

Normal craniovascular variation in two modern European adult populations

Stanislava Eisová,^{1,2}  Hana Pířová,¹ Petr Velemínský²  and Emiliano Bruner³ 

¹Department of Anthropology and Human Genetics, Charles University, Prague, Czech Republic

²Department of Anthropology, National Museum, Prague, Czech Republic

³Centro Nacional de Investigación sobre la Evolución Humana, Burgos, Spain

Abstract

The vascular networks running into the meningeal layers, between the brain and braincase, leave imprints on the endocranial surface. These traces are visible in osteological specimens and skeletal collections, providing indirect evidence of vascular patterns in those cases in which bone remains are the only source of anatomical information, such as in forensic science, bioarchaeology and paleontology. The main vascular elements are associated with the middle meningeal artery, the venous sinuses of the dura mater, and the emissary veins. Most of these vascular systems have been hypothesized to be involved in endocranial thermal regulation. Although these traits deal with macroanatomical features, much information on their variation is still lacking. In this survey, we analyze a set of craniovascular imprints in two European dry skull samples with different neurocranial proportions: a brachycephalic Czech sample ($n = 103$) and a mesocephalic Italian sample ($n = 152$). We analyzed variation and distribution, correlation with cranial metrics, and sex differences in the dominance of the branches of the middle meningeal artery, the patterns of confluence of the sinuses, and the size of the emissary foramina. The descriptive statistics provide a reference to compare specimens and samples from different case studies. When compared with the Italian skulls, the Czech skulls display a greater dominance of the anterior branch of the middle meningeal artery and more asymmetric right-dominance of the confluence of the venous sinuses. There is no sex difference in the middle meningeal vessels, but males show a greater prevalence of the occipito-marginal draining system. Differences in the middle meningeal vessels or venous sinuses are apparently not influenced by cranial dimensions or proportions. The mastoid foramina are larger in larger and more brachycephalic skulls, which increases the emissary potential flow in the Czech sample and males, when compared with the Italian samples and females, respectively. The number of mastoid foramina increases in wider skulls. This anatomic information is necessary to develop further morphological and functional inferences on the relationships between neurocranial bones and vessels at the genetic, ontogenetic, and phylogenetic levels.

Key words: blood flow; cranial foramina; emissary veins; middle meningeal artery; venous sinuses.

Introduction

Craniovascular traits

Human head vasculature relies on networks bridging the endocranial and ectocranial spaces. Besides the internal cerebral system and the external drainage of the scalp, it includes vessels running into the meninges between the

brain and skull (Patel & Kirmi, 2009; Adeeb et al. 2012), the diploic veins within the bones of the cranial vault (e.g. Hershkovitz et al. 1999; García-González et al. 2009; Rangel de Lázaro et al. 2016), and the emissary veins crossing the cranial bones and bridging intra- and extra-cranial regions (e.g. Boyd, 1930; Louis et al. 2009). The dura mater is the outer meningeal sheet and is composed of two layers which are separated by the dural venous sinuses. The middle meningeal vessels run into the endosteal (periosteal) layer of the dura mater. This layer is adherent to the inner table of the skull (Kerber & Newton, 1973; Patel & Kirmi, 2009; Adeeb et al. 2012). The brain cortex exerts a physical pressure on these vascular systems against the endocranial wall, inducing osteoclastic activity with consequent formation of traces and imprints on the bones of the braincase (Moss & Young, 1960; Holloway, 1974; Bruner & Sherkat, 2008;

Correspondence

Emiliano Bruner, Centro Nacional de Investigación sobre la Evolución Humana, Paseo Sierra de Atapuerca 3, 09002 Burgos, Spain. E: emiliano.bruner@cenieh.es

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Bruner, 2015). The development of the middle meningeal vessels increases at 1–2 years of age and reaches a stable morphology around 5–6 years of age, although the network only becomes fully operative in adulthood (Saban, 1995). The early endocranial vascular imprints are due to bone modeling, whereas the imprints in adults must be interpreted as the result of remodeling (see Ralston, 2017 and Walsh, 2017). Bone remodeling is influenced by hormones, microfractures, and mechanical stimuli, and it is based on a balance between osteoclastic and osteoblastic activity. Mechanical load has been hypothesized to have an effect on osteocytes, activating the remodeling cycle. A cycle has an average duration of 200 days and therefore we must assume that vascular traces are continuously shaped by active vessels during adulthood. If a vessel is lost or if it does not exert sufficient mechanical pressure, the trace is likely to smooth or disappear after remodeling. The expression of the traces and imprints depends on various local factors including vessel size, blood and brain pressure, meningeal thickness, and cerebrospinal fluid pressure (Moss & Young, 1960; Holloway, 1974; Zollikofer & Ponce de León, 2013). Although these imprints are a partial representation of the original vascular network, neurosurgical practice suggests a good general correspondence between the bone impressions and the equivalent vessels, at least in terms of gross morphology (Bruner & Sherkat, 2008). Imprints on the endocranial surface tend to smooth gradually during adulthood (Neubauer et al. 2009, 2010; Zollikofer & Ponce de León, 2013) and, in macaques, there is a significant age-related decrease of the endocranial sulcal impressions, mostly after 20 years of age (Minh & Hamada, 2017). It has been hypothesized that age-related brain shrinkage and thinning of the cranial vault bones both contribute to increasing the endocranial volume, with subsequent reduction of the pressure between the soft tissues and the skull. This reduction of meningeal pressure may lead to smoothing of the vascular and brain imprints on the endocranial wall (Zollikofer & Ponce de León, 2013; Bruner, 2015; Minh et al. 2015; Minh & Hamada, 2017). Nonetheless, it is also worth noting that, with aging, bone resorption exceeds formation (Walsh, 2017). This unbalanced deposition is probably a major factor responsible of the smoothing of the imprints. Bone formation is also related to hematopoietic functioning, and bone loss is generally associated with anemia or specific blood pathologies (Valderrábano & Wu, 2019). This association provides a further causal relationship between aging and vascular imprints, bridging variations in blood supply and bone formation in both normal and pathological conditions.

In adults, the gross vascular patterns associated with meningeal endocranial traces are apparently not influenced by normal braincase form variation (Bruner et al. 2009). However, vessel morphology and distribution can display specific changes in those cases in which cranial shape is profoundly altered, such as in pathological conditions or when

the skull is deformed after cultural practices (Dean, 1995; O'Loughlin, 1996). Visual inspection of the cranial cavity is sufficient to detect the traces of the middle meningeal vessels and dural venous sinuses, whereas medical imaging is necessary to reveal the diploic channels running in the trabecular layer of vault bones (e.g. Hershkovitz et al. 1999; Jivraj et al. 2009; Tsutsumi et al. 2013; Rangel de Lázaro et al. 2016).

Vascular networks

The middle meningeal artery usually arises from the maxillary branch of the external carotid artery and enters the cranial cavity through the foramen spinosum. On the endocranial surface, it splits into anterior (bregmatic), middle (obelic), and posterior (lambdoidal) branches (Bruner & Sherkat, 2008; Patel & Kirmi, 2009; Adeeb et al. 2012; Pišová et al. 2017). Vessel branching patterns follow a dichotomous pseudo-fractal model and are otherwise difficult to quantify in terms of geometry (Zamir, 1999, 2001). The main vessels (first order branches) split into smaller vessels (second order branches) and so on, and the branching orders follow geometric schemes which can be partially recognized on the endocranial traces. In adults, generally at least five orders of middle meningeal branches can be detected in dry skulls, with the mean lumen size (i.e. the diameter) of the vessel ranging between 2.46 ± 0.51 mm for the first (larger) order and 1.11 ± 0.28 mm for the fifth (smaller) order (Eisová et al. 2016). The main branches of the arteries are accompanied by satellite, usually paired, veins. Endocranial traces generally associated with the middle meningeal artery may thus also include the imprints of these parameningeal veins (Falk & Nicholls, 1992; Saban, 1995). We must therefore take into account that when dealing with osteological samples we are not investigating the morphology of the artery alone, but instead of a more diverse set of vessels. Accordingly, we use term 'traces of the middle meningeal vessels' (TMV) to indicate the actual anatomic features concerned in the study of the middle meningeal artery in cranial remains.

