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Internal carotid supply to the parietal meninges: a comparative study based on cranio-orbital vascular traces in modern humans and Indonesian *Homo erectus*

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Abstract The recurrent branch of the ophthalmic artery which originates from the internal carotid artery, or the recurrent meningeal artery (RMA), often extends to the parietal meninges in non-human haplorrhines. The RMA usually enters the cranial cavity via the superior orbital fissure (SOF) in modern humans and generally via the cranio-orbital foramen (COF) in non-human haplorrhines. The present study aimed to clarify how often the RMA extends its territory to the parietal meninges and via which pathway it enters the cranial cavity in Indonesian *Homo erectus*. This study also aimed to enhance our knowledge of cranial vascular traces in modern humans. The caliber of the COF and the associated vascular trajectories were examined in 156 sides of 78 modern Japanese crania and 12 sides of eight Indonesian *H. erectus* specimens. The results showed that two Indonesian *H. erectus* crania (Sambungmacan 4 and Ngawi) had a large COF unilaterally, via which the RMA probably extended its territory to the parietal region. The prevalence of RMA reaching the parietal region in Indonesian *H. erectus* (16.7%) was not as high as that in the extant great apes, but significantly higher than that in *Homo sapiens* (0.6% in this study; 3% at most in general). These results suggest that the SOF-related RMA became predominant in *H. sapiens* or the ancestor sometime in the Pleistocene, while the middle meningeal artery (MMA) arising from the external carotid–maxillary artery might not have been so enhanced in *H. erectus* and their ancestral hominins versus modern humans. The possible influence of encephalization and other factors on the evolutionary changes of the RMA and MMA can be hypothesized based on ontogenetic and hemodynamic assumptions.

Key words: recurrent meningeal artery, cranio-orbital foramen, middle meningeal artery, sphenoidal artery, *Homo erectus*

Introduction

Phylogenetic variations of the craniovascular system in human lineages have been studied, with a particular focus on the middle meningeal vessels, venous sinuses, diploic vessels, and internal carotid artery (Grimaud-Hervé, 2004; Bruner and Sherkat, 2008; Bruner et al., 2011; Rangel de Lázaro et al., 2016; Pišová et al., 2017; Seymour et al., 2019). Involvement of the internal carotid–ophthalmic artery in parietal meningeal vascularization also shows arresting species differences; in non-human haplorrhines, the ophthalmic arterial system often gives off the branch, known as the anterior/lacrimal meningeal artery, to the anterior or entire parietal region (Castelli and Huelke, 1965; Bugge, 1974; Müller, 1977; Falk and Nicholls, 1992; Falk, 1993; Diamond, 1994). In contrast, in *Homo sapiens*, the recurrent

ophthalmic branch rarely extends its territory to the parietal region, while the middle meningeal artery originating from the external carotid–maxillary artery dominantly supplies blood to the parietal meninges (McLennan et al., 1974; Dilenge and Ascherl, 1980; Maiuri et al., 1998; Manjunath, 2001; Bonasia et al., 2020b). Despite the unique human condition, the evolutionary history of this trait in human lineages has rarely been studied, mainly because intact sphenoorbital bone structures are rarely available in the human fossil record.

Abbreviations

In-text abbreviations are used for the following anatomic structures: COF, cranio-orbital foramen; FO, foramen ovale; FS, foramen spinosum; MMA, middle meningeal artery; POF, periorbital foramen; RMA, recurrent meningeal artery; SOF, superior orbital fissure; SPS, sphenoparietal sulcus; and TC, sphenoparietal canal of Trolard. The definitions adopted in this paper for the terms COF, POF, RMA, and SPS are described later. See each legend for the other abbreviations used only in Figure 1 and Figure 2.

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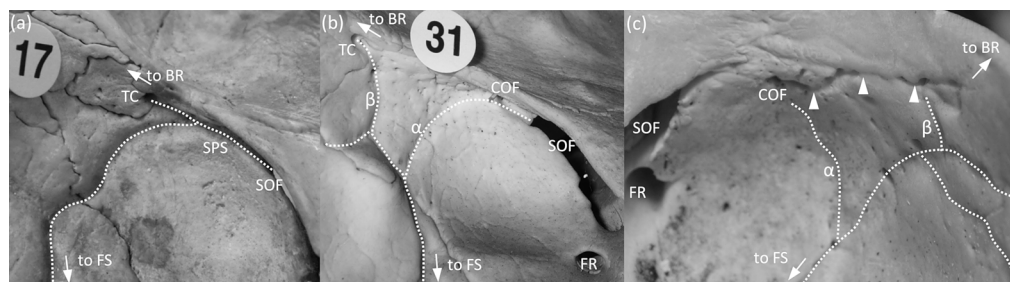


Figure 1. Endocranial vascular traces on the anterior part of the middle cranial fossa. BR, bregmatic region; FR, foramen rotundum. See text for other abbreviations. Arrows with labels (to BR, to FS) denote destinations of the grooves. Dotted lines denote the trajectory of vascular grooves. (a) A left middle cranial fossa of *H. sapiens* in which the groove of the MMA's anterior ramus joins the SPS. (b) A left middle cranial fossa of *H. sapiens* in which the SPS is not developed. The groove of the MMA's anterior ramus bifurcates into the orbital and bregmatic branches. The former (denoted by α) reaches the COF and then the SOF, while the latter (denoted by β) runs to the bregmatic region via the TC. (c) A right middle cranial fossa of *P. troglodytes* in which the groove of the COF-related RMA (denoted by arrowheads) was developed; a deep chiseled vascular groove arises from the COF and ascends toward the bregmatic region. The groove of the MMA gives off two branches toward the anterior end of the middle cranial fossa; the medial one (denoted by γ) is feeble and reaches the COF, while the lateral one (denoted by δ) joins the aforementioned chiseled groove at the pterion region.

Cranio-orbital foramen and superior orbital fissure as alternative pathways

In modern humans, the SOF and/or COF provide pathways for the ophthalmic or lacrimal meningeal branches or the orbital branches of the MMA (Diamond, 1991a). To avoid terminological confusion (Lasjaunias et al., 1975; Diamond, 1991a; Erdogmus and Govsa, 2005; Kier et al., 2021), in this study, the terms 'sphenoidal artery' and 'meningolacrimal artery' are used to refer to the orbital branch of the MMA via the SOF and the COF, respectively (Diamond, 1991a). The term RMA is used here to refer to the ophthalmic branch that enters the middle cranial fossa from the orbit via the SOF or the COF (Hayreh, 1962; Erdogmus and Govsa, 2005; for the different usage of this term, see Toma, 2016; Bonasia et al., 2020a). Thus, it includes the anterior/lacrimal meningeal artery of non-human primates (Falk and Nicholls, 1992; Falk, 1993). The COF also has ambiguous definitions (i.e. including/excluding the POF mentioned hereafter) and various synonyms such as Hyrtl's canal, lacrimal foramen, speno-orbital foramen, and meningo-orbital foramen (Diamond, 1991a; O'Brien and McDonald, 2007; Bonasia et al., 2020a). Hereafter, the term COF is used to refer to the foramen that penetrates the orbital wall lateral to the SOF and contains a vessel that travels between the orbit and middle cranial fossa, as distinguished from the POF (Diamond, 1991b), which penetrates the lateral part of the orbital roof and contains a vessel that travels between the orbit and the anterior cranial fossa. The COF and POF are synonymous with the M- and A-subtypes of the orbitomeningeal foramen, respectively (Macchi et al., 2016). Two or more COFs can occur on one side of the skull (Georgiou and Cassell, 1992; Erturk et al., 2005; O'Brien and McDonald, 2007; Macchi et al., 2016).

