

# The middle meningeal artery: from clinics to fossils

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## Abstract

**Introduction** Although research today ranges from molecular to universe scale, many issues regarding gross anatomy remain totally neglected. Within the framework of the endocranial morphogenesis and evolution, understanding the role and variation of the middle meningeal artery relies upon the very limited, scattered, and descriptive information available. The meninges are supplied by branches originating from both the internal and external carotid arteries, often converging in the same networks and hence raising questions on the homology and embryogenesis of these vessels. The middle meningeal artery is often ligated during craniotomies, with no apparent impairment of the cerebral functional processes. The exact physiological role of this extended vascular system, together with the adaptations and selective pressure associated with its evolutionary characterization, have generally been ignored.

**The middle meningeal vessels in nonhuman primates** Anthropologists have made many attempts to quantify and qualify the differences and variation between and within human and nonhuman primates, with scarce results due to the blurry morphology of the vascular networks. Living apes and humans probably have meningeal vessels originating from different embryogenetic processes, further hampering easy phylogenetic comparisons. Generally, monkeys and apes

display a larger component derived from the internal carotid artery and its ophthalmic branch.

**Evolution and morphological variation in fossil hominids** The fossil endocasts partially show the traces of the middle meningeal vessels, allowing some hypotheses on the evolution of these structures. In contrast with modern humans, some extinct groups show a dominance of the posterior branch over the anterior one. The most interesting features are associated with the variation of the middle branch, which supplies the parietal areas. In any case, the most striking difference between the modern and non-modern humans regard the definite increase in the number and complexity of the anastomoses and reticulation in the former. This may be either the simple result of a larger percentage of traces left by the soft tissue or be associated with a more developed vascular network.

**Perspectives** Tools are needed to quantify and qualify the morphogenesis and variations of the middle meningeal artery. Supposing these vessels are not strictly necessary in the adult age, the evolutionary pressure shaping their structure may have been associated with early life stages. Apart from oxygenation, another function which deserves attention is thermoregulation, considering the metabolic loadings of the cerebral mass.

**Keywords** Endocranium · Vascular system · Human evolution · Paleoneurology

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## Introduction

The scale of scientific investigation has considerably extended in range over the past century, from molecules to galaxies. Naturally, micro- and macroscopic studies represent the vast majority of scientific projects because of the consequent fas-

cinating challenges and possible pragmatic applications. Nonetheless, the recent application of computed modeling, biomedical imaging, and multivariate analytical approaches, supports a renewed interest for medium-sized targets investigated in anatomy and morphology [12]. At the same time, concepts such as morphological integration [22], heterochrony [47], and modularity [23, 48], have been reevaluated and developed. Hence, the phenotype is no more intended as a mere sum of anatomical traits, but as a single anatomical system, in which all the traits are related through a network of functional and structural relationships. Morphometrics aims to study such relationships, ontogenetic or evolutionary, associated with the normal morphogenesis or with pathological and subpathological variations.

Naturally, the skull represents one of the major topics in this sense because of the large amount of evolutionary information available within its structures and its fundamental role in almost every biomedical field [4, 6, 13]. In particular, one of the most intriguing topics concerns the study of the evolutionary and morphogenetic dynamics between neurocranium and brain [59].

The first true and helpful information available after these early years of morphometric revolution was to recognize that we almost entirely ignore the dynamics and the variations of macroscopic anatomical organization. The correlations between traits, their morphogenetic patterns, the population and sexual differences, the external and internal influences affecting the final phenotype have been never investigated in a quantitative manner, or through the use of robust analytical models. Naturally, if the variation and dynamics of many anatomical characters are ignored for current human populations (for which large sample sizes are clearly available), one can imagine how little they can be considered in evolutionary studies due to the limited number of fossil specimens.

One of these characters is the middle meningeal artery. The size of these vessels makes them a clear morphological component of the endocranial anatomy. Their position, intermediate between the cortical volumes of the brain and the endocranial wall, would seem to indicate some form of biological relevance. Taking into account the fact that the vessels leave their traces on the endocranial bones, this vascular system also represents a good opportunity to investigate physiological processes in fossil species [10]. Apart from this general lack of information concerning its embryological nature and homology compared to primate variability [26, 32, 33], the difficulties in applying categories to such a complex morphology [17, 38] means that these structures are quite often neglected in morphometrics.

This review aims to provide a simple but multidisciplinary synthesis of the current knowledge concerning the morphogenesis, variation, and evolution of the middle meningeal artery, and to promote possible future applications and studies in this area.