The dural venous sinuses are enlarged venous channels which mainly collect the blood from cerebral, meningeal, diploic, and extracranial circulation. They drain the endocranial blood flow into the internal jugular veins through the jugular foramina (Gray & Carter, 1858; Knott, 1881; Baló, 1950; Curé et al. 1994; Adeeb et al. 2012). Many dural venous sinuses leave traces on the endocranial surface, supplying information about the superior sagittal sinus, transverse and sigmoid sinuses, occipital and marginal sinuses, and sphenoparietal sinus (Durgun et al. 1993; Curé et al. 1994; San Millán Ruíz et al. 2004; Takahashi et al. 2007; Adeeb et al. 2012; Pišová et al. 2017). In the internal occipital protuberance, the confluence of sinuses (*torcular Herophili*) connects the superior sagittal sinus, the right and left transverse sinuses, the straight sinus (from the inner volume

of the endocranial space, not in contact with the bone) and, if present, the occipital sinus, redistributing the blood flow towards the right and left sides of the endocranial base (Browning, 1953; Bisaria, 1985; Curé et al. 1994; Singh et al. 2004; Fukusumi et al. 2010; Adeeb et al. 2012; Bayaroğulları et al. 2018). The pattern of the confluence may vary, with a different degree of asymmetries, and such variability must also be taken into account. We use the term 'traces of dural venous sinuses' (TVS) when referring to the imprints of the dural venous sinuses in cranial remains.

Emissary veins cross the cranial bones to link the ectocranial and endocranial vascular systems. They are associated with foramina and bony canals which are generated after the ossification process. In adults, emissary veins vary in prevalence, number, location, and expression. The largest and most frequent ones are usually the parietal, mastoid, and condylar emissary veins, which respectively generate parietal, mastoid, and condylar canals (Boyd, 1930; Shapiro & Robinson, 1967; Falk, 1986; Ginsberg et al. 1994; Berge & Bergman, 2001; San Millán Ruiz et al. 2004; Louis et al. 2009; Mortazavi et al. 2013). The parietal foramen may also serve as a passage for an anastomosis between the middle meningeal and scalp arteries (Yoshioka et al. 2006), and the condylar and the mastoid foramina may also transmit the occipital artery (Choudhry et al. 1996; Kiyosue et al. 2007). Therefore, although the presence and size of these channels can be used as a proxy for their respective vessels, correspondence may not always be complete. In some cases, a sphenoparietal emissary vein is also present, linking the cavernous sinus with the pterygoid venous plexus through the foramen of Vesalius (*foramen Vesalii*, sphenoidal emissary foramen, *foramen venosum*, *canaliculus sphenoidalis*) (Boyd, 1930; Lanzieri et al. 1988; Kale et al. 2009; Rossi et al. 2010; Shinohara et al. 2010; Chaisuksunt et al. 2012; Ozer & Govsa, 2014; Raval et al. 2015). Rarely, the occipital emissary vein may develop and cross the occipital bone, forming the occipital foramen (Boyd, 1930; Berge & Bergman, 2001; San Millán Ruiz et al. 2004; Louis et al. 2009). The importance of these emissary veins in normal physiological conditions is probably negligible, although during altered physiological conditions (such as hyperthermia) their role is more relevant because of the contribution to the management of endocranial blood flow and thermoregulation (Cabanac & Brinnet, 1985). Some pathological conditions may cause enlargement or narrowing of these foramina (Shapiro & Robinson, 1967; Lanzieri et al. 1988; Shinohara et al. 2010), suggesting anatomical plasticity to specific physiological responses.

Applications and aims

The analysis of the cranial vascular traces may be useful in forensic sciences, biological anthropology, evolutionary studies, and medicine (Přisová et al. 2017). In bioarchaeology, craniovascular traits can be used for testing

biodistances, kinship, and interbreeding level (Hauser & De Stefano, 1989). Some craniovascular traits are considered to be population-specific, according to the presence of the cranial foramina, prevalence of the O/M sinuses or morphology of the diploic veins (Matiegka, 1923; Buikstra & Ubelaker, 1994; Hershkovitz et al. 1999). In paleoanthropology, craniovascular features display specific phylogenetic variations, and a general increase of the vascular networks has been described in our species, *Homo sapiens* (Grimaud-Hervé, 1997; Bruner et al. 2005; Bruner & Sherkat, 2008; Rangel de Lázaro et al. 2018). Nonetheless, information on normal variation in our species is still scanty. A preliminary survey described the frequency of some major craniovascular features in adult humans in a European population (Bruner et al. 2003). In this study, we provide a more comprehensive analysis of the endocranial vascular traces in two distinct European adult populations, so as to evaluate the ranges and patterns of normal variation, testing the influence of sex, cranial size and symmetry, under the null hypothesis of no association between these factors and the expression of the craniovascular features.

Materials and methods

Two cranial samples of adult modern humans ($n = 255$) were analyzed to describe and quantify the normal variation of major craniovascular traits. Both samples represent European populations, although from distinct regions. The first one is the Pachner collection housed in the Department of the Anthropology and Human Genetics of Charles University (Czech Republic), collected in the second half of the 19th century. This autopsy collection from the 1930s contains individuals belonging to the Czech urban working class. Contemporary documentation (name, gender, age at death, body height, health state, and cause of death) is available for this sample (Borovanský, 1936; Pachner, 1937). We measured 103 individuals, 81 of them with known age at death (median age: 46 years; interquartile range 37–62 years) and 101 of them with known sex (56 males, 45 females). The second sample is part of the collection of the Museum of Anthropology Giuseppe Sergi at the University La Sapienza in Rome (Italy), representing a local Italian population, collected at the beginning of the 20th century (Bruner et al. 2003). We measured 152 adult individuals, 77 of them determined as males, 54 as females, and 21 indeterminate, according to Ferembach et al. (1979). In this case, therefore, sexual assessment is an estimation based on cranial morphology and must be intended as a statistical inference based on the expression of anatomical traits. The skulls of both collections were transversally sectioned during autopsy, which allows a direct inspection of the endocranial cavity. Only anatomically normal adult individuals are included in this survey.

Cranial measurements included cranial length (glabella – opisthocranium), cranial breadth (eurion – eurion), and cranial height (basion – bregma). Mean size, cephalic index (width-length index), height-length index, and height-width index were also calculated. Mean size is computed as the mean value of the cranial length, width, and height, whereas the indexes are ratios multiplied by 100 (e.g. Knussmann, 1988).

TMV pattern was classified following Adachi (1928) according to the origin of the middle branch, namely from the anterior (Adachi

type I), posterior (Adachi type II) or both (Adachi type III) branches (Fig. 1). A further general classification was based on the visual assessment of the distribution and complexity of the vessels, namely separating skulls with most developed anterior vs. posterior branches (anterior vs. posterior dominance). Therefore, TMV 'pattern' deals with the origin of the branches, whereas TMV 'dominance' deals with the complexity of the anterior and posterior regions (Fig. 2). Often, networks with the middle branch originating from the anterior branch display more complex anterior vascularization. However, these two features do not always agree, and there are situations in which the origin of the middle branch and the region of development of the major vessels do not coincide topologically (for example, cases in which the middle branch does originate posteriorly, but the vessels are more developed anteriorly, and vice versa).

TVS were categorized according to the morphology of the confluence (Fig. 3), and depending on whether the superior sagittal sinus runs mainly into the right (Type I) or left (Type II) transverse sinuses, equally into both (Type III) or with unclear traces (IV), (Brunner et al. 2003). The pattern was also scored according to the dominant (largest) transverse sinus as right, left or unclear, and according to the degree of expression of the imprint (depth) as light (hardly visible), clear (clearly visible) or marked (deep). We also considered the presence of the sphenoparietal, occipital, and marginal sinuses as present or absent.