The orbital branch of the MMA anastomoses with the RMA (Hayreh and Dass, 1962; Lasjaunias et al., 1975; Diamond, 1991a; Shimada et al., 1995; Bonasia et al., 2020a, 2020b, 2021), or instead of the ophthalmic arterial branches, it supplies blood to the orbital contents such as the lacrimal gland, extraocular muscles, and periorbital connective tissues and occasionally travels further to the anterior

cranial fossa (Diamond, 1991a; Shimada et al., 1995; Bonasia et al., 2020a; Kier et al., 2021). Some cadaver dissection studies suggest that the orbital branch of the MMA often anastomoses with the RMA when it passes through the SOF, while it does less frequently when it passes through the COF in modern humans (Diamond, 1991a; Shimada et al., 1995; Perrini et al., 2007).

Based on the observation of a series of sectioned embryos, Padgett (1948) explained the anastomosis between the MMA and ophthalmic artery as a result of the fetal stapedal artery. According to Padgett (1948), the stapedal artery arises from the hyoid artery at 16–18 mm. In 20- to 24-mm embryos, the maxillomandibular and supraorbital rami of the stapedal artery anastomose to the external carotid–maxillary and internal carotid–ophthalmic arteries, respectively. The stem of the stapedal artery is then involuted. In 40-mm embryos, the proximal and distal parts of the supraorbital ramus are incorporated into the MMA and the ophthalmic arterial branches, respectively, while the intermediate part involutes or remains the anastomosis between the MMA and the ophthalmic artery. Although many researchers assume such a developmental process (Dilenge and Ascherl, 1980; Diamond, 1991a, 1991b; Gailloud et al., 2009; Komiyama, 2011; Macchi et al., 2016; Toma, 2016; Bonasia et al., 2020a; contra: Müller, 1977), some disagreement persists; Diamond (1991a) argued that anastomosis via the COF is the true remnant of the stapedal's supraorbital ramus, which is commonly seen in the haplorrhines, while the anastomosis via the SOF is an additive collateral that evolved in *Homo* and *Pongo* lineages. In contrast to Diamond (1991a), Georgiou and Cassell (1992) argued that the sphenoidal artery may be a remnant of the supraorbital ramus of the medially translocated stapedal artery. In contrast to Padgett (1948), Müller (1977) doubted the stapedal involvement in the anastomosis between the MMA and ophthalmic artery and alternatively argued that the bregmatic branch of the MMA initially appears in the form of the RMA in the early fetal stage, and is then annexed by the MMA stemming from the maxillary artery in the latter fetal stage. Thus, the ontogeny and phylogeny of the RMA and the sphenoidal artery remain controversial.

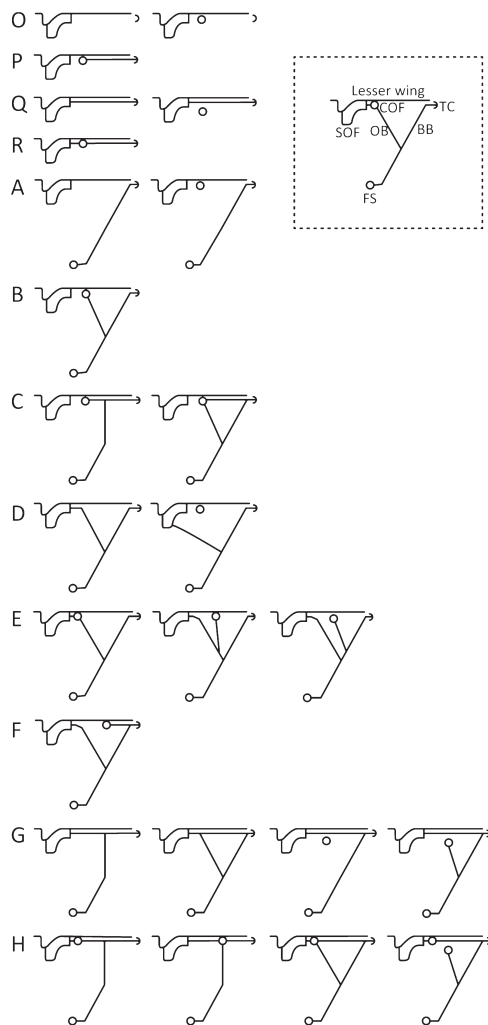


Figure 2. Twelve types (O–R and A–H) of vascular trace variations across the anterior part of the middle cranial fossa. The definitions are presented in Table 2. The diagrams represent the configurations of the vascular traces on the right side. Anatomic names are shown in a diagram surrounded by the dashed line. Solid lines represent vascular groove trajectories and the lesser wing of the sphenoid. Regarding the grooves of the MMA (and accompanying veins), the branches other than bregmatic (BB) and orbital branches (OB) are omitted from the diagrams. Although not illustrated here, cases with multiple COFs also can be classified in the same manner.

Cranial vascular traces and the aims of this study

The trajectory of the meningeal arteries is suggested by the grooves on the endocranial surface which are left by the accompanying meningeal veins as well as the arteries themselves (Jones, 1912; Diamond, 1991b, 1992). In primates, the COF generally provides a pathway for an artery only or for both an artery and the accompanying vein, and rarely for a vein only (Diamond, 1992; Erturk et al., 2005). Owing to these associations, fossil records could be useful for clarifying the evolutionary history of the above-noted arteries. Falk (1993) argued that the meningeal arterial branch of the anterior parietal region (i.e. the bregmatic branch) probably arose from the orbit in three *Homo erectus* crania from Zhoukoudian (ZKD), China: on the left side of ZKD V (skull

of Locus H) and ZKD XI (skull II of Locus L), and on both sides of ZKD III (skull of Locus E). Similarly, Wu et al. (2006) argued that the same characteristic was found on both sides of the *H. erectus* cranium from Hexian, China (contra: Wu and Dong, 1982). However, the sphenoid wings of these Chinese *H. erectus* specimens, except for that on the left side of ZKD III, were severely damaged (Weidenreich, 1938, 1943; Wu et al., 2006, 2010), which hampers inference of where the bregmatic branch came from: the FS/FO, SOF, or COF. Black (1933), Weidenreich (1938), and Grimaud-Hervé (1997) described the bregmatic branch of ZKD III as part of the MMA rather than the RMA. To my knowledge, undoubted evidence of RMA vascularizing the parietal meninges in archaic *Homo* has not been reported.

This study aims to clarify how often the RMA extends its territory to a part of the parietal meninges and via which pathway the RMA entered the cranial cavity in Indonesian *H. erectus*. Among the fossils examined here, the almost intact braincases of Sambungmacan 4 (Baba et al., 2003; Baab and Zaim, 2017) and Ngawi crania (Sartono, 1991; Kaifu et al., 2015; Baab and Zaim, 2017) provide certain evidence of these issues. The present study in particular focuses on whether and how vascular traces arising from COF, PO, SOF, and/or FS/FO merge and reach the anterior parietal region (hereinafter called the ‘bregmatic region’, where the bregmatic branch of the MMA/RMA ranges).

