These differences may be important at the global level (heat accumulation throughout the whole endocranial system) and local level (heat accumulation in specific cortical areas). The colour version of this figure is available at the JASs website.

volume after parietal bulging. Interestingly, this area correspond to the precuneus, which has a very variable extension among adult humans (Bruner *et al.*, 2014b, 2015), with very high metabolic and thermal loads (Cavanna & Trimble, 2006; Sotero & Iturria-Medina, 2011). This may be even more relevant when we consider that metabolic impairments of the precuneus have been described in the early stages of Alzheimer's disease, which is a pathology that is basically associated only with our own species (Jacobs *et al.*, 2012a,b).

The specific morphology of the meningeal and diploic vessels in our species and the persistence of these branches in adults suggest active roles for these vascular systems, which are currently not well understood. The blood flow is low or absent in adults at rest, at least in the main branches of the meningeal channels (Bruner *et al.*, 2011), which may suggest that their role is more crucial during earlier ontogenetic stages, or that these vessels probably function mainly during heat accumulation (physical activity, pathology, and alert). Furthermore, a mechanical role in hydrostatic protection cannot be excluded. Finally, it may also be hypothesized that the peculiar development of these vessels in our species is a consequence of physiological and evolutionary processes that targeted the cerebral vessels, which had secondary effect on the meningeal and diploic system via shared growth factors.

Reciprocal influences and associations can be expected among the brain size, brain shape,

metabolism, thermoregulation, and vascular system. In evolution and paleoneurology, these relationships may have adaptive value (Falk, 1990). In modern populations, the same issue may have relevance for biomedical and clinical fields. The particular arrangement and physiology of the sinuses and emissary veins led to the so called "radiator theory" (Falk, 1990). Anatomical and experimental physiological studies of recent humans have determined the presence of an extensive network of small vessels and it is mandatory to investigate the impact of this vascular small-scale component on thermal management. (Canabac & Brinnel, 1985; Zenker & Kubik, 1996). The direction of the blood flow in some emissary veins can be altered by changes in temperature. During hyperthermia, the blood in the emissary veins flows from the skin into the endocranial cavity to prevent acute damage to sensitive brain tissue. In the hypothermic state, the blood flow from the endocranial cavity to the extracranial surface is minimal or undetected. Falk (1990) assumed that the inverse flow of the cooled blood from the extracranial surface, which may be facilitated by the absence of valves, could serve as a selective brain cooling mechanism to release thermal stress during hyperthermia. This cooling system is expected to be necessary when dealing with encephalization and brain mass increases. Criticisms of this theory include the lack of a quantitative approach and the general absence of data or evidence for the physiological processes involved (e.g., Braga & Boesch, 1997). However, this hypothesis is generally accepted in paleoanthropology and it is considered to explain the evolution of the emissary foramina and the dural sinuses (Falk, 1986; Cartmill & Brown, 2009; Lieberman, 2011).

Craniovascular system and methodological issues

Working with the craniovascular morphology involves related methodological and statistical issues. Craniovascular traits are frequently scored according to categories (e.g., Berry & Berry, 1967; Falk, 1993; Bruner *et al.*, 2003a; Saunders

& Rainey, 2008), but nominal and ordinal data are difficult to analyze when dealing with correlations and multivariate approaches, and most of the methods employed are sensitive to operational choices (e.g., sample size, distance metrics, and clustering algorithms). Many characteristics can be scored only as present or absent using binary values, but these scores refer strictly to the general phenotypic appearance, and they could even be biased by the fact that similar phenotypic expressions can be the result of different biological processes, associated with non-homologous physiological responses, or due to independent functional mechanisms. Groups and classes assigned according to categories related to the expression of traits are often descriptive, and thus they are not based on clear underlying factors (e.g., Giuffrida-Ruggeri, 1912; Adachi, 1928). These limits are even more obvious when dealing with group values, particularly when using parameters to compare populations by computing means or distances (Irish, 2010; Nikita, 2015).

When establishing classes based on phenotypic expression, general grouping criteria (i.e., based on general and gross variations) are reliable but rarely informative, whereas specific grouping criteria (i.e., based on specific and detailed variations) are informative but highly subjective.

Due to all of these methodological problems, variables should be described and specified clearly, appropriate methods must be selected, and results must be tested carefully by checking for intra- and inter-observer errors. When dealing with multivariate statistics, the results must be adequately supported by statistical evaluations of their stability and reliability. All these recommendations should be carefully acknowledged during any numerical analysis, but they are particularly important when using discrete traits. Most of the available statistical methods for discrete traits are based on non-parametric approaches and, given their high variability and small inter-group differences, usually require very large samples to obtain reliable and robust statistical outputs.

A further concern arises when dealing with vascular form variation. Vessels have a fuzzy and irregular geometry but most importantly, they

are organized according to a dichotomous and pseudo-fractal structure (see Zamir, 1999, 2001). Variables such as *fractal dimension* (space-filling capacity) or *lacunarity* (the homogeneity of distribution) can be very useful when trying to quantify physical vascular properties, but we still lack a general agreement on how to recognize different geometrical or spatial groups of vascular patterns. Furthermore, thresholds are necessary to select a given range of vascular sizes, according to the resolution available for the analysis and the dimension of the vascular section. Such choices use to leave out the smaller vessels, like capillaries or sub-trabecular networks, which can have a major role in the overall vascular balance because of their fractal properties.

In terms of anatomy and sampling, a major issue concerns the digital tools that are currently available for segmentation and rendering craniovascular characteristics. CT is the only useful imaging method when working with bone remains but resolution is a crucial factor when setting the minimum vascular size for detection using densitometric data. At present, micro-CT can readily supply information at a resolution of a few microns, but this high resolution requires very large memory budgets and this causes problems with computational resources, thereby limiting its application to small areas or specific features. For diploic channels, high resolution beyond the trabecular dimensions can even introduce noise associated with the diploic spaces, which confounds the recognition of the main channels (Rangel de Lázaro *et al.*, 2016).

population, and species levels. However, we still lack much information related to variability and the mechanisms that underlies these vascular features because of methodological limits and the scarcity of analytical studies. Thus, the functional and structural relationships among cranial, cerebral, and vascular elements must be investigated carefully in living samples to provide a robust theoretical background for any hypothesis related to evolutionary processes or population dynamics. Normal, pathological, and ontogenetic variability are still ignored for most of these characteristics, which may be important for their adaptive or medical value. Compensatory mechanisms during early ontogenesis can act to maintain a functional balance in the whole system (Solter & Paljan, 1973; Schelling, 1978; Chen *et al.*, 2007; Qureshi, 2014). In addition to the internal relationships associated with intrinsic anatomical factors, genetic and environmental components should also be carefully considered. Finally, more studies are required to address the relationships between hard and soft tissues to evaluate the actual capacity for investigating these characteristics in osteological or fossil samples. This issue is a multidisciplinary field, and thus biologists, anthropologists, and medical doctors should collaborate to understand the many different sources of variation. Due to the limited information available about these vascular elements, large anatomical surveys of modern populations are required before proposing any hypotheses concerning the evolutionary and functional meaning of craniovascular features.

Final remarks

Cranial bones preserve parts of the information about the pre-existing vascular system via imprints, foramina, and channels, which can serve as evidence to address various anthropological objectives. The craniovascular imprints are morphological remnants of physiological processes related to metabolism and thermoregulation. This review describes the differences and patterns associated with variation at the individual,

Acknowledgments

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Associate Editor, Markus Bastir