In the case of the bony vascular canals, we considered the parietal, condylar, mastoid, occipital, spinous and Vesalius foramina presence on both the right and left sides for each specimen. Multiple mastoid foramina can be detected in the same individual. Closed foramina were scored as absent, since they are not functionally active. Where foramina are present, we measured their size using probes (steel wires) of different sizes (0.3, 0.5, 0.8, 1, 1.2 and 1.8 mm) according to the best fit for the passage. This metric information is assumed to be proportional to the lumen diameter of the associated vessels. We also calculated cumulative indexes based on the sum of the values for the canals, as proxies for the overall blood flow capacity of the foramina (Rangel de Lázaro et al. 2018). For

each specimen, we computed the sum of the right-left dimensions for paired canals, the sum of the right and left side emissary canals, and the sum of all the emissary canals (Table 1).

Data were collected by a single operator (H.P.) for the right (R) and left (L) sides. The distributions of quantitative and discrete traits were calculated and tested by Student *t*-test, *F*-test for equal variances, Mann-Whitney test (Agresti & Finlay, 2009), Epps-Singleton test (Epps & Singleton, 1986; Goerg & Kaiser, 2009), and Spearman's rank correlation (Press et al. 1992). Statistics were computed with PAST 3.18 (Hammer et al. 2001).

Results

Cranial size

Table 2 shows the cranial metrics for the two populations, and for males and females. The Czech skulls are more brachycephalic than the Italian skulls. According to the cephalic (width-length) index (Williams et al. 1995), the former group actually tends to a brachycephalic distribution, whereas the latter's main figure is mesocephalic (Table 3). The two groups do show differences in cranial proportions, but not in the mean cranial size. In contrast, males and females do not show different cranial proportions, but male skulls are larger than female ones (Table 4).

Middle meningeal vessels

Table 5 shows the distribution of the features associated with the middle meningeal vessels, for the two populations, and for males and females. In the total sample, Adachi type I is most prevalent (50%), followed by type II (28%) and type III (23%). The anterior branch very often occurs close to the coronal suture and reticulates posteriorly. The

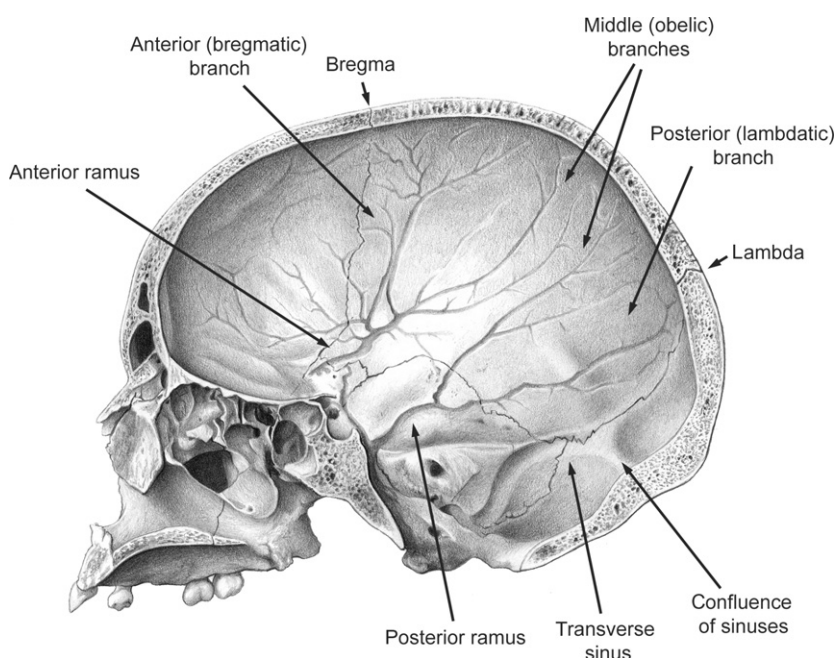


Fig. 1 Main craniovascular features of the human endocranial cavity.



Fig. 2 The middle branch of the middle meningeal artery can originate from the anterior (A,B) or posterior (C) branch. Independently from the origin, the network can be more developed anteriorly (A) or posteriorly (B,C). So there are subjects in which the origin is anterior, but the network is more developed posteriorly (B). [Colour figure can be viewed at wileyonlinelibrary.com]

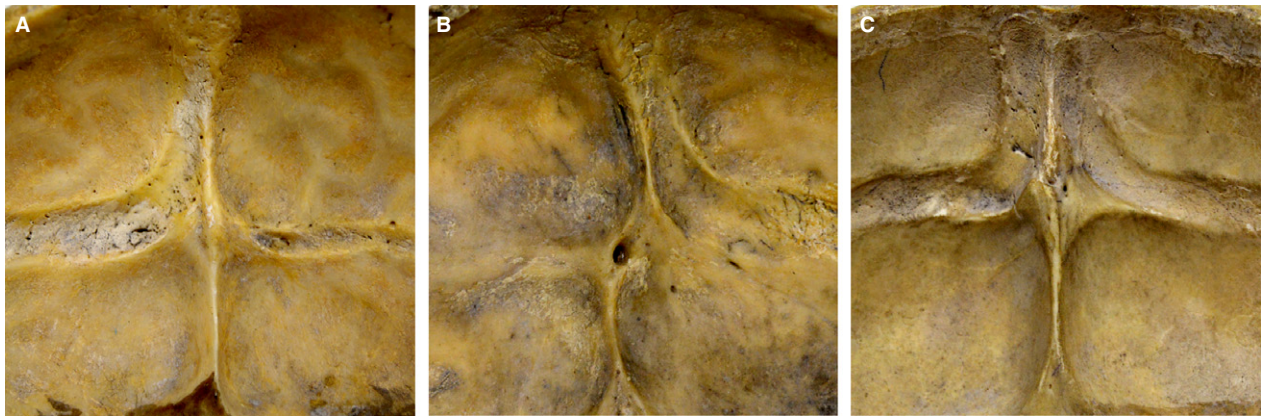


Fig. 3 At the confluence of sinuses (*torcular Herophili*), approaching the internal occipital protuberance, the main flow of the superior sagittal sinus can be deviated on the right transverse sinus (A), on the left transverse sinus (B) or distributed equally on both sides (C). [Colour figure can be viewed at wileyonlinelibrary.com]

Table 1 Foramina (f) cumulative indexes

Variable	Description
Parietal index	Sum of right and left size of parietal f.
Condylar index	Sum of right and left size of condylar f.
Mastoid index	Sum of right and left size of mastoid f.
Vesalius index	Sum of right and left size of Vesalius f.
Spinous index	Sum of right and left size of spinous f.
R index	Sum of right size of parietal, condylar, and mastoid f.
L index	Sum of left size of parietal, condylar, and mastoid f.
Emissary index	Sum of all size of parietal, condylar, mastoid, and occipital f.

anterior network is more developed in 70% of the skulls, and the posterior in 10%. In 18% of the cases, there was no patent dominance of one of the two sectors. Most figures are similar in the two populations, although the Czech skulls display more frequent anterior dominance of the branches (Fig. 4, Table 6). There is no significant difference

between males and females in the distribution of these vascular patterns. The Italian skulls display a different right-left figure in 52% of the individuals for the branching patterns and 38% of the individuals for the antero-posterior dominance, whereas in the Czech skulls, subjects with distinct right-left morphology are less frequent (46 and 12%, respectively). However, these differences between the right and left sides are not statistically significant. There is no significant association between the cranial dimensions or proportions and the morphology of the middle meningeal vessels (anterior vs. posterior branch pattern or dominance), when only symmetric individuals (i.e. with the same figure on both sides) are considered.