This study also aims to enhance our knowledge of the cranial vascular traces in modern humans, which is needed in osteological and paleontological approaches to the cranial vascular anatomy. There are different views regarding the feasibility of inferring from the cranial vascular traces the attribution of the bregmatic branch (i.e. whether the branch is primarily supplied by the RMA or the MMA); Falk (1993) determined the territory of the RMA in all cases from endocast samples of great apes. On the other hand, Diamond (1994) noted that it is often difficult to infer from vascular traces whether the RMA supplies blood to the parietal meninges. The present author also realizes that it is often difficult to infer the territory of the RMA, especially when the SPS is present and it merges with the groove of the anterior ramus of the MMA and the accompanying vein (Figure 1a versus Figure 1b). The SPS is a seemingly continuous groove formed by the two venous entities, the sinus of the lesser sphenoid wing and the middle meningeal vein (San Millán Ruiz, et al., 2004; Tubbs et al., 2007; Adeeb et al., 2012); it courses along and under the lesser wing and reaches the SOF medially and the bregmatic region laterally, making it impossible to retrieve the nuanced arterial trajectories of the RMA and the bregmatic and orbital branches of the MMA from the endocranial surface. Hence, the present study attempts to infer the attribution of the bregmatic branch unless the groove of the MMA merges with the SPS. Comparatively, this study examined the variations in the vascular trace pattern and foramen caliber in a modern human cranial sample as well as the Indonesian *H. erectus* sample, and it refers to a selected chimpanzee cranium. Finally, based on these observations, some ontogenetic and evolutionary issues of the COF- and SOF-related conduits and the different arterial supply routes to the parietal meninges in the human lineages are discussed.

Table 1. Indonesian *H. erectus* sample examined in the present study

Specimen	Observable side	Preservation of the middle cranial fossa	Medium of observation
Sangiran 10 (Pithecanthropus VI)	Both sides	Medial part missing	A silicone endocast made from the fossil cranium
Skull IX (Tjg-1993.05)	Right side	Medial part missing	CT images with isotropic 0.34-mm voxels and secondary products (virtual and stereolithographic endocasts)
Bukuran	Left side	Medial part missing	CT images with isotropic 0.34-mm voxels and virtual endocast
Sambungmacan 3	Left side	Medial part missing	A silicone endocast made from the fossil cranium
Sambungmacan 4	Both sides	Almost intact	CT images with isotropic 0.34-mm voxels and secondary products (virtual endocast and stereolithographic cranium)
Ngawi	Both sides	Almost intact	CT images with isotropic 0.34-mm voxels and virtual endocast
Ngandong 7	Right side	Anterior part damaged	CT images with isotropic 0.32-mm voxels and secondary products (virtual endocast and stereolithographic cranium)
Ngandong 12	Both sides	Anterior part damaged	CT images with isotropic 0.34-mm voxels and secondary products (virtual endocast and stereolithographic cranium)

Materials and Methods

Materials

As a modern human sample, this study selected 78 dry skulls (47 male, 31 female) among Japanese cadavers from the early 20th century. The skulls are housed at the University Museum of the University of Tokyo. Their vaults are cut horizontally so that it is convenient to observe the cranial cavities. All but three specimens (a 14-year-old male and 10- and 14-year-old females) were from adults. Although the age at death was not recorded for two males and four females, the other adult specimens were 18–76 years (mean, 38.5 years) for males ($n = 44$) and 22–74 years (mean, 51.1 years) for females ($n = 25$). Observations were made on the right and left sides of each cranium (156 sides total).

This study also refers to an adult female skull of a *Pan troglodytes* cadaver housed at the Primate Research Institute of Kyoto University, because it provides a good example of a vascular trace pattern not found in the modern human sample. This represents a case in which a deeply engraved vascular groove arising from the COF ascends to the bregmatic region, indicating that the parietal meninges were supplied with blood by the RMA that enters the cranial cavity via the COF together with the MMA (Figure 1c).

Based on the preservation states, 12 sides of eight Indonesian *H. erectus* crania (Table 1) were selected for the present study, while the other eight crania (Trinil 2; Sangiran 2, 4, 12, 17, and 38; Ngandong 6 and 11) were excluded from the analysis because of missing or damaged spheno-orbital regions. Among the selected specimens, the Sangiran 10 (Pithecanthropus VI), Skull IX (Tjg-1999.05), and Bukuran crania are derived from the layers dated to c. 880–790 kya in the Bapang Formation of the Sangiran dome, Central Java (Hyodo et al., 2011; Grimaud-Hervé et al., 2012; Matsu'ura et al., 2020). The Ngandong crania are derived from the terrace dated to 117–108 kya of the Solo River, Central Java (Rizal et al., 2020). The Sambungmacan 3 and 4 and Ngawi crania were discovered from the bed of the Solo River by local inhabitants (Sartono, 1991; Kaifu et al., 2006), and their stratigraphic origins remain controversial (Kaifu et al., 2015; Baab and Zaim, 2017; Kaifu, 2017). The cranial morphology suggests that the Sambungmacan and Ngawi crania

are chronologically younger than the Sangiran series (Widianto and Zeitoun, 2003; Baab and Zaim, 2017) and possibly older than the Ngandong series (Baba et al., 2003; Kaifu et al., 2015).

The morphology of the fossil sample was examined based on the silicone endocasts for Sangiran 10 and Sambungmacan 3, and using computed tomography (CT) and the virtual mesh and stereolithographic models reconstructed from the CT images for the other six specimens (Table 1). The vascular trace toward the bregmatic region often traverses the TC in the vicinity of the Sylvian crest (Eberlova et al., 2020). Sediments cover the COF, SOF, POF, and TC as well as part of the endocranial and orbital cavities in some fossil specimens. Thus, the vascular trajectories on the bone surface and the intracranial courses were inspected by segmentation of the sediments on the CT images. The calibers of the COF of the fossil specimens were measured on the CT images with 0.1-mm isotropic voxels, which were reconstructed from the original CT images with 0.34-mm resolution. Analyses based on CT data were performed using the software Analyze 11.0 (Mayo Clinic, Rochester, MN, USA), Amira 5.4.0 (Konrad-Zuse-Zentrum, Berlin), and Geomagic XOS (3D Systems, Rock Hill, SC, USA).

Observation and measurement

The number and caliber of the COF and POF on each side and the presence/absence of the vascular grooves on the middle cranial fossa, which ran between the FS/FO, COF, SOF, and/or bregmatic region, were recorded. In addition, to evaluate the arterial contribution to the parietal meninges via the POF, the following grooves were also recorded: (1) the vascular groove called the 'periorbital sulcus' (Diamond, 1991b), which is related to the COF, POF, and/or SOF on the inferior surface of the orbital roof; and (2) the groove on the anterior cranial fossa that is related to the POF and merges with the bregmatic branch ascending from the middle cranial fossa, hereinafter referred to as the 'POF-related anastomosis with the bregmatic branch'.

The penetration of each COF and POF of the modern human specimens was verified by the insertion of nylon wires with diameters of 0.3, 0.4, 0.5, 0.6, 0.8, 1.0, and 1.25 mm, and the approximate caliber was recorded as the class (e.g.