## Anatomy and morphogenesis

The middle meningeal artery (MMA) in most individuals arises from the maxillary branch of the external carotid artery and enters the skull through the foramen spinosum (or in some rare cases through the petrosphenoid fissure). It then divides into anterior and posterior branches to supply the dura and adjacent calvarium. There have been a few reports of different origins of the middle meningeal artery from branches of the internal carotid artery. In the most common variation, the middle meningeal artery originates from the ophthalmic artery (ophthalmic middle meningeal artery). Dilenge and Ascherl [27] found 17 cases of MMA arising from the ophthalmic artery among 3,500 cerebral angiograms examined (0.5%). The earliest cases of MMA arising from the ophthalmic artery were described by Curnow [24] and Zuerkandl [71]. In some cases, this anomaly is associated with the absence of any external carotid artery contribution to the middle meningeal artery and agenesis of the foramen spinosum [54]. A less common origin of the middle meningeal artery from the internal carotid artery circulation is the “stapedial-middle meningeal artery”. This variation, first documented by Altmann [3], is very rare. House and Patterson [45] encountered this pattern only twice during 8,000 procedures on the middle ear, whereas Steffen [64] noticed only two cases during 10,000 middle ear operations. First reported by Hyrtl in 1836 [46], only around 30 cases of this variation reported in the literature are probably the result of failure of the embryonic stapedial artery to involute. The stapedial artery derives from the second aortic arch and connects to the developing internal carotid artery (third arch) via the hyoid artery. The stapedial artery then develops two main branches: a supraorbital division from which the extraocular arteries and intracranial middle meningeal artery arise and a maxillofacial division. As the embryo develops, the stapedial artery involutes, and the maxillofacial division joins the external carotid artery to form the maxillary artery, including the segment that will later become the extracranial middle meningeal artery. A persistent stapedial artery enters the middle ear, passes through the stapes, travels through the facial canal, exits via the stapedial foramen near the geniculate ganglion, continues between the dura and bone of the middle cranial fossa, and anastomoses with the middle meningeal artery.

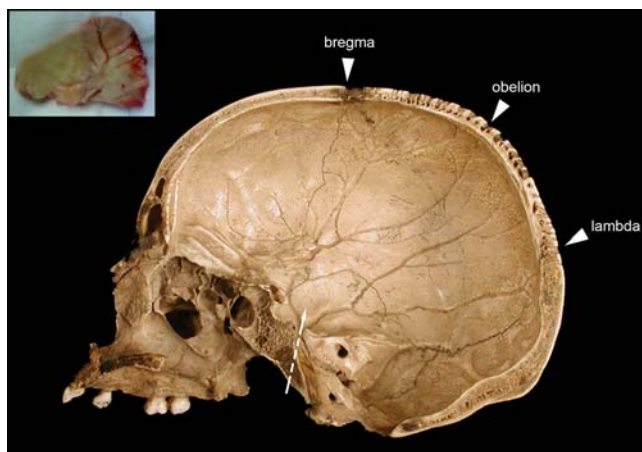
Generally, the middle meningeal artery is organized in three main branches. The anterior (or bregmatic) branch runs posteriorly to the coronal suture, the middle branch (obelic) lies along the area of the lateral sulcus reaching the parietal regions, and the posterior branch (lambdatic) follows the lower border of the temporal lobe. The associated meningeal veins originate from lacunae lateral to the superior sagittal sinus, draining into the pterygoid venous plexus. According to Saban [62], the first anastomotic channels can be detected at the 40th day, the vascular complexity increases during the

first year of life, the rate of growth decreases at around 2.5 years, being almost fully developed at the age of 5 and complete at 6.5. Since neonatal age, the right vascular network seems to be more reticulated and developed than the left system. Nonetheless, the hemispheric differences are not so clear. It has been suggested that the right network develops faster [62] and also that modern humans show a left dominance [41]. Currently, no marked differences have been confirmed regarding asymmetries, age, sex, or race [32, 53, 57].

Of course, minor but interesting variations cannot be evidenced using the descriptive and subjective approaches generally available for these kinds of anatomical surveys. The traces of middle meningeal vessels (Fig. 1) have been investigated in anthropology since the beginning of the 20th century. It was soon recognized that a certain kind of information could be obtained from the presence and derivation of the middle branch (the obelic ramus), associated with the vascularization of the parietal areas. In particular, this branch can originate from the anterior ramus, from the posterior one, or from both [36]. Many different classifications were then proposed [see 17 and 38 for further information], but with scarce results because of the extreme heterogeneity of the patterns, the elusive and complex nature of the vascular morphology, and the large subjectivity involved in the scoring procedures. After many attempts, the most applied scoring method is still the one based on the derivation of the obelic branch, namely, the Adachi classes: obelic branch from the anterior ramus (Adachi type I), from the posterior ramus (Adachi type II), or from both (Adachi

type III) [32]. Even if largely used, also the Adachi typologies suffer from certain subjectivity, mainly related in modern humans to the large anastomotic networks converging on the middle branch from both the anterior and posterior districts. In fact, the prevalence of the three patterns may vary consistently between different authors [see 17, 32, 38].