Venous sinuses

Distributions of values for the venous sinuses (TVS) are shown in Table 7. The main confluence pattern is type I (56%), followed by type IV (24%), type II (18%) and type III (2%). The right sinus is dominant in 45% of cases and the left in 25% of cases; in the rest of the subjects there was no

Table 2 Cranial metrics

Czech sample	All (<i>n</i> = 103)					Males (<i>n</i> = 56)					Females (<i>n</i> = 45)				
	Mean	SD	Q1	Q2	Q3	Mean	SD	Q1	Q2	Q3	Mean	SD	Q1	Q2	Q3
Gla-Opist	175	7	171	175	179	179	7	174	179	183	171	5	168	171	174
Eu-Eu	146	7	142	147	150	148	6	145	148	151	144	6	139	144	148
Bas-Bre	128	6	124	127	132	130	6	125	130	135	125	4	123	125	128
Mean size	150	5	146	149	153	152	5	149	152	155	146	4	144	147	149
Width-length index	83	3	82	83	85	83	3	81	83	85	84	3	82	84	86
Height-length index	73	3	71	73	75	73	3	71	72	76	73	3	72	73	75
Height-width index	88	5	85	88	91	88	4	84	88	91	87	5	85	88	91

Italian sample	All (<i>n</i> = 152)					Males (<i>n</i> = 77)					Females (<i>n</i> = 54)				
	Mean	SD	Q1	Q2	Q3	Mean	SD	Q1	Q2	Q3	Mean	SD	Q1	Q2	Q3
Gla-Opist	178	7	174	178	184	181	6	177	182	186	174	5	171	175	177
Eu-Eu	139	6	134	138	142	142	6	137	141	146	135	4	133	136	138
Bas-Bre	130	6	126	130	134	133	6	129	133	137	127	5	124	127	130
Mean size	149	5	146	149	152	152	4	149	152	155	146	3	144	146	148
Width-length index	78	4	75	78	80	78	4	75	78	82	78	3	76	78	79
Height-length index	73	3	71	73	76	73	3	72	74	76	73	3	71	73	75
Height-width index	94	5	91	94	97	94	5	90	94	97	94	4	91	94	97

Q1, first quartile, Q2, second quartile (median), Q3, third quartile; SD, standard deviation.

Table 3 Cranial proportions

Range of cephalic index (Williams et al. 1995)	Mean		Frequency	
	Czech sample	Italian sample	Czech sample	Italian sample
Dolichocephalic < 74.9			1 (1%)	35 (23%)
Mesocephalic 75–79.9		77.7	14 (14%)	83 (55%)
Brachycephalic 80–84.9	83.5		52 (50%)	27 (18%)
Hyperbrachycephalic > 85			36 (35%)	7 (5%)

Table 4 Cranial differences

	Czech (<i>n</i> = 103) vs. Italian (<i>n</i> = 152) sample				Males (<i>n</i> = 133) vs. Females (<i>n</i> = 99)			
	<i>t</i> -test		<i>F</i> -test		<i>t</i> -test		<i>F</i> -test	
	<i>t</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>F</i>	<i>P</i>
Mean size	0.8	0.425	1.3	0.181	11	0.0001***	1.8	0.002**
Width-length index	11.9	0.0001***	1.4	0.035*	−0.8	0.433	1.1	0.761
Height-length index	0.0	1.000	1.2	0.536	−0.3	0.779	1.1	0.838
Height-width index	10.6	0.0001***	1.1	0.571	0.6	0.545	1.0	0.960

**P* < 0.05.

***P* < 0.01.

****P* < 0.001.

Table 5 Patterns of middle meningeal vessels

Czech sample	All (<i>n</i> = 100)		Male (<i>n</i> = 54)		Female (<i>n</i> = 44)	
	R	L	R	L	R	L
TMV pattern						
Adachi type I	47 (47%)	51 (51%)	28 (52%)	29 (54%)	19 (43%)	21 (48%)
Adachi type II	26 (26%)	27 (27%)	11 (20%)	12 (22%)	14 (32%)	14 (32%)
Adachi type III	27 (27%)	22 (22%)	15 (28%)	13 (24%)	11 (25%)	9 (20%)
TMV dominance						
Anterior	88 (88%)	83 (83%)	47 (87%)	42 (78%)	40 (91%)	40 (91%)
Posterior	7 (7%)	8 (8%)	3 (6%)	6 (11%)	3 (7%)	1 (2%)
Unclear	5 (5%)	9 (9%)	4 (7%)	6 (11%)	1 (2%)	3 (7%)

Italian sample	All (<i>n</i> = 149)		Male (<i>n</i> = 76)		Female (<i>n</i> = 53)	
	R	L	R	L	R	L
TMV pattern						
Adachi type I	65 (44%)	83 (56%)	29 (38%)	40 (53%)	27 (51%)	31 (58%)
Adachi type II	51 (34%)	35 (23%)	32 (42%)	19 (25%)	12 (23%)	12 (23%)
Adachi type III	33 (22%)	31 (21%)	15 (20%)	17 (22%)	14 (26%)	10 (19%)
TMV dominance						
Anterior	87 (58%)	96 (64%)	47 (62%)	49 (64%)	28 (53%)	34 (64%)
Posterior	21 (14%)	16 (11%)	10 (13%)	8 (11%)	6 (11%)	5 (9%)
Unclear	41 (28%)	37 (25%)	19 (25%)	19 (25%)	19 (36%)	14 (26%)

clear asymmetry. Imprints were absent in 7% of the cases, feeble in 43% of the cases, clear in 30% of the cases, and marked in 19% of the cases. Traces compatible with a sphenoparietal sinus were detected in 49% of the specimens. Traces of the occipito-marginal vascular system were detected in 9% of the skulls. The Czech skulls display a more frequent right-dominance of the transverse sinus, whereas the Italian sample shows fewer right-left differences (Fig. 5). Minor differences in the other patterns do not reach significance (Table 6). There are minor sex differences for TVS patterns.

In the Czech sample, the Type I (superior sagittal sinus runs to the right transverse sinus) category of confluence pattern appears more frequently in females (71%) than in males (46%) (Table 7). Males were more often rated as Type IV category (unclear traces), which may possibly cause the lower frequency of Type I rate in this group. However, the only significant result is a larger prevalence of the occipito-marginal system in males (9%) than in females (3%), (Epps–Singleton test: $P = 0.045$). Table 6 summarizes the differences between the two populations according to the Epps–Singleton test for equal distributions. There is no significant association between cranial dimensions or proportions and the right-left dominance of the confluence of sinuses.

Foramina

Table 8 shows the prevalence of the foramina in the two populations, and in males and females. Table 9 displays

the number of specimens with 0–4 foramina. Overall prevalences are as follows: parietal foramen 56%, condylar foramen 75%, mastoid foramen I and II 83 and 18%, respectively, occipital foramen 3%, foramen of Vesalius 46%, and foramen spinosum 99%. The only significant difference between the two populations is a larger number of mastoid foramina in the Czech skulls (Tables 6 and 10). Also, the number of mastoid foramina increases in wider skulls ($P = 0.0002$; Fig. 6), as measured by the eurion–eurion distance. There are no significant differences between males and females or between right and left sides.

Table 11 shows the descriptive statistics for foramina size. The overall mean diameters are as follows: parietal foramen 0.6 mm, condylar canal 1.6 mm, mastoid foramen 1.2 mm, occipital foramen 0.8 mm, foramen of Vesalius 0.6 mm, foramen spinosum 1.5 mm. Table 12 displays the values of the cumulative indexes. Larger mastoid foramina are detected in the Czech sample than in the Italian skulls, and in males than in females (Table 13). This difference influences the side-specific indexes and the total emissary value, which in the Czech skulls is 14% larger than in the Italian skulls, and in males is 10% larger than in females (6 and 15% in the Czech and Italian samples, respectively).