Table 2. Classification of the vascular trace patterns related to the foramen spinosum/ovale, cranio-orbital foramen, superior orbital fissure, and the bregmatic region

Type	Definition
O	The origin of the bregmatic branch cannot be traced to the FS/FO, COF, or SOF
P	The origin of the bregmatic branch can be traced to a COF rather than the SOF or the FS/FO
Q	The origin of the bregmatic branch can be traced to the SOF rather than the COF or the FS/FO
R	The SOF gives off the SPS which meets COF(s) and reaches the bregmatic region, while the origin of the bregmatic branch cannot be traced to the FS/FO
A	The origin of the bregmatic branch can be traced to the FS/FO rather than the COF or the SOF, while the MMA does not give off the orbital branch
B	The origin of the bregmatic branch can be traced to the FS/FO rather than the COF or the SOF, and the MMA gives off the orbital branch(es) to COF(s)
C	A COF gives off the RMA's bregmatic branch, and the MMA's anterior ramus joins it, while both the SPS and the MMA's orbital branch to the SOF are absent
D	The origin of the bregmatic branch can be traced to the FS/FO rather than the COF or the SOF, and the MMA gives off the orbital branch to the SOF
E	The origin of the bregmatic branch can be traced to the FS/FO rather than the COF or the SOF, and the MMA gives off the orbital branch(es) to both COF(s) and the SOF
F	A COF gives off the RMA's bregmatic branch, and the MMA's bregmatic branch joins it, while the SPS is absent and the MMA's orbital branch reaches the SOF
G	The SOF gives off the SPS which meets the MMA's anterior ramus and reaches the bregmatic region, while the COF does not meet the SPS
H	The SOF gives off the SPS which meets both COF(s) and the MMA's anterior ramus and reaches the bregmatic region

0.3–0.39 mm). This study did not record foramina smaller than 0.3 mm in diameter, which is rare in modern human samples and presumably contributes little to the blood supply. In addition to nylon wires, more deformable copper wires were used to verify the penetration of the TC because the canal is sometimes too tortuous to probe with nylon wires.

To provide criteria to evaluate the contribution and route of the RMA to the bregmatic region, this study introduced a classification system for composite vascular trace patterns across the middle cranial fossa. The definitions and diagrams of the 12 types (O–R and A–H) are shown in Table 2 and Figure 2. Types A, B, D, and E suggest that the MMA of the external carotid origin supplies blood to the bregmatic region. Types P, Q, and R suggest that the RMA supplies blood to the bregmatic region. Type C suggests that the RMA via the COF and the MMA supply blood to the bregmatic region, and the contribution of the RMA is likely predominant if the COF is large and the groove of the anterior ramus of the MMA is relatively weak. In Type F, it is difficult to postulate the internal carotid supply to the bregmatic region via the COF because the sphenoidal artery might return to the cranial cavity via the COF, although such a variant was not found in the literature. In Types G and H, the arterial blood flow direction via the SOF is unclear. Hence, it is difficult to infer the contribution of the RMA to the bregmatic region in Types F–H.

The groove bridging the FS/FO and the SOF indicates the sphenoidal artery in Types D–F and may be true for Types G and H. However, it has not been demonstrated whether the SPS is always accompanied by the sphenoidal artery. Hence this study examined the prevalence of the following two indicators of the sphenoidal artery: the groove bridging the FS/FO and the SOF excluding the SPS (sum of Types D–F) and that including the SPS (sum of Types D–H).

Statistical analysis

Fisher's exact test was used to statistically evaluate the following: (1) sex and left–right differences in the occurrences of the COF, POF, SPS, the periorbital sulcus bridging the COF and the POF, and the groove bridging the FS/FO and the SOF excluding the SPS; (2) independence of occurrences of the COF and the POF in the modern human sample; and (3) species differences between Indonesian *H. erectus* and extant great apes and humans in the prevalence of the RMA that extends its territory to the bregmatic region. Comparable data for the great ape samples were reported by Falk (1993). Those of modern human samples were reported by Diamond (1991a), Klisović et al. (1993), and the present study.

Results

Variation observed in the modern Japanese sample

Table 3 summarizes the prevalence of vascular trace features across the middle cranial fossa and the orbital roof in the Japanese sample. POF-related anastomosis with the bregmatic branch was observed only in males. Except for this feature, sex and left–right differences were not remarkable; Fisher's exact test did not show statistically significant sex or left–right differences in the prevalence of the COF ($P = 0.62$ for sex, $P = 0.87$ for sides), the POF ($P = 0.21$ for sex; $P = 0.53$ for sides), the SPS ($P = 0.73$ for sex; $P = 0.61$ for sides), the periorbital sulcus bridging the COF and the POF ($P = 0.19$ for sex, $P = 1$, for sides), or the groove bridging the FS/FO and the SOF excluding the SPS ($P = 1$ for sex; $P = 0.52$ for sides). Hence, the following descriptions focus on the pooled sample.

At least one COF was found in 84 cases (54%). There was one COF linked to an orbit in 60 cases (38%) and two COFs linked to an orbit in 24 cases (15%). None of the orbits had

Table 3. Prevalence of vascular trace features on the middle cranial fossa and the orbital roof in the Japanese sample

	Total (<i>n</i> = 156)	Male (<i>n</i> = 94)	Female (<i>n</i> = 62)	Left (<i>n</i> = 78)	Right (<i>n</i> = 78)
Cases with the COF(s)	84 (54%)	49 (52%)	35 (56%)	41 (53%)	43 (55%)
Cases with multiple COFs or COF's orifices	24 (15%)	18 (19%)	6 (10%)	13 (17%)	11 (14%)
Cases with the POF	28 (18%)	20 (21%)	8 (13%)	12 (15%)	16 (21%)
Cases with the periorbital sulcus bridging between the COF and the POF	17 (11%)	13 (14%)	4 (6%)	9 (12%)	8 (10%)
Cases with POF-related anastomosis with the bregmatic branch	7 (4%)	7 (7%)	0 (0%)	3 (4%)	4 (5%)
Cases with the SPS	50 (32%)	29 (31%)	21 (34%)	23 (29%)	27 (35%)
Cases with the groove bridging between the FS/FO and the SOF excluding the SPS	69 (44%)	42 (45%)	27 (44%)	37 (47%)	32 (41%)
Cases with the groove bridging between the FS/FO and the SOF including the SPS	118 (76%)	70 (76%)	48 (77%)	60 (77%)	58 (76%)
Cases in which the bregmatic branch was annexed by the RMA	1 (1%)	1 (1%)	0 (0%)	0 (0%)	1 (1%)
Cases in which the bregmatic branch was annexed by the MMA	106 (68%)	65 (69%)	41 (66%)	55 (71%)	51 (65%)
Cases in which attribution of the bregmatic branch was undetermined	49 (31%)	28 (30%)	21 (34%)	23 (29%)	26 (33%)
Type R	1 (1%)	1 (1%)	0 (0%)	0 (0%)	1 (1%)
Type A	24 (15%)	15 (16%)	9 (15%)	13 (17%)	11 (14%)
Type B	13 (8%)	8 (9%)	5 (8%)	5 (6%)	8 (10%)
Type D	27 (17%)	17 (18%)	10 (16%)	13 (17%)	14 (18%)
Type E	42 (27%)	25 (27%)	17 (27%)	24 (31%)	18 (23%)
Type G	28 (18%)	15 (16%)	13 (21%)	13 (17%)	15 (19%)
Type H	21 (13%)	13 (14%)	8 (13%)	10 (13%)	11 (14%)
Types O, P, Q, C, and F	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)

more than two COFs. In six of the 24 cases with two COFs, the foramina shared an opening on the middle cranial fossa, diverged within the orbital wall, and had separate orifices on the orbital side. The POF was found in 28 cases (18%), of which 61% (17/28 cases) and 4% (1/28 cases) were linked to the COF and the SOF by the periorbital sulcus. None of the orbits had more than one POF. The prevalence of the POF was significantly higher in the cases with the COF (21/84 cases) than in those without the COF (7/72 cases, Fisher's exact test: $P = 0.02$). A POF-related anastomosis with the bregmatic branch was found in seven cases (4%), among which six coexisted with the periorbital sulcus bridging the COF and the POF; they were classified as Type R (one case), E (three cases), or H (two cases). The other one, in which the periorbital sulcus was absent, was classified as Type H.