The morphogenetic variables involved in shaping this vascular system are far from understood. Nerves and vessels often share common molecular factors [28]. On the other hand, the angiogenesis is directly associated with neurocranial growth, physically through mechanical transduction or by biochemical signaling [42]. Accordingly, the study of the vascular system must be necessarily related to the evolutionary and ontogenetic adaptations and constraints of both the brain and bone structures. In fact, because of the intimate relationship between vessels, neurocranium, and cortical surfaces, the study of meningeal vascularization represents a good opportunity to investigate the brain vs. braincase dynamics. Interestingly, both the artificial deformations of the skull for aesthetical practices and the craniosynostoses are associated with consequential changes in the vascular organization, with the vessels following the altered direction of the brain growth forces [57]. On the other hand, plagiocephaly has been hypothesized to influence the vascular development more than the shape of the vascular networks [53]. Taking into account all these observations, it seems clear that vascular morphogenesis is the ultimate result of the interaction between a phylogenetic background (genes), functional and physiological environment (molecules), and biomechanical framework (strains, forces).



**Fig. 1** Midsagittal section of a modern human skull, showing the imprints of the middle meningeal vessels and some neurocranial craniometric landmarks: bregma (fronto-parietal junction), lambda (parieto-occipital junction), and obelion (parietal foramina for the passage of the parietal emissary veins). The *arrow* shows the entrance of the middle meningeal artery, through the foramen spinosum. The *upper frame* shows an endocranial fragment after neurosurgical removal, with traces of the middle meningeal vessels. Generally, the pattern of the vascular network and the resulting imprints are very similar, at least in their general morphology

### Current neurosurgery and clinical relevance

Epidural hematoma (EDH) is a traumatic accumulation of blood between the inner table of the skull and the stripped-off dural membrane. The inciting event is often a direct blow to the head. In 85–95% of patients, this type of trauma results in an overlying fracture of the skull [2, 8, 35]. Blood vessels in close proximity to the fracture are the sources of the hemorrhage in the formation of an EDH. Because the underlying brain has usually been minimally injured, prognosis is excellent if treated aggressively. Outcome from surgical decompression and repair is related directly to a patient's preoperative neurological condition. EDH occurs in 1–2% of all head trauma cases and in about 10% of patients who go into a traumatic coma. The temporo-parietal region and the middle meningeal artery are involved most commonly (66%), although the anterior ethmoidal artery may be involved in frontal injuries, the transverse or sigmoid sinus in occipital injuries, and the superior sagittal sinus in traumas at the vertex. Bilateral epidural hematomas account for 2–10% of all acute epidural hematomas in adults but are ex-

ceedingly rare in children. Posterior fossa epidural hematomas represent 5% of all cases of epidural hematomas [70].

The middle meningeal artery represents the source of bleeding in 85% of epidural hematomas. The endocranial arterial blood accumulation dislocates the cerebral structures that herniate and cause fatal brain stem compression. Therefore, the epidural hematoma is a life-threatening complication of skull fractures and needs to be surgically evacuated. In supra-tentorial hematomas, the surgical treatment includes a bone flap made over the greater diameter of the clot, with the exposure of the foramen spinosum. After removing the blood clot, the middle meningeal artery is ligated as close as possible to the foramen, in order to stop the arterial bleeding from its main trunk. In the absence of brain injuries, a dramatic recovery of neurological impairment is usually observed, soon after the surgical procedure. The patient is frequently discharged within a week after surgery. At present, no functional impairments are known to be associated with the suppression of the middle meningeal vascularization.

Some neurosurgical risks are associated with uncommon meningeal patterns. The preoperative embolization of dural lesions supplied by meningeal vessels of ophthalmic origin is dangerous due to the risk of embolization into the ophthalmic circle [52]. Also, a persistent stapedia artery can cause dangerous bleeding during middle ear surgery.