Figure 7 shows the proportions of the parietal, condylar, and mastoid indexes. In general, the condylar and mastoid contributions are similar, and dominant when compared with the parietal contribution, which is definitely smaller. The distribution of the Czech sample and of the male

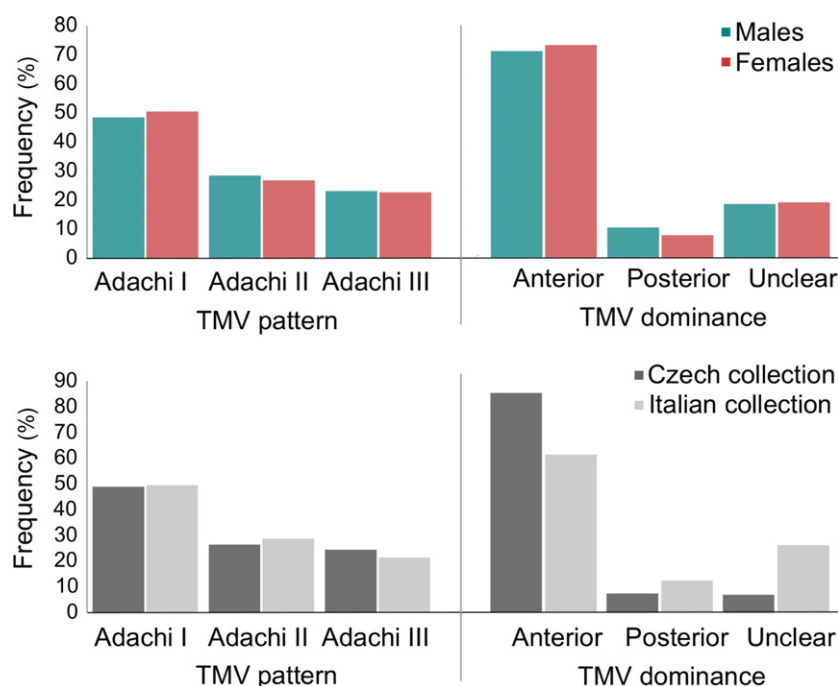


Fig. 4 Traces of the middle meningeal vessels (TMV): pattern and dominance. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 6 Comparison between Czech ($n = 103$) and Italian ($n = 152$) samples (Epps-Singleton test for equal distributions)

	W_2	P
Traces of middle meningeal vessels		
TMV pattern	0.808	0.937
TMV dominance	46.649	< 0.0001***
Traces of dural venous sinuses		
Confluence pattern	2.857	0.582
Transverse s. dominance	16.64	0.002**
Transverse s. expression	2.468	0.650
Sphenoparietal s. presence	0.037	1.000
Occipital or marginal s. presence	2.357	0.670
At least one O/M s.	0.457	0.978
Cranial foramina		
Parietal foramen	2.549	0.636
Condylar canal	2.464	0.651
Mastoid foramen	18.395	0.001***
Foramen Vesalii	5.849	0.211
Occipital foramen	0.029	1.000
Foramen spinosum	0.761	0.944

W_2 is the test statistic.

** $P < 0.01$.

*** $P < 0.001$.

sample is slightly skewed toward a condition with more mastoid and less condylar contribution, as compared with Italian and female samples, respectively.

According to Spearman's correlation test, there is no correlation between the parietal, condylar, and mastoid

indexes. There is a significant correlation between the mastoid index and cranial proportions, as well as between the mastoid index and mean cranial size (Table 14).

Discussion

Overview

Craniovascular traits concern the imprints left by arteries and veins on the cranial bones, and represent the only vascular information available when dealing with osteological remains, as found in bioarchaeology, forensic science, and paleontology (Písová et al. 2017; Rangel de Lázaro et al. 2018). Most of these features are termed 'epigenetic traits' because of the uncertain morphogenetic mechanisms, and probable influence of both genetic and developmental factors (Hauser & De Stefano, 1989). Their prevalence and degree of expression can be variable among different populations, although the reasons for these differences are not clear. In general, much information is missing on the association between these vascular features and other cranial traits, as well as on the exact functions of these anatomical elements. Such information is valuable in clinical and pathological situations, bridging anthropology and medicine (e.g. Kobayashi et al. 2006; Ribas et al. 2006).

In this study, we provide a quantitative analysis of the prevalence and expression of major craniovascular features that can be easily scored on dry skull collections, with two main aims. First, this study supplies a quantitative reference for further comparison with other samples or specific case

Table 7 Patterns of dural venous sinuses

Czech sample	All (n = 103)		Male (n = 56)		Female (n = 45)	
Confluence pattern						
Type I	60 (58%)		26 (46%)		32 (71%)	
Type II	20 (19%)		14 (25%)		6 (13%)	
Type III	3 (3%)		1 (2%)		2 (4%)	
Type IV	20 (19%)		15 (27%)		5 (11%)	
Transverse s. dominance						
Right	53 (51%)		27 (48%)		25 (56%)	
Left	32 (31%)		19 (34%)		12 (27%)	
Unclear	18 (17%)		10 (18%)		8 (18%)	
	R	L	R	L	R	L
Transverse s. expression						
No imprint	6 (6%)	12 (12%)	4 (7%)	3 (5%)	2 (4%)	9 (20%)
Light imprint	43 (42%)	50 (49%)	27 (48%)	34 (61%)	16 (36%)	15 (33%)
Clear imprint	35 (34%)	26 (25%)	19 (34%)	10 (18%)	15 (33%)	15 (33%)
Marked imprint	19 (18%)	15 (15%)	6 (11%)	9 (16%)	12 (27%)	6 (13%)
Sphenoparietal sinus	47 (46%)	52 (50%)	27 (48%)	30 (54%)	19 (42%)	21 (47%)
Occipital or marginal sinus	12 (12%)	8 (8%)	7 (13%)	7 (13%)	3 (7%)	0 (0%)
At least one O/M s.	13 (13%)		8 (14%)		3 (7%)	
Italian sample	All (n = 141)		Male (n = 71)		Female (n = 50)	
Confluence pattern						
Type I	76 (54%)		40 (56%)		29 (58%)	
Type II	25 (18%)		13 (18%)		6 (12%)	
Type III	2 (1%)		1 (1%)		1 (2%)	
Type IV	38 (27%)		17 (24%)		14 (28%)	
Transverse s. dominance						
Right	57 (40%)		27 (38%)		23 (46%)	
Left	28 (28%)		19 (27%)		5 (10%)	
Unclear	56 (40%)		25 (35%)		22 (44%)	
	R	L	R	L	R	L
Transverse s. expression						
No imprint	8 (6%)	10 (7%)	5 (7%)	4 (6%)	1 (2%)	4 (8%)
Light imprint	53 (38%)	66 (47%)	27 (38%)	34 (48%)	16 (32%)	23 (46%)
Clear imprint	43 (30%)	42 (30%)	19 (27%)	21 (30%)	17 (34%)	15 (30%)
Marked imprint	37 (26%)	23 (16%)	20 (28%)	12 (17%)	16 (32%)	8 (16%)
Sphenoparietal sinus	63 (45%)	70 (50%)	37 (52%)	39 (55%)	19 (38%)	21 (42%)
Occipital or marginal sinus	6 (4%)	11 (8%)	2 (3%)	7 (10%)	1 (2%)	7 (14%)
At least one O/M s.	14 (10%)		8 (11%)		2 (4%)	

studies. A preliminary survey was performed on a single collection and on fewer traits (Bruner et al. 2003). The current analysis includes more specimens, different geographical samples, more variables, and a more comprehensive statistical analysis. Secondly, in the current analysis we have considered the association between traits and the differences associated with factors such as cranial form and sex. This information is mandatory in evaluating whether the expression of the features represents a primary and independent genetic/physiological trait, or a secondary consequence of cranial architecture (for example associated with size and allometric effects). In particular, the two geographical populations analyzed in this survey have different mean cranial forms (the Czech sample is more brachycephalic, whereas

the Italian sample is more mesocephalic) but the same cranial size, in agreement with North–South craniometric trends (e.g. Beals et al. 1983, 1984; Relethford, 2004; Roseman, 2004; Harvati & Weaver, 2006; Hubbe et al. 2009). In contrast, males and females differ in cranial size (larger in males) but not in cranial proportions.