The bregmatic branch of the MMA was observed in all but one case. The exceptional case, classified as Type R, had the FS but lacked the bregmatic branch of the MMA, which suggests that the bregmatic branch was annexed by the RMA. In addition, as noted above, this case had a periorbital sulcus bridging the COF and the POF, suggesting that the RMA entered the cranial cavity via the SOF and then ascended to the bregmatic region, giving off a branch which returns to the orbit via the COF as shown in Figure 4b of Diamond (1991a). The SPS was found in 50 cases (32%), which were classified as Type R (1%), G (18%), or H (13%). The other 106 cases (68%) were classified as Type A (15%),

B (8%), D (17%), or E (27%), which suggests an exclusive blood supply from the external carotid system to the parietal meninges. No cases exhibited Type O, P, Q, C, or F. Groove bridging the FS/FO and the SOF excluding the SPS and that including the SPS were found in 69 cases (44%) and 118 cases (76%), respectively, indicating that at least 44% and possibly about 76% of the cases had the sphenoidal artery.

Table 4 shows the approximate calibers of the COF and POF in the Japanese sample. The average calibers of the COF and the POF were respectively estimated to be 0.56–0.62 mm and 0.41–0.45 mm based on the minimum and class values of each class. Seven COF (6.5% of all COF) were larger than 1.0 mm in caliber; five of them were associated with Type E, thus suggesting a well-developed meningo-lacrimal artery,

Table 4. Calibers of the cranio-orbital and periorbital foramina in the Japanese sample

Caliber class	COF (<i>n</i> = 108)	POF (<i>n</i> = 28)
0.3–0.39 mm	16 (15%)	9 (32%)
0.4–0.49 mm	16 (15%)	9 (32%)
0.5–0.59 mm	26 (24%)	9 (32%)
0.6–0.79 mm	32 (30%)	1 (4%)
0.8–0.99 mm	11 (10%)	
1.0–1.24 mm	4 (4%)	
1.25–1.39 mm	3 (3%)	

and the remaining two were found on both sides of a skull whose vascular traces were classified as Type H.

Variation observed in Indonesian *H. erectus* sample

An enlarged COF provided a pathway for the RMA that extended its territory to the bregmatic region in two cases (the right sides of Sambungmacan 4 and Ngawi; Figure 3a–c, e–g), in which the posterior parietal meningeal region was supplied by the MMA of the maxillary arterial origin. In the other 10 cases, the MMA of the maxillary arterial origin extended its territory to the entire region of the parietal meninges (Figure 3d, h, Figure 4). The definitive vascular groove of the sphenoidal artery or the SOF-related RMA was not found in four cases (the right sides of Skull IX and Sambungmacan 4, both sides of Ngawi), and the presence or absence could not be confirmed in the other cases, mainly due to breakage. The SPS was not found in any of the cases. The COF was found in three cases (the right side of Sambungmacan 4, both sides of Ngawi; Figure 3). Details of the observations are as follows.

On both sides of the Sangiran 10 endocast (Figure 4a, b), the vascular trace of the bregmatic branch was interrupted near the Sylvian crest, presumably due to the TC. Despite the interruption, the bregmatic branch was most likely continuous with the MMA of the maxillary arterial origin because the only vascular trace observed underneath the Sylvi-

an crest was that of the MMA arising from the bottom of the middle cranial fossa. On the right side of Skull IX (Figure 4c), a trace of the MMA was observed from the bottom of the middle cranial fossa to the bregmatic region without interruption or branching toward the orbit. On the left side of Bukuran (Figure 4d), the TC penetrating the Sylvian crest was detected on CT scans. The trace of the anterior ramus of the MMA bifurcated into the orbital (medial) and ascending (lateral) branches. Although the adherent matrix masked the inferior orifice of the TC, the barely observable trace of the lateral branch suggests continuity to the bregmatic region via the TC. The orbital branch ends at breakage.

On the left side of Sambungmacan 3 (Figure 4e), the trace of the MMA's anterior ramus bifurcated into the orbital and lateral ascending branches, and the latter reached the bregmatic region, crossing over the Sylvian crest. The orbital branch ends at breakage. On the right side of Ngandong 7 (Figure 4f), the TC was detected on CT scans. This canal connected the vascular trace of the anterior ramus of the MMA arising from the vicinity of the FS/FO with that of the bregmatic branch. The orbital branch of the MMA is unclear due to the irregular bone surface. On both sides of Ngandong 12 (Figure 4g, h), the trace of the bregmatic branch was continuous with that of the MMA, which arose from the FS and crossed over the Sylvian crest. The orbital branch of the MMA was partly observed on the left side and faintly on the