### The middle meningeal vessels in nonhuman primates

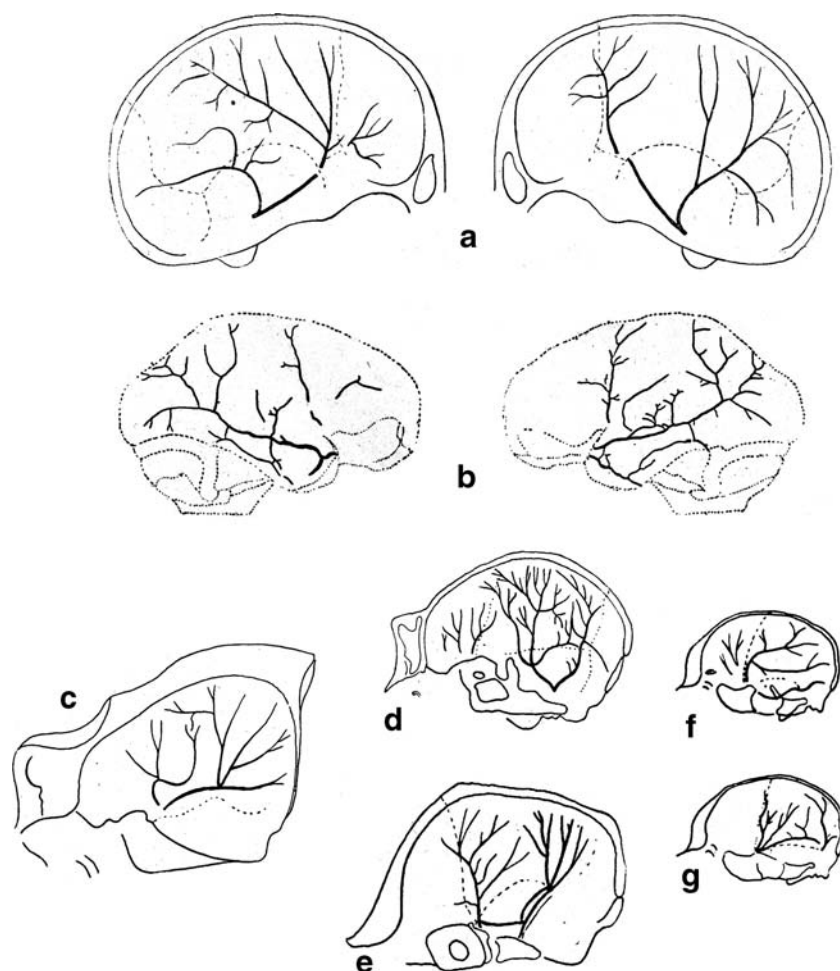
The data concerning the variation within and between species for the meningeal vessels are mainly based on the imprints left on the endocranial wall. The samples available for such investigations (i.e., museal collections; Fig. 2) are definitely larger than those available for dissection and direct visual inspection of the soft tissues. However, the precise source of such imprints remains unclear. Some authors refer to the imprints as arterial marks, while others suggest that they are mainly related to veins. This second approach is based on the consideration that veins are generally more superficial than their arterial counterpart. Because of the close contact between the middle meningeal artery and a couple of parameningeal veins, it has been suggested that the traces are left by the veins, but following the pattern of the artery [see 32]. It has also been hypothesized that arterial pressure influences the generation of the traces indirectly [62], and when the cerebral pressure is increased (as in craniosynostoses), the arteries may contribute to the imprinting process providing more convoluted marks [57]. Of course, a source of confusion is associated with the incautious use of the words “arteries” and “veins” (the original anatomical elements) instead of “imprints” (their residual evidence). Apart from the uncertain origin of the endocranial marks, it must always be



**Fig. 2** The morphological studies on the phylogenetic variation of the endocranial vessels are mostly based on endocast collections from zoological and anthropological museums (here, a chimpanzee endocast on the left, and a gorilla endocast on the right). The endocranial casts are generally moulded with plaster of Paris, silicon, or epoxy resins [44]. In recent years, computed tomography and digital reconstruction have substituted the physical replicas [10, 63]. When the original specimen is not available or the endocranium cannot be explored, the casting technique largely influences the rendering of the middle meningeal imprints

taken into account that the traces are related to a certain percentage of the preexisting soft tissues. Local factors (like meningeal thickness or endocranial pressure) change the relationship between vessels and bones, leading to a lack of complete correspondence between the vascular network and the consequent endocranial pattern. In any case, neurosurgical practice, in general, suggests that there is a good and reliable correspondence between soft tissue and bone traces, at least regarding the overall appearance.

The major problem in assessing the current and phylogenetic variation of these vascular systems in primates is a probable lack of homology between the vessels characterizing the different species [26] (Fig. 3). In nonhuman primates, the vascular network associated with the internal carotid artery (ophthalmic artery and its lacrimal branch) is definitely more relevant than in modern humans. In macaques, the anterior areas are supplied by an anterior meningeal artery, which may be homologous with the lacrimal artery of the great apes or with the anterior branch of the middle meningeal artery of modern humans [33]. The anterior branch of the middle meningeal artery could be even homologous to the lacrimal artery itself [56]. In any case, the anterior meningeal system is associated with the ophthalmic branch of the internal carotid. Falk and Nicholls [33] detected a dominant anterior system in macaques in 69% of the cases, anterior–middle codominance in 24% of the cases, and a dominant middle meningeal network in the remaining 6% of cases. Posteriorly, the middle meningeal vascularization is inversely proportional to the development of the posterior meningeal artery. Macaques show no evident sexual or hemispheric differences in the distribution of these vascular patterns.