Prevalence and distribution

The middle meningeal artery in our sample is more developed in the anterior endocranial regions (70% of cases) and through the development of the anterior branches (50% of cases), and the superior sagittal sinus frequently runs into the right sinus (56% of cases), which is often much larger

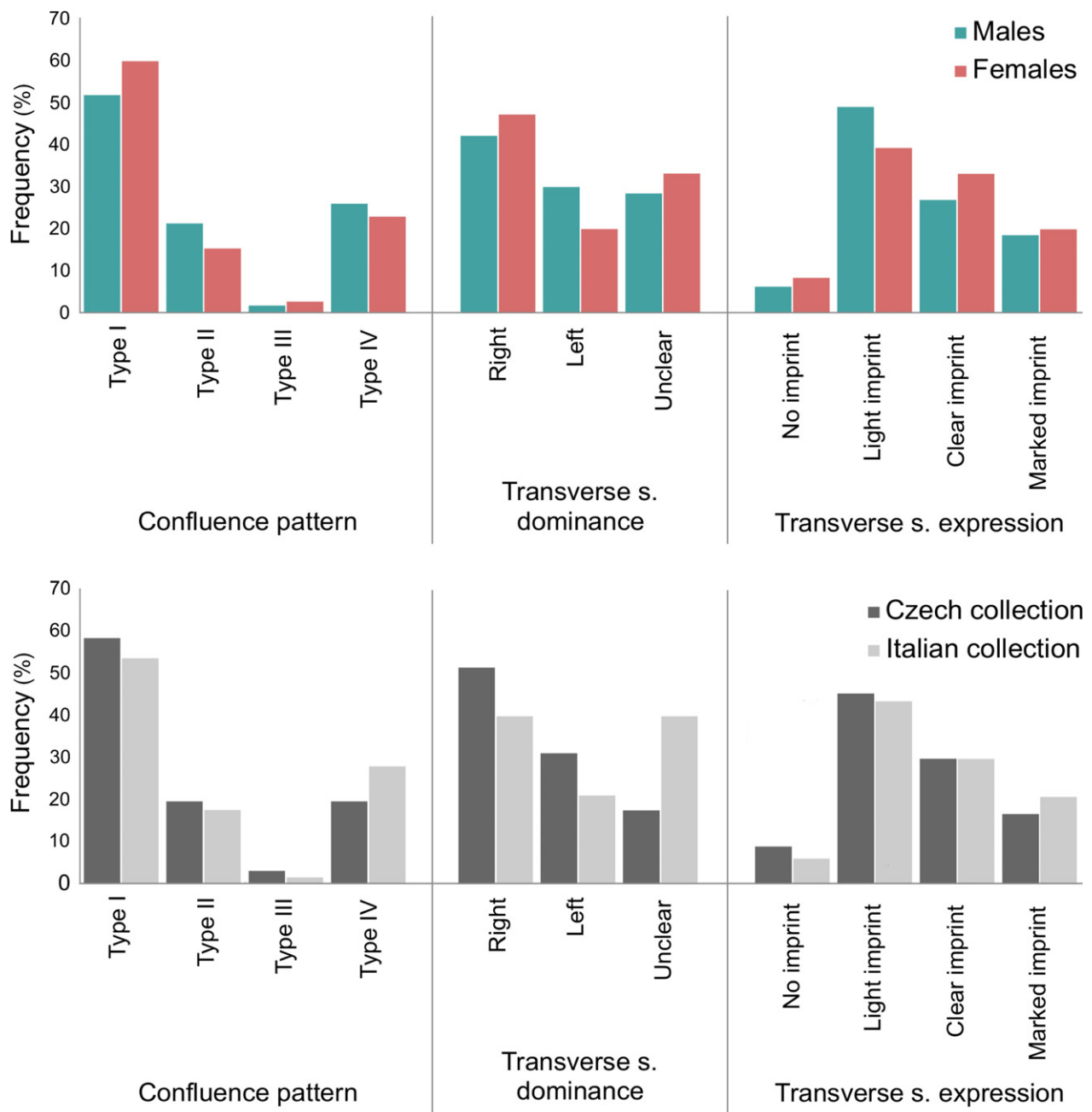


Fig. 5 Traces of dural venous sinuses (TVS): pattern, dominance, and expression. [Colour figure can be viewed at wileyonlinelibrary.com]

than the left (45% of cases). Similar patterns have been described in other samples, suggesting a general consistency among human populations (e.g. Kaplan et al. 1972; Durgun et al. 1993; Goto & Koda, 2000; Hirata, 2000; Bruner et al. 2005). For the traces of the middle meningeal artery, Saban (1995) suggested that these vessels are more developed on the right side, although without supplying a quantitative assessment (Saban, 1995). However, differences in right–left vascularization were not confirmed after a quantitative analysis using fractal dimension (Bruner et al. 2005).

At least for the features considered in the current survey, our data do not reveal a consistent or a significant pattern of asymmetries. We could then conclude that asymmetries in these vascular traces, if any, must be subtle. In some cases, vascular asymmetry can be a consequence of cerebral asymmetry (Bruner et al. 2009). For example, in adult humans the left occipital lobe is generally much larger than the right (Kimbel, 1984), and a different distribution of endocranial pressure may therefore facilitate the development of the sinuses on the right side. However, at present

Table 8 Foramina prevalence

Czech sample	All (n = 85)		Male (n = 48)		Female (n = 35)	
	R	L	R	L	R	L
Presence of:						
Parietal foramen	54 (64%)	50 (59%)	30 (63%)	30 (63%)	23 (66%)	19 (54%)
Condylar canal	63 (74%)	63 (74%)	35 (73%)	38 (79%)	27 (77%)	25 (71%)
Mastoid foramen I	74 (87%)	71 (84%)	43 (90%)	40 (83%)	29 (83%)	29 (83%)
Mastoid foramen II	14 (16%)	30 (35%)	7 (15%)	18 (38%)	6 (17%)	11 (31%)
Foramen Vesalii	44 (52%)	50 (59%)	24 (50%)	23 (48%)	20 (57%)	27 (77%)
Occipital foramen		3 (4%)		1 (2%)		2 (6%)
Foramen spinosum	84 (99%)	85 (100%)	47 (98%)	48 (100%)	35 (100%)	35 (100%)

Italian sample	All (n = 134)		Male (n = 68)		Female (n = 49)	
	R	L	R	L	R	L
Presence of:						
Parietal foramen	72 (54%)	66 (49%)	41 (60%)	37 (54%)	23 (47%)	24 (49%)
Condylar canal	100 (75%)	103 (77%)	51 (75%)	50 (74%)	36 (73%)	38 (78%)
Mastoid foramen I	115 (86%)	103 (77%)	59 (87%)	58 (85%)	42 (86%)	34 (69%)
Mastoid foramen II	18 (13%)	15 (11%)	14 (21%)	9 (13%)	4 (8%)	5 (10%)
Foramen Vesalii	61 (46%)	51 (38%)	30 (44%)	26 (38%)	23 (47%)	18 (37%)
Occipital foramen		5 (4%)	2 (3%)			2 (4%)
Foramen spinosum	132 (99%)	132 (99%)	68 (100%)	68 (100%)	48 (98%)	48 (98%)

Table 9 Prevalence of multiple foramina

	Number of foramina per individual				
	0	1	2	3	4
Parietal foramen	63 (27%)	90 (38%)	83 (35%)		
Condylar canal	27 (11%)	145 (61%)	64 (27%)		
Mastoid foramen	15 (6%)	48 (20%)	110 (46%)	52 (22%)	12 (5%)
Foramen Vesalii	91 (39%)	71 (31%)	69 (30%)		
Occipital foramen	229 (97%)	8 (3%)			
Foramen spinosum	0 (0%)	5 (2%)	224 (98%)		

Table 10 Multiple mastoid foramina

Number of mastoid foramina per specimen	Czech sample (n = 103)	Italian sample (n = 152)
0	4 (4%)	9 (6%)
1	19 (18%)	35 (23%)
2	36 (35%)	80 (53%)
3	35 (34%)	20 (13%)
4	9 (9%)	8 (5%)

there is no experimental evidence to support or contradict this hypothesis. In terms of the antero-posterior distribution of the vessels, general cranial shape differences seem to

have no or a negligible effect on the gross vascular morphology (Bruner et al. 2009), although extreme deformation may influence the orientation of the vessels (O'Loughlin, 1996). If structural influences between skull anatomy and vessels distribution are minor or negligible, functional hypotheses must be considered to explain the vascular differences between groups and among individuals. These vessels may be involved in endocranial thermoregulatory processes, and particularly in heat dissipation (Cabanac & Brinnel, 1985; Falk, 1990; Zenker & Kubik, 1996; Caputa, 2004; Bruner et al. 2011, 2012). The middle meningeal artery is particularly developed on the parietal surface, which is likely a crucial region of heat interchange (Bruner & Sherkat, 2008; Bruner et al. 2014). In this sense, it is worth