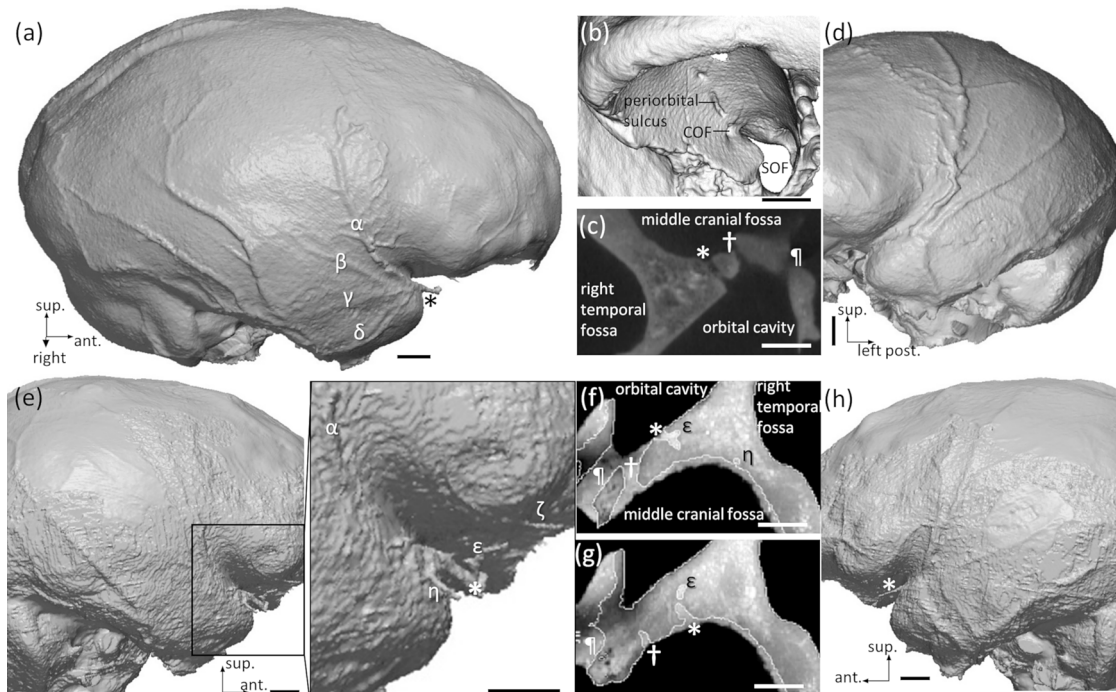


Figure 3. Indonesian *H. erectus* specimens (a–d, Sambungmacan 4; e–h, Ngawi) in which the large COF provides the pathway for the RMA which extended its territory to the parietal region. (a) Virtual endocast, right side. (b) A CT-rendered image of the right orbit, frontal view. (c) A transverse CT section at the level of the COF. (d) Virtual endocast, left side. (e) Virtual endocast, right side with a close-up. (f) A transverse CT section at the level of the COF's orifice to the orbit. (g) A transverse CT section at the level of the COF's orifice to the middle cranial fossa, or 1.7 mm above the level of (f). The fossil bone surface is delineated by white lines in (f) and (g), and the bright voxels outside the lines denote the adherent matrix on the bone surface. (h) Virtual endocast, left side. Symbols denote the following features: *, COF; †, SOF; ¶, optic canal; α, the bregmatic branch, or the most superior branch associated with the COF; β, the second branch associated with the COF; γ, the third branch associated with the COF; δ, the fourth branch associated with the COF, or the MMA's anterior ramus; ε, the intracanalicular branch of the COF which turns back to the orbit; ζ, the intracanalicular part of the POF; η, the passage of the anastomotic branch for the temporal fossa. Scale bar = 10 mm.

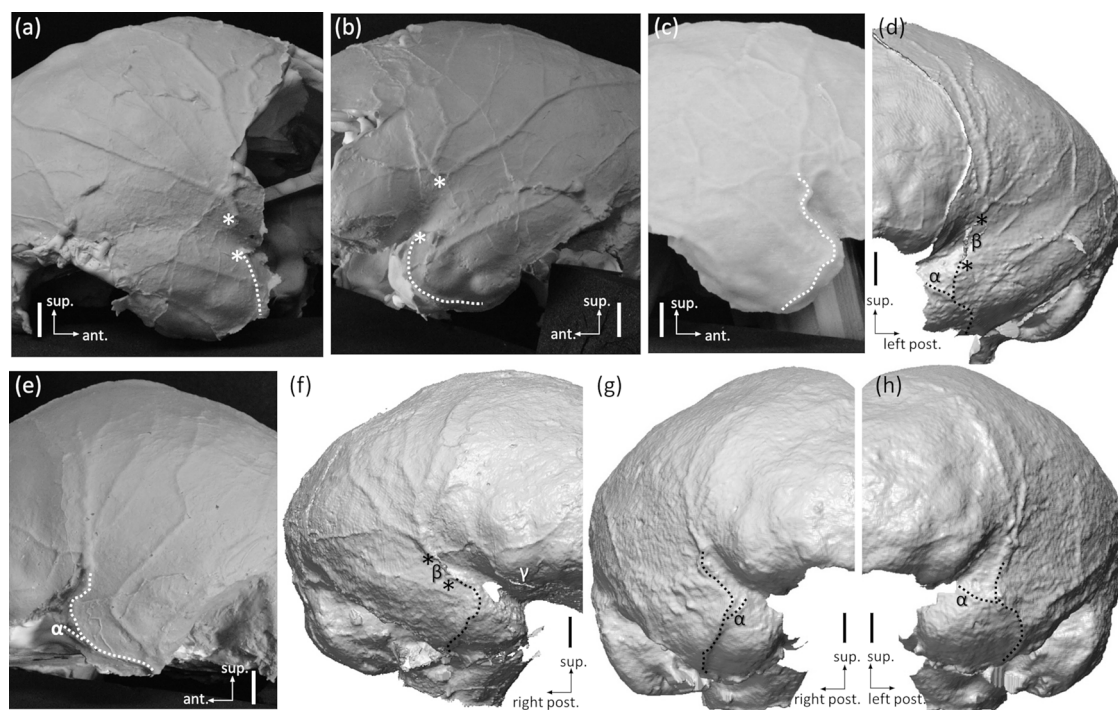


Figure 4. Endocasts of the Indonesian *H. erectus* specimens in which the MMA of maxillary arterial origin predominantly supplied blood to the entire region of the parietal meninges. (a) Sangiran 10, right. (b) Sangiran 10, left. (c) Skull IX, right. (d) Bukuran, left. (e) Sambungmacan 3, left. (f) Ngandong 7, right. (g) Ngandong 12, right. (h) Ngandong 12, left. Silicone endocasts (a, b, e), a CT-based stereolithographic model (c), and CT-based virtual endocasts (d, f, g, h) are shown. Dotted lines indicate the trajectories of the MMA's anterior ramus on the middle cranial fossa. Symbols denote the following features: α , the MMA's orbital branch. β , TC. *, the orifice position of TC. γ , the intracanalicular part of the POF. Scale bar = 10 mm.

right side, although breakages obscured the termination.

Regarding Sambungmacan 4, the right orbit had a 1.0-mm-caliber COF (Figure 3b, c) and the periorbital sulcus, although the POF was absent. In the right middle cranial fossa, a distinct vascular trace arose from the lateral rim of the COF, ascended 7–8 mm along the sphenoid ridge laterally, and then diverged into four branches (Figure 3a). The most superior stoutest branch further ascended, crossing over the Sylvian crest and reaching the bregmatic region. The second branch coursed more posteriorly and ascended to the inferior parietal region. These branches indicate that the COF-related RMA extended its territory to the anterior parietal region. The third and feeblest branch coursed posteriorly and probably joined the obelic branch of the posterior ramus of the MMA. The fourth and most inferior branch corresponds to the trace of the anterior ramus of the MMA. It declined on the lateral wall of the middle cranial fossa and then reached the bifurcation point of the MMA arising from the FS. The bifurcation point was located 18 mm lateral and slightly posterior to the FS. Thus, the vascular trace pattern can be classified as Type C. On the left side of Sambungmacan 4 (Figure 3d), the bregmatic region was predominantly supplied by the MMA arising from the FS. Although the anterior ramus of the MMA probably had a feeble medial branch, it could not be confirmed whether it reached the SOF.

Regarding Ngawi, the right orbit had a 1.5-mm-caliber COF (Figure 3e–g). The intracanalicular part of the COF

had a 0.8-mm-caliber branch that coursed laterally and turned back to the orbit. In the right middle cranial fossa, the orifice of the COF was laterally oriented, although its continuation to the bregmatic branch could not be traced because it was difficult to discern the details of bone surface features covered by the adhesive matrix on the present CT images. As for the MMA on the right side, the groove of the anterior ramus was too faint to discern, while that of the posterior ramus was clearly visible. The vascular trace pattern can be classified as Type P or possibly Type C. Despite the unclear vascular continuation around the Sylvian crest, a combination of the considerably large COF and the absence or faintness of the anterior ramus of the MMA suggests that the bregmatic branch was most likely annexed by the RMA via the COF. The POF and a passage toward the temporal fossa were also found (Figure 3e), although their calibers were less than 0.5 mm. On the left side of Ngawi (Figure 3h), the orbit had a 0.5-mm-caliber COF. The groove of the anterior ramus of the MMA was well-developed and predominantly supplied the bregmatic branch (Figure 3h).