**Fig. 3** The middle meningeal vessels of the extant and extinct primates show very different patterns. The homology between the different branches and their embryologic and morphogenetic origin is still cause for debate, due to the scarce information available on these structures and their variation. **a** Modern human, showing the middle branch originating

from the anterior (*left*) and posterior (*right*) ramus; **b** Asian *H. erectus* (Zhoukoudien III, between 300.000 and 500.000 years before present); **c** Gorilla; **d** Chimp; **e** Orangutan; **f** Gibbon; **g** Macaque (after Marcozzi [53])

Also in apes, the anterior vascularization is often fused with the middle meningeal system through additional channels [26]. The vessels joining the two systems pass through the superior orbital fissure (sphenoidal artery) or through the cranio-orbital foramen (meningo-lacrimal artery—maybe homologous with the superior branch of the stapedial artery). The former passage is associated with the sphenoparietal sulcus, which houses the sphenoparietal sinus (sometimes called Breschet’s sinus, while others call it the great anterior vein) and the sphenoidal artery. A high prevalence of this trait is evident in humans and orangs, both genera also showing a lateral expansion of the superior orbital fissure. The latter passage is localized on the great wings of the sphenoid, and it is also called lacrimal foramen, Hyrtl foramen, meningo-orbital foramen, or spheno-frontal foramen. In modern humans, this foramen is present in 42% of the hemicrania [26]. When the ophthalmic artery substitutes the

middle meningeal network entirely, the foramen spinosum is absent, and there are no imprints on the middle fossa.

Gibbons have a vascularization which is mainly based on the anterior (ophthalmic) system, passing antero-posteriorly through the superior orbital fissure and lacking the foramen spinosum [53]. In general, orangs also show a larger contribution of the orbital system, while chimps show a dominance of the middle meningeal network, as described in humans [32]. The middle meningeal artery in chimps is mainly developed anteriorly, and interestingly, its traces are even more reticulated than in humans [53]. On the other hand, the main middle meningeal vessels in orangs are associated with the obelic/parietal branches, from the posterior ramus. There are some differences between chimps and gorillas, but there is no statistical evidence regarding this matter. Gorillas display more heterogeneous patterns, often showing a developed “pre-obelic” branch [53]. There is also

no evidence of differences in the vascular patterns between hemispheres, age classes, or sexes. Figure 4 synthesizes the relationships between the main vascular elements associated with the middle meningeal network.

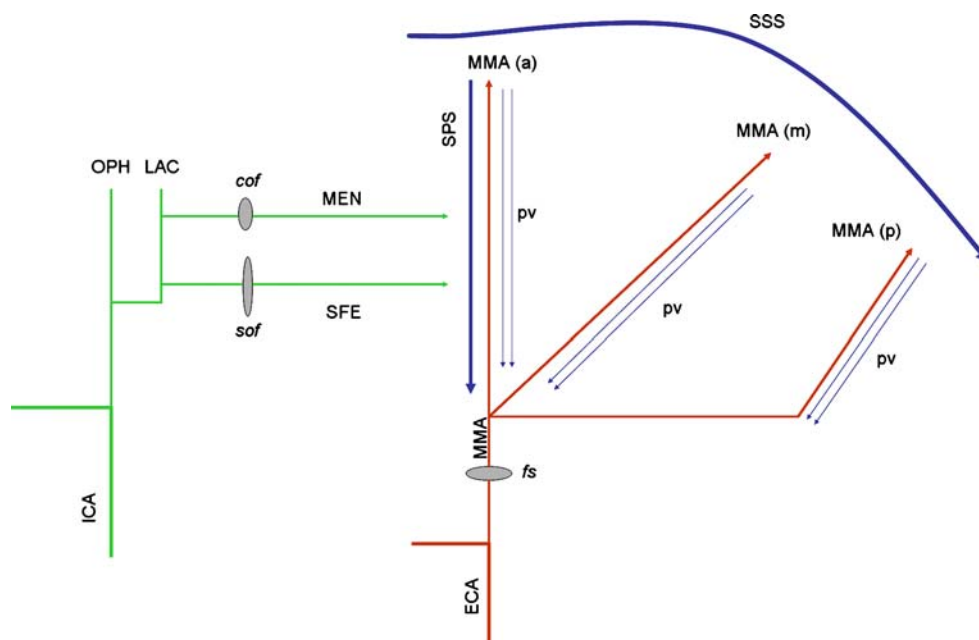
### Evolution and morphological variation in fossil hominids

Information concerning the fossil record is rather scattered, and the problems encountered in the quantification of the middle meningeal patterns are accentuated because of the small and fragmented samples available in paleontology. Paleoneurology (the morphological study of the endocranial anatomy in extinct species) [10, 30, 43, 66] deals with the reconstruction of endocranial casts (or endocasts; Fig. 5) [44].