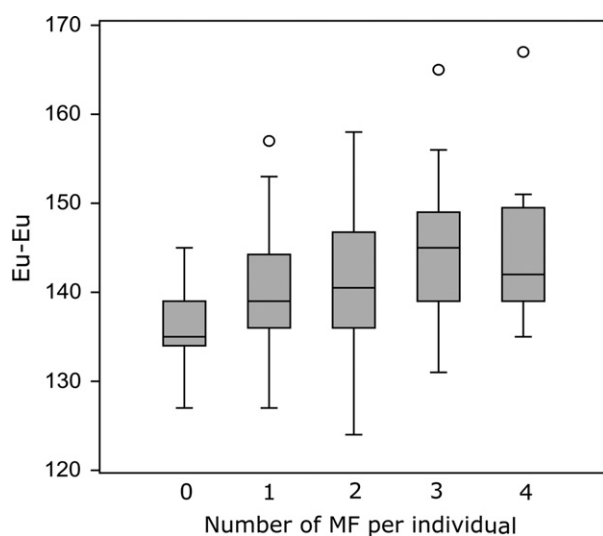


Fig. 6 Cranial breadth (median, interquartile, range) in individuals with different number of mastoid foramina.

noting that more developed posterior branches are often associated with a reduced vascular complexity (Bruner et al. 2005).

Geographical differences

When compared with the Italian sample, the Czech skulls display a greater dominance of the anterior branches of middle meningeal vessels, and the confluence of the sinuses is more asymmetrical, more frequently deviated toward the right side. Conversely, the Italian skulls display on average more developed posterior networks, and show more vascular differences between right and left sides. We found no association between the craniovascular features investigated in this survey and cranial main diameters or general proportions. Therefore, cranial size and form have apparently a null or negligible effect on the expression of these morphological features, which accordingly must be interpreted in terms of genetic or physiological responses, and not as allometric structural consequences. In this sense, the described differences between the two geographical populations are likely to be due to geographic/genetic differences, and not to secondary features due to distinct cranial proportions. Accordingly, we can hypothesize that geographical distances, climate, and migration flow can influence cranial proportions (e.g. Cheverud, 1982; Relethford, 2004; Roseman, 2004; Harvati & Weaver, 2006; Smith, 2009; Hubbe et al. 2009) and vascular traits (Hanihara & Hajime, 2001) independently.

Sexual differences

There are no apparent sex differences in the morphology of the middle meningeal artery, but males display a greater prevalence of occipito-marginal (O-M) sinuses. Males and

females have similar cranial proportions but different cranial sizes. It should be evaluated, therefore, whether the retention of this additional or complementary drainage system in males is associated with size-dependent variations or constraints. However, the O-M sinus prevalence and pattern in modern human populations is low and irregular, making such analysis problematic in terms of sample size and statistical power. Kobayashi et al. (2006), in their study of the anatomical features of the occipital sinus, also found no statistically significant sex-related differences. They analyzed 555 individuals by contrast-enhanced magnetic resonance venography and found the presence of the occipital sinus in 37.7% of cases, respectively 34.6% of males and 40.4% of females (Kobayashi et al. 2006). The prevalence of the O-M sinus system has been considered by several authors. Studies with a sample size of at least 100 specimens provide distinct results for prevalence, e.g. 65% (Das & Hasan, 1970), 53% (Dora & Zileli, 1980), 10% (Ayanzen et al. 2000), 18% (Goto & Koda, 2000), 7% (Bruner et al. 2003), 38% (Kobayashi et al. 2006), and 17% (Narayanam & Livingstone, 2006). In general, the enlarged form of these O-M sinuses which can substitute for the transverse-sigmoid (T-S) system is rarer (Kimbel, 1984; Ayanzen et al. 2000; Bruner et al. 2003; Kobayashi et al. 2006), as the current study also confirms. In addition, age-related changes have also been hypothesized, suggesting that the O-M system is more developed in early stages of ontogeny, and that its diminution and replacement by the T-S and by the vertebral plexus in adulthood is connected to the change in posture to the upright position, when it becomes functionally redundant (Falk, 1986; Widjaja & Griffiths, 2004; Kopuz et al. 2010). However, Kobayashi et al. (2006) found a larger prevalence of the occipital sinus in older age (> 50 years), suggesting that there are discrepancies and differences among different studies. It is worth noting that possible group-specific vascular differences must in any case be better interpreted as tendencies, because individual variation is nonetheless noticeable, and all of these traits are likely to be the result of multifactorial influences, which generates a marked overlap in the distribution of the characters, with an important idiosyncratic component.

Emissary canals

Our results show that mastoid and condylar foramina have a major importance for the endocranial blood flow associated with the emissary canals, followed by the parietal foramina, and then by the occipital foramina, at least when taking into account their size and prevalence. There is no apparent correlation among the presence or dimensions of these canals, which should thus be considered, at present, independent traits. Only the mastoid canals show a correlation with cranial form and, interestingly, they are apparently influenced by both size and proportions. Accordingly, mastoid channels are more developed in larger or

Table 11 Descriptive statistics of foramina size

Czech sample													Italian sample													
	n	R	Mean	SD	Q1	Q2	Q3	n	Mean	SD	Q1	Q2	Q3	n	R	Mean	SD	Q1	Q2	Q3	n	Mean	SD	Q1	Q2	Q3
			L	L	L	L	L	L	L	L	L	L	L			L	L	L	L	L	L	L	L	L	L	L
All																										
Parietal size	53	0.6	0.3	0.3	0.5	0.8	52	0.6	0.3	0.3	0.5	0.8	84	0.7	0.3	0.3	0.5	0.5	0.8	76	0.6	0.2	0.3	0.5	0.8	
Condylar size	62	1.6	0.4	1.2	1.8	1.8	63	1.5	0.4	1.2	1.8	1.8	113	1.6	0.3	1.6	0.3	1.8	1.8	113	1.6	0.3	1.8	1.8		
Mastoid size I	73	1.4	0.4	1.0	1.2	1.8	70	1.3	0.5	1.0	1.2	1.8	120	1.2	0.5	1.2	0.5	1.8	1.8	114	1.1	0.5	0.8	1.0		
Mastoid size II	12	0.9	0.4	0.8	0.9	1.2	25	1.0	0.4	0.8	1.0	1.2	21	0.8	0.3	0.5	0.8	1.1	18	0.9	0.3	0.7	1.0			
Vesal size	43	0.6	0.3	0.3	0.5	0.8	48	0.6	0.3	0.3	0.5	0.8	64	0.6	0.4	0.3	0.5	1.0	51	0.6	0.3	0.3	0.5			
Spinous size	83	1.5	0.3	1.2	1.8	1.8	83	1.5	0.3	1.2	1.8	1.8	144	1.5	0.3	1.2	1.2	1.8	143	1.5	0.3	1.2	1.8			
Occipital size*	2	0.5	0.0	0.4	0.5	0.4							4	1.0	0.2	0.8	0.9	1.2								
Males																										
Parietal size	27	0.7	0.3	0.3	0.5	0.9	29	0.6	0.3	0.3	0.5	0.9	46	0.7	0.3	0.5	0.7	1.0	41	0.6	0.2	0.5	0.5			
Condylar size	33	1.6	0.4	1.8	1.8	1.8	36	1.5	0.4	1.2	1.8	1.8	56	1.6	0.4	1.2	1.8	1.8	54	1.6	0.3	1.2	1.8			
Mastoid size I	41	1.4	0.4	1.1	1.8	1.8	38	1.4	0.5	1.0	1.8	1.8	62	1.3	0.4	1.0	1.2	1.8	64	1.2	0.5	0.8	1.2			
Mastoid size II	6	0.9	0.2	0.7	0.9	1.1	14	1.0	0.4	0.8	1.0	1.2	15	0.8	0.3	0.5	0.8	1.2	11	1.0	0.3	0.8	1.0			
Vesal size	21	0.6	0.4	0.3	0.5	0.8	21	0.7	0.4	0.3	0.5	1.0	31	0.7	0.5	0.3	0.5	1.2	25	0.6	0.4	0.3	0.5			
Spinous size	45	1.5	0.3	1.2	1.8	1.8	45	1.5	0.3	1.2	1.8	1.8	74	1.5	0.3	1.2	1.8	1.8	73	1.5	0.3	1.2	1.8			
Occipital size*	1	0.5	0.0	0.3	0.5	0.3							1	1.0	0.0	0.5	1.0	0.5								
Females																										
Parietal size	25	0.5	0.2	0.3	0.5	0.8	22	0.6	0.3	0.3	0.7	0.8	27	0.6	0.3	0.5	0.5	0.8	26	0.5	0.2	0.3	0.5			
Condylar size	28	1.5	0.4	1.1	1.8	1.8	27	1.4	0.4	1.0	1.8	1.8	40	1.7	0.2	1.8	1.8	1.8	41	1.6	0.3	1.5	1.8			
Mastoid size I	30	1.4	0.4	1.0	1.2	1.8	30	1.3	0.5	0.8	1.2	1.8	43	1.1	0.5	0.8	1.0	1.2	37	1.0	0.5	0.5	1.0			
Mastoid size II	5	1.0	0.5	0.6	1.0	1.5	10	1.0	0.4	0.7	0.9	1.2	5	0.7	0.3	0.5	0.5	1.0	5	0.8	0.4	0.5	1.2			
Vesal size	22	0.5	0.2	0.3	0.5	0.8	27	0.5	0.3	0.3	0.5	0.8	24	0.6	0.4	0.3	0.5	0.8	19	0.6	0.3	0.3	0.5			
Spinous size	36	1.5	0.3	1.2	1.8	1.8	36	1.6	0.3	1.2	1.8	1.8	51	1.4	0.3	1.2	1.2	1.8	50	1.5	0.3	1.2	1.2			
Occipital size*	1	0.5	0.0	0.3	0.5	0.3							2	1.0	0.3	0.6	1.0	0.9								