The RMA that extended its territory to the bregmatic region was found in 16.7% (2/12 cases) of the Indonesian *H. erectus* specimens. Compared with the great apes (Falk, 1993), this rate was lower than but not significantly different from that in *Pan paniscus* (36.8% or 7/19 cases, $P = 0.42$, Fisher's exact test) or *P. troglodytes* (45.9% or 17/37 cases, $P = 0.09$) and significantly lower than that in *Gorilla* (67.7% or 21/31 cases, $P < 0.001$) and *Pongo* (100% or 13/13 cas-

es). On the other hand, it was significantly higher ($P < 0.05$, Fisher's exact test) than that in three *H. sapiens* samples (0.6% or 1/156 cases, the present study; 2.7% or 17/638 cases, Diamond, 1991a; about 2% or 6–9/372 cases, recalculated from the percentage, Klisović et al., 1993).

Discussion

Variations within modern humans

The prevalence of having at least one COF and that of multiple COFs linked to an orbit is reportedly 28–59% and 4.3–15%, respectively, in *H. sapiens* populations (Diamond, 1988; Georgiou and Cassell, 1992; Kwiatkowski et al., 2003; Macchi et al., 2016). These features were found with a relatively high frequency in the present Japanese sample (54% and 15%, respectively). The POF was found in 18% of the Japanese sample, which is higher than the previously reported value (8.2%) for the other *H. sapiens* cranial sample (Macchi et al., 2016). The present study found that the POF occurs more frequently in orbits with the COF than in orbits without the COF, and 61% of the POF had a periorbital sulcus continuous to the COF. The COF-related artery would be the meningolacrimal artery in most cases with the periorbital sulcus bridging the COF and the POF. However, it would be the orbital branch of the RMA in the only case whose bregmatic branch was annexed by the RMA; the vascular trajectory, classified as Type R, suggests that the RMA initially entered the middle cranial fossa via the SOF and then bifurcated into the orbital and bregmatic branches. Similar cases were reported in previous studies (Diamond, 1991a; Liu and Rhoton, 2001).

Cadaver dissection studies provide distinct results on the prevalence of the sphenoidal artery: 13% (20/150 cases, Shimada et al., 1995), 54% (38/70 cases, Ducasse et al., 1985), 79% (12/14 cases, Perrini et al., 2007), and 100% (59/59 cases, Hayreh and Dass, 1962). The present study estimated it to be at least 44% and possibly 76% in the Japanese sample. The estimate is compatible with most of the aforementioned studies but incompatible with the quite low prevalence reported by Shimada et al. (1995). This discrepancy cannot be attributed to the ancestry of the populations because Shimada et al. (1995) also examined the Japanese population. Although the present study suggests that Japanese individuals also have a high frequency of the sphenoidal artery, this should be confirmed in future studies.

Anastomosis between the RMA and the MMA via the SOF is frequently observed in *H. sapiens*. Among cases in which the sphenoidal artery is present, the prevalence of the anastomosis is reportedly 60% (12/20 cases, Shimada et al., 1995), 92% (11/12 cases, Perrini et al., 2007), and 100% (59/59 cases, Hayreh and Dass, 1962) in cadaver dissection studies. Similarly, Liu and Rhoton (2001) reported that all 10 human cadaver specimens had the RMA passing through the SOF, of which nine had an anastomosis with the MMA.

In contrast, some evidence suggests that the anastomosis between the RMA and the MMA via the COF rarely occurs in *H. sapiens*. Shimada et al. (1995) reported that the meningolacrimal artery was found in 45% (116/258 cases) of a Japanese cadaver sample, of which only 3.4% (4/116 cases) anastomosed with an ophthalmic arterial branch. Other ca-

daver dissection studies (Diamond, 1991a; Perrini et al., 2007) also showed that the ophthalmic arterial system anastomosed with the MMA via the SOF rather than the COF. Erdogmus and Govsa (2005) reported that 11% (4/38 cases) of a human cadaver sample exhibited anastomosis via the COF.

Reports on the ophthalmic artery of MMA origin and the MMA of ophthalmic origin provide another line of evidence of frequent anastomosis via the SOF rather than the COF in *H. sapiens*. Based on data compiled from the literature, Diamond (1991a) showed that the SOF provide the passage for 96% (23/24 cases) of the ophthalmic artery annexed by the MMA and 86% (6/7 cases) of the MMA annexed by the ophthalmic artery. In addition, he reported that the groove of the RMA that extended its territory to the parietal meninges was found in 2.7% (17/638 cases) of the human skulls, all of which exhibited a trajectory related to the SOF. This tendency is supported by recent case reports of the ophthalmic artery of MMA origin (Liu and Rhoton, 2001) and the MMA of ophthalmic origin (Pretterklieber and Krammer, 1996; Nikolova et al., 2012; Cvetko and Bosnjak, 2014), all of which exhibited SOF-related trajectories. As noted above, the present study also found that the RMA probably entered the middle cranial fossa via the SOF in the only case in which the bregmatic branch was annexed by the RMA.

Summary of Indonesian *H. erectus* characteristics

The prevalence of the RMA that extends its territory to the bregmatic region was found to be significantly higher in Indonesian *H. erectus* than in *H. sapiens*, although not as high as that of the extant great apes. Although based on a quite small sample, this result is compatible with Falk's (1993) hypothesis that the RMA supplied blood to the parietal meninges more frequently in archaic *Homo* species as well as in extant great apes than in *H. sapiens*.

All of the Indonesian *H. erectus* specimens had the posterior ramus of the MMA originating from the bottom of the middle cranial fossa. Falk (1993) found the prevalence of the RMA annexing the entire territory of the MMA to be 0% (0/19 cases) in *P. paniscus*, 8% (3/37 cases) in *P. troglodytes*, 39% (12/31 cases) in *Gorilla*, and 15% (2/13 cases) in *Pongo*. Diamond (1994) reported it as 0% (0/44 cases) in *P. troglodytes*, 11% (4/37 cases) in *Gorilla*, 44% (20/45 cases) in *Pongo*, and 1% (1/100 cases) in *H. sapiens*. In short, Indonesian *H. erectus* is comparable to *H. sapiens* (and possibly *Pan*) in terms of usually having MMA of maxillary arterial origin, but is distinct from *Gorilla* and *Pongo*.

The Sambungmacan 4 and Ngawi crania had a large COF in the right orbit, where the COF probably provided the pathway for the RMA that supplied blood to the bregmatic region. In this respect, they resemble extant non-human haplorrhines rather than *H. sapiens*. According to Diamond (1991a), who examined eight cadavers of seven non-human haplorrhine species, the anastomosis between the MMA and the ophthalmic artery via the COF was found in all species other than *Pongo* and a non-anastomotic RMA with a vein via the COF was found in a *Pongo* cadaver. Diamond (1991a) also noted that the anastomotic artery of a *Pan* cadaver was weak within the middle cranial fossae but much better developed within the COF, suggesting COF-related

arterial blood flow from the orbit to the cranial cavity. The groove of the COF-related RMA was also found in the *Pan* cranium referred to in this study (Figure 1c).