According to the available fossil record, gracile Australopithecinae (genus *Australopithecus*) display only two middle meningeal branches, a developed anterior (ophthalmic) vascular system [62], and the superior orbital fissure show a morphology comparable with the African apes [26, 58]. Therefore, it may be hypothesized that these species possibly lacked the derived traits which connect the anterior and posterior endocranial systems, possibly evolved through parallelism in humans and orangs.

The human genus evolved in Africa around two million years ago, and then produced divergent lineages which popu-

lated Africa, Europe, and Asia [see 13 for a general overview]. Compared with anatomically modern humans, almost all the extinct species show very simple meningeal networks, at least when considering their endocranial imprints. It has been suggested that the encephalization process was associated with an increasing degree of complexity of the vascular system, paralleling the ontogenetic trajectory [62]. Of course, this interpretation was based on an old-fashioned linear, gradual, and progressive perspective of evolutionary change, which is unlikely considering current knowledge in paleontology and evolutionary biology [e.g., 67, 68]. Recently, the complexity of the middle meningeal traces in the human genus has been investigated with fractal analysis, which is able to quantify the degree of reticulation of linear networks [20]. The results suggest that all the extinct humans share the same low level of reticulation, independent of their cranial capacity, while only *Homo sapiens* display a significant increase of imprint complexity. Clearly, more traces could mean more vessels or, alternatively, simply more imprints. In the first case, a functional/physiological interpretation would be required, while the second hypothesis would involve some changes in the structural relationship between brain and braincase, with a larger percentage of vessels leaving their imprints on the endocranial wall. It is worth noting that reticulation in modern humans is particularly evident at the parietal surface, ever since many Late Pleistocene modern populations [that is, between 20 and 50 thousands years ago (ka); 38, 61]. This is quite interesting if one considers that

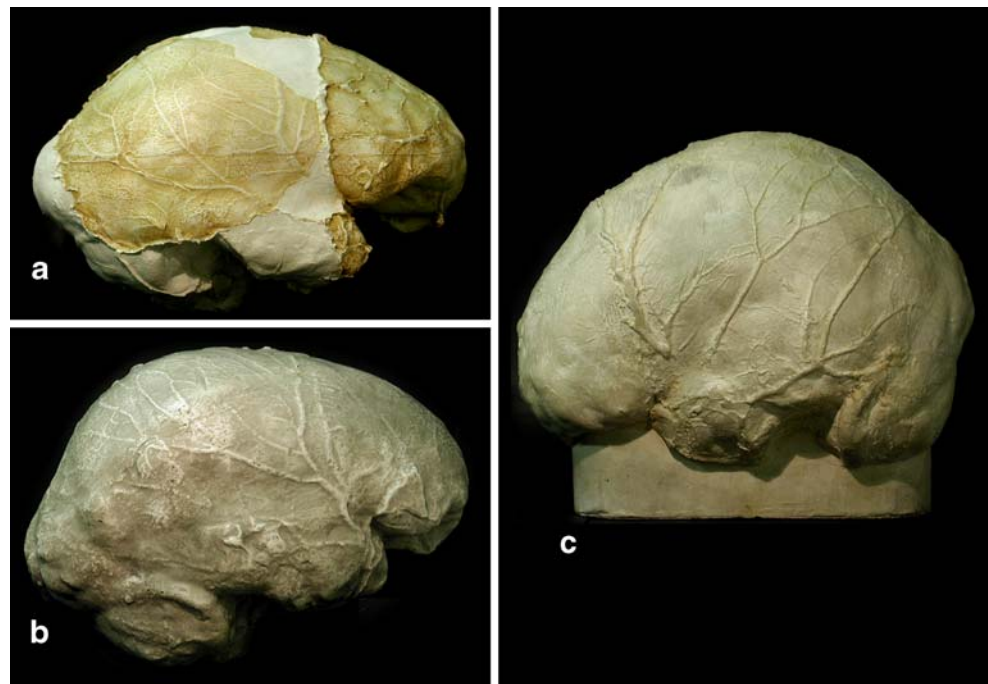


**Fig. 4** Schematic diagram of the main vascular elements associated with the middle meningeal network (mostly according to Diamond [26]). The arrows show the direction of the blood flow. Green Ophthalmic system, red middle meningeal artery, blue venous system. Arteries: ECA external carotid artery, ICA internal carotid artery, LAC lacrimal artery, MEN