This study failed to demonstrate whether and how often Indonesian *H. erectus* had a sphenoidal artery because the vicinity of the SOF was broken in most of the specimens. Diamond (1991a) argued that Sangiran 10 on the right side exhibited the earliest evidence of the sphenoidal artery (or the SOF-related RMA) in the *Australopithecus–Homo* lineage, although it was based on an illustration of the endocast drawn by Saban (1984, p. 149). Against Diamond (1991a) and compatible with Grimaud-Hervé (1997), the present observation of the Sangiran 10 endocast confirmed that the region around the SOF was broken and the only groove discernible on the preserved middle cranial fossa was that of the MMA's bregmatic branch ascending from the bottom of the middle cranial fossa. Therefore, it is most likely that the vascular groove that Saban (1984) drew and Diamond (1991a) regarded as part of the sphenoidal artery is that of the bregmatic branch of the MMA.

Ontogenetic issues

According to Müller (1977), a presumed remnant of the stapedia's supraorbital ramus was observed in estimated 20- and 24-week-old human fetal specimens as a twiggy artery, which arises from the stem of the MMA and courses lateral to the anterior ramus of the MMA; hence the persistent MMA's anterior ramus may not be the true remnant of the fetal stapedia artery. In this hypothesis, the persistent anastomosis between the MMA and the ophthalmic artery is explained by secondary connection, while the bregmatic branch of the MMA is considered the extraorbital part of the RMA annexed by the MMA; if this were true, the bregmatic branch would always arise near the orbit. However, the bregmatic branch often occurs at a point closer to the stem of the MMA and then runs anteriorly on the middle cranial fossa, even in fetal specimens (see also the 18-week fetus of Kier et al. (2021)). Such a branching pattern would be more compatible with the generally accepted hypothesis that persistent anastomosis is the remnant of the stapedia's supraorbital ramus (Padget, 1948; Georgiou and Cassell, 1992), although identification of the twiggy artery that Müller (1977) described as the stapedia's vestige is also needed.

Compared to the meningolacrimal artery or the COF-related RMA, the sphenoidal artery or the SOF-related RMA usually follows a long and tortuous path (Diamond, 1991a; Gailloud et al., 2009). The latter also joins the definitive lacrimal artery at a point closer to the stem of the ophthalmic artery (Diamond, 1991a). According to Diamond (1991a), these features imply that the sphenoidal artery is a late-acquired collateral rather than a remnant of the supraorbital ramus of the stapedia artery. However, this hypothesis has not yet been demonstrated by ontogenetic evidence. Georgiou and Cassell (1992) provided a more parsimonious model, in which the sphenoidal artery or the SOF-related RMA is considered the remnant of the medially translocated supraorbital ramus of the stapedia artery, and the coexistence of the sphenoidal and meningolacrimal arteries, which is sometimes observed in modern humans, is explained by extraorbital branching of the lacrimal artery. At this time, the afore-

mentioned difference between Indonesian *H. erectus* and modern humans is parsimoniously explained by the model of Georgiou and Cassell (1992), although the ontogeny of the sphenoidal artery remains unclear, and the possibility that some sphenoidal arteries are late-acquired collaterals and others are the remnant of the stapedia's supraorbital ramus cannot be excluded.

Evolutionary implications

The sphenoidal artery or the RMA passing through the SOF is prevalent in *H. sapiens* and *Pongo* (Diamond, 1988, 1991a), although it probably occurs at low frequencies in other extant hominoids (Weidenreich, 1938; Marcozzi, 1942; Diamond, 1988). The present finding that the RMA passed through the COF in Indonesian *H. erectus* suggests that they and their ancestral hominins likely retained the plesiomorphic COF-related RMA while the SOF-related RMA or sphenoidal artery became prevalent in *H. sapiens* or the ancestor sometime in the Pleistocene. This hypothetical evolutionary change should be tested based on chronologically and geographically diverse hominin specimens. Meanwhile, if the RMA almost always passes through the COF, the prevalence of the RMA which extends its territory to the parietal meninges should not exceed that of the COF. Diamond (1988) reported that the COF was found in less than 20% of *P. troglodytes* and *Gorilla* specimens, a rate that is too low compared to that of the RMA that extends its territory to the parietal meninges (45.9% in *P. troglodytes*, 67.7% in *Gorilla*) reported by Falk (1993) unless the SOF-related RMA is prevalent in African apes. This incompatibility might be attributable to sampling or observer errors; thus, it should be resolved in further studies.

Although it remains unclear how often the common chimp–human ancestor, australopithecines, and early *Homo* had the RMA that extends its territory to the parietal meninges, the currently known fossil record suggests that the early hominins usually had the MMA arising from the bottom of the middle cranial fossa (Schepers, 1946, 1950; Tobias, 1967; Saban, 1984; Beaudet et al., 2019). However, together with the variations observed in the extant great apes (Falk, 1993; Diamond, 1994), the present finding that Indonesian *H. erectus* probably had an enhanced RMA with a higher frequency than that of *H. sapiens* still suggests that the MMA of the maxillary arterial origin might not have been so enhanced in the early hominins as in *H. sapiens*.

If the external carotid–maxillary arterial route to the parietal meninges versus the internal carotid–ophthalmic route was enhanced in the human lineage, what factors were involved in the evolutionary transition? Candidates include encephalization with brain reorganization, facial size reduction, and posture and locomotion, which would have influenced the basicranial morphology, metabolism, and cranial hemodynamics (Bastir et al., 2010, 2011; Bruner et al., 2014; Neaux et al., 2018; Seymour et al., 2019). Jamniczky and Hallgrímsson (2011) reported that the circle of Willis and basicranium are interacted in morphogenesis in mice. If postulating a similar interaction in humans, the aforementioned candidates might have influenced the evolution of the meningeal arteries through their effects on basicranial morphology.

Blood-flow-derived mechanical stresses to the endothelium are major physiological factors that drive angiogenesis and arterial remodeling; they are involved in sprouting, elongation, anastomosis, pruning, and caliber regulation of vessels (Hoefler et al., 2013; Campinho et al., 2020). Hypoxia is also another physiological factor essential to angiogenesis; tissue expansion outpacing the accompanying angiogenesis leads to highly hypoxic environments, where vascular growth is promoted (Fong, 2008). These factors would be likely reciprocally associated with heterochronic changes in embryonic development of the stapelial, internal carotid–ophthalmic, and external carotid–maxillary arteries (Padgett, 1948), which result in various branching patterns of the RMA/MMA in the second trimester (Müller, 1977). Sakai et al. (2012) reported that the brain size of chimpanzee fetuses was half that of human fetuses at 16 weeks of gestation. Because the difference likely occurs with the corresponding vascular growth at earlier stages, encephalization could influence the aforementioned presumed heterochronic changes due to the hemodynamic and metabolic demands.

Because the blood flow rate of the ophthalmic artery is generally less than twice that of the MMA in humans (Zarrinkoob et al., 2015), it is expected that the RMA with a large territory would enlarge the caliber of the ophthalmic artery stem. However, Pretterklieber and Krammer (1996) reported that the caliber of the ophthalmic artery was smaller on the same side of the MMA of ophthalmic origin in a human cadaver. This leads to the speculation that the RMA with a large territory could impinge on the development of the eye. Regarding intraspecific variation of *H. sapiens*, higher-latitude populations have larger eyes, probably due to adaptation to lower-daylight environments (Pearce and Dunbar, 2012). Assuming conflict over the blood supply in the ophthalmic arterial system, it is expected that the selective pressure for larger eyes might reduce the RMA's territory and could partially account for the low prevalence of the RMA with a large territory in modern humans. Clarification of the detailed ontogenetic changes and intra- and intergroup variations in the ophthalmic arterial system is needed to test this speculative hypothesis.

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Conflict of interest

The author declares no competing interests.

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