meningo-orbital artery, MMA middle meningeal artery (*a* anterior branch, *m* middle branch, *p* posterior branch), OPH ophthalmic artery, SFE sphenoidal artery. Veins: *pv* parameningeal veins, SPS sphenoparietal sinus, SSS superior sagittal sinus. Endocranial passages: *cof* cranio-orbital foramen, *fs* foramen spinosum, *sof* superior orbital fissure

**Fig. 5** Endocasts from European human fossil specimens, showing the imprints of the middle meningeal vessels:

**a** Arago (France, about 450,000 years before present); Combe Capelle (France, about 25,000 ybp); Vatte di Zambana (Italy, about 8,000 ybp)



changes at the parietal lobes are hypothesized to be a distinctive trait associated with the evolution of the modern lineage [11, 14, 15, 18]. Naturally, neural differences can be responsible for both the functional or structural hypotheses concerning the increased reticulation of the parietal vascular marks.

Although the presence of extended anastomotic channels was easily recognized as a supposed autapomorphic trait of *H. sapiens*, there are nonetheless some relevant exceptions in which non-modern specimens display very complex and reticulated traces, such as in the Neandertals from Biache [60] and Krapina [21], or in the Middle Pleistocene specimens from Arago [39] (Fig. 5a) and Swanscombe [62].

Other features have been tentatively associated with specific human lineages. The Asian *Homo erectus* endocranial cast shows a large prevalence of codominance between the anterior and posterior middle meningeal traces (the Indonesian specimens) or dominance of the posterior branch (the Chinese populations) [20, 37, 38, 41]. On the other hand, Neandertals and modern humans show a definite dominance of the anterior branch. Of course, the situation is not always so easy to interpret and describe. Some early humans (*Homo ergaster*) show a very light dominance of the anterior network [5], while some early Neandertals display more developed posterior channels [16, 21]. A posterior dominance of the meningeal network was once interpreted as a primitive trait, both in phylogenetic and even racial terms. Nonetheless, considering the heterogeneous situation described for modern humans, extinct humans, and nonhuman primates, it seems clear that no progressive and linear changes can be identified in this framework and that the posterior dominance in some

fossil morphs could be a specialization associated with neurocranial constraints. Interestingly, as previously mentioned, a posterior dominance has been described for Asian *H. erectus* and early Neandertals: both are very platycephalic, and the former also have a marked posterior projection of the occipital lobes. That is, their meningeal configuration can be simply a structural consequence of the antero-posterior stretching of the endocranial morphology. Interestingly, the *H. erectus* specimen showing the most rounded (that is, the less platycephalic) neurocranial morphology, Sambungmacan 3, also displays a well-developed anterior meningeal vascular network [9]. In any case, a more developed posterior network has also been described for other European Middle Pleistocene specimens, such as the skull from Reilingen [25], and the very limited sample size hampers any statistical modeling of the variation.

Furthermore, it should be also taken into account that in some *H. erectus* endocasts, the anterior vascular network has been hypothesized to be derived from the orbital system, namely, from the internal carotid artery and not from the middle meningeal vessels [32, 69]. If this is the case, of course, the interpretation of the bregmatic, obelic, and lambdatic branches (as well as the Adachi classification) is misleading not only for nonhuman primates and Australopiths, but also for the archaic human species. It must be noted that an anterior branch which is quite isolated from the posterior system and which originates around the anterior portion of the lateral sulcus (i.e., possibly entering the endocranium from the superior-orbital fissure/cranio-orbital foramen) can be similarly hypothesized for other Afro-European Middle Pleistocene specimens [compare figures in references 7 and 25].

Concerning *H. sapiens*, the origin of modern humans is still poorly described in terms of fossils, but there is a general agreement in recognizing anatomically modern populations in Africa/Near East at about 100–200 ka [65]. The fossil skull from Jebel Irhoud found in Morocco and dated at about 150 ka shows some modern facial traits, but a quite archaic neurocranium [18, 19]. Although its endocast does not show a modern-like morphology [15], the middle meningeal artery shows anterior dominance and a vascular network which is quite reticulated and anastomized [40]. Nonetheless, another late Middle Pleistocene African endocast possibly related with the modern human lineage [the skull from Eliye Springs from Kenya—see 7] seems to have a more developed posterior branch and a very simply vascular system.

In any case, as soon as modern cranial morphology becomes fully evolved, the middle meningeal traces show a definite increase in the whole vascularization pattern and anastomoses, notably around the parietal surface [34, 38, 61] (Fig. 5b,c). Concerning left–right dominance and vascular asymmetry, if these traits are yet to be defined for modern humans, for the fossil record they are even more uncertain and cause for debate [41].

## Perspectives

At the beginning of the 21st century, we have at least one certainty concerning the middle meningeal artery: its morphogenesis, functions, variations, and evolution have been largely ignored. This is quite odd considering it concerns macroanatomy, which requires no extreme technical investigations or expensive tools. We can imagine that such a lack of information is due to at least three raw reasons. Firstly, after the age of molecular studies, macroanatomical topics have been neglected, precisely in a period in which the technical and conceptual advances could have provided an interesting improvement in these issues. Secondly, there is a lack of large anatomical/osteological collections in which such investigations can be successfully performed through inferential statistics on robust sample sizes. Thirdly, the fragile tissutal nature of the middle meningeal vascular system and its fuzzy morphology prevent most of the classical quantification approaches, allowing only subjective and descriptive analyses.

The morphogenetic framework deserves attention, taking into consideration both the functional and structural variables involved in this vascular system. The spatial relationships between the skull components and their physical interaction play a major role in shaping the cranial architecture [29]. Furthermore, the vascular channels are strictly associated with the meningeal layers, which, in turn, represent the principal tensors within the neurocranial structural context [55]. During embryogenesis, as well as during the following life-

time, biomechanical and molecular signals can concur to generate the functional context underlying the physiological and anatomical processes characterizing some relevant endocranial dynamics. Undoubtedly, the function itself of this vascular network requires robust hypotheses to be tested using neontological and paleontological information. On one hand, the middle meningeal artery is generally eliminated during neurosurgical treatments with no known physiological consequences. On the other hand, the variation associated with the modern and non-modern humans (and generally in the whole Order of Primates) suggests a certain “evolutionary investment”, which can far be explained in terms of adaptations or phylogeny. This evidence may suggest that the role of the meningeal vessels can be mainly exerted (and selected, in terms of evolution) during the embryogenesis, or at least before the adult stage. Naturally, longitudinal studies may be a very interesting tool to analyze this possibility.

There are two basic possible functional roles for the middle meningeal vessels: oxygenation and thermoregulation. Oxygenation is associated with the dura layers more than with cortical brain volumes. The degree of continuity between the arterial and venous systems (superior sagittal sinus, parameningeal veins) may suggest a short persistence of the hematic flow in these channels, and a consequent scarce molecular exchange. According to this supposed minor relevance in tissutal oxygenation, the hypothesis of a relevant role in thermoregulation gains more weight. The brain is the most expensive organ in modern humans in terms of energy requirement. Nonhuman primates allocate less than 8% of the basal metabolism to the brain mass, while an adult human spends about 21% of its energy budget on the central nervous system [49, 50, 51]. This percentage in infants and newborns is definitely higher, reaching 80% for some ontogenetic early stages. Because humans have the same total metabolism of any other mammal according to their body size, it has been suggested that such reallocation of energy in human evolution has been achieved at the expense of other tissues, namely, those involved in the digestive system [1]. The basic way in which the brain regulates inner temperature is by arranging the input/output of the blood volume, i.e., introducing and eliminating heat via the vascular channels. Heat loading associated with encephalization has already been hypothesized for some hominid species preceding the evolution of the human genus [31]. It is therefore not unlikely that the most marked encephalized species of the human lineage did experience adaptations required to evolve such a large brain mass or at least such an expensive organ. In this sense, the observation that Neandertals and modern humans share the same cranial capacity but not the same meningeal traces raises the interesting question regarding the possible association between the vascular system and metabolic rates of the brain. It must be taken into account that the cranium has four basic vascular systems: cerebral (in

the depth of the brain mass), meningeal (at the brain/bone interface), diploic (within the bone volumes), and pericranial (outside the braincase) [62]. These cranial vascular systems are quite different in terms of anatomical localization, but they are in continuous contact and exchange. They work as a single functional hydrodynamic system, able to shift blood flow from one level to another whenever necessary. Accordingly, inferences considering only one of these four sub-systems are surely partial.

Any functional relevance of the middle meningeal vessels, possibly more exerted in the early life stages, must be properly interpreted within the endocranial structural context (brain vs. braincase morphogenesis) and within the evolutionary and phylogenetic variation. This means that only integrated efforts using different approaches and the information from different disciplines can provide reliable and robust hypotheses on the biological framework underlying the morphology and evolution of these vascular systems.

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