Q1, first quartile; Q2, second quartile (median); Q3, third quartile; SD, standard deviation. Raw data have an interval character, * unpaired midsagittal value.

Table 12 Summary statistics of the foramina indexes in the Czech and Italian sample

	All						Males						Females					
	<i>n</i>	Mean	SD	Q1	Q2	Q3	<i>n</i>	Mean	SD	Q1	Q2	Q3	<i>n</i>	Mean	SD	Q1	Q2	Q3
Czech sample																		
Parietal index	81	0.9	0.5	0.5	0.8	1.2	45	1.0	0.5	0.6	0.8	1.2	35	0.9	0.4	0.5	0.8	1.2
Condylar index	93	2.6	0.9	1.8	2.8	3.6	51	2.5	1.0	1.8	2.6	3.6	41	2.6	0.9	1.8	2.8	3.6
Mastoid index	98	2.9	1.3	1.8	2.9	3.6	52	3.1	1.1	1.9	3.0	3.8	44	2.6	1.4	1.7	2.7	3.6
Vesalius index	64	0.9	0.6	0.5	0.8	1.2	31	0.9	0.7	0.5	0.6	1.2	33	0.9	0.5	0.5	0.8	1.3
Spinous index	101	3.0	0.6	2.4	3.0	3.6	56	3.0	0.6	2.4	3.0	3.6	43	2.9	0.7	2.4	3.0	3.6
R index	103	2.9	1.1	2.1	3.0	3.6	56	3.0	1.1	2.1	3.1	3.8	45	2.8	1.1	2.1	2.8	3.6
L index	103	2.9	1.2	2.0	2.8	3.8	56	3.0	1.2	2.1	3.0	3.9	45	2.8	1.2	1.9	2.8	3.6
Emissary index	103	5.8	1.8	4.6	5.8	7.1	56	5.9	1.7	4.7	6.0	7.2	45	5.6	1.8	4.1	5.4	7.1
Italian sample																		
Parietal index	107	0.9	0.4	0.6	0.8	1.2	59	1.0	0.4	0.6	1.0	1.3	35	0.9	0.4	0.6	0.8	1.0
Condylar index	132	2.8	0.9	1.8	3.0	3.6	65	2.7	0.9	1.8	3.0	3.6	47	2.9	0.9	1.8	3.0	3.6
Mastoid index	140	2.2	1.1	1.3	1.8	3.0	75	2.5	1.2	1.7	2.3	3.2	48	1.8	1.1	1.0	1.5	2.6
Vesalius index	83	0.9	0.5	0.5	0.8	1.2	42	1.0	0.6	0.5	1.0	1.2	29	0.9	0.6	0.5	0.8	1.1
Spinous index	151	2.9	0.7	2.4	3.0	3.6	77	3.0	0.7	2.4	3.0	3.6	53	2.8	0.7	2.4	3.0	3.3
R index	150	2.7	1.1	1.8	2.7	3.5	76	2.8	1.1	2.0	3.0	3.6	54	2.5	1.0	1.8	2.4	2.9
L index	147	2.5	1.1	1.8	2.6	3.1	75	2.7	1.1	2.1	2.6	3.4	53	2.3	1.0	1.8	2.2	2.7
Emissary index	152	5.1	1.8	3.8	5.2	6.2	77	5.4	1.8	4.4	5.7	6.9	54	4.7	1.7	3.6	4.7	5.8

Q1, first quartile, Q2, second quartile (median), Q3, third quartile; SD, standard deviation.

Table 13 Foramina indexes differences (Mann-Whitney test)

	Czech (<i>n</i> = 103) vs. Italian (<i>n</i> = 152) sample		Males (<i>n</i> = 133) vs. Females (<i>n</i> = 99)	
	<i>z</i>	<i>P</i>	<i>z</i>	<i>P</i>
Parietal index	−0.951	0.347	−1.580	0.112
Condylar index	−1.246	0.211	−0.781	0.432
Mastoid index	−4.373	0.0001***	−3.282	0.002**
Vesalius index	−1.015	0.308	−0.965	0.340
Spinous index	−0.581	0.572	−1.831	0.071
R index	−1.853	0.064	−2.036	0.039*
L index	−2.772	0.005**	−2.084	0.036*
Emissary index	−2.858	0.004**	−2.377	0.019*

**P* < 0.05.

***P* < 0.01.

****P* < 0.001.

brachycephalic skulls, and more numerous in wider skulls. Larger mastoid channels increase the overall emissary capacity of endocranial blood flow which, accordingly, is higher in the Czech individuals and in male individuals. It is worth noting that larger skulls generally present more hyperostotic traits, and mastoid size is a feature usually associated with cranial robustness. It is then likely that more developed mastoid canals are associated with larger mastoid bones. The correlation with cranial proportions is less easy to explain, and in this case a candidate shared factor between brachycephaly and the mastoid veins is the cranial

base, which arrangement is profoundly involved in the differences between long and short braincases (Lieberman et al. 2000; Zollikofer & Ponce de León, 2013; Bastir & Rosas, 2016).

Because of the large individual variation, it must be expected that any possible association or correlations between these traits will be subtle and hard to detect in statistical terms. Subtle differences between groups may be irrelevant at an individual level but are important to understand the biological relationships behind phenotypic expression. Future efforts on this topic should therefore be devoted to improving the resolution of these quantitative analyses. Future studies should be also aimed at increasing the geographical diversity, at including ontogenetic variations, and at providing more detailed vascular metrics (for example, on the exact dimensions of traces and vessels). Nonetheless, major advances in this topic will depend upon a proper knowledge of the vessels themselves, and on a more detailed understanding of the mechanical and physiological relationships between the vessels and their bony traces. Vessel anatomy and structure should be investigated with dissections and histology, and the functioning, morphogenesis and physiological responses to behavioral and environmental factors should be studied through the employment of digital imaging and animal models.

Conclusion

In this survey, we have investigated the prevalence and correlation between the major craniovascular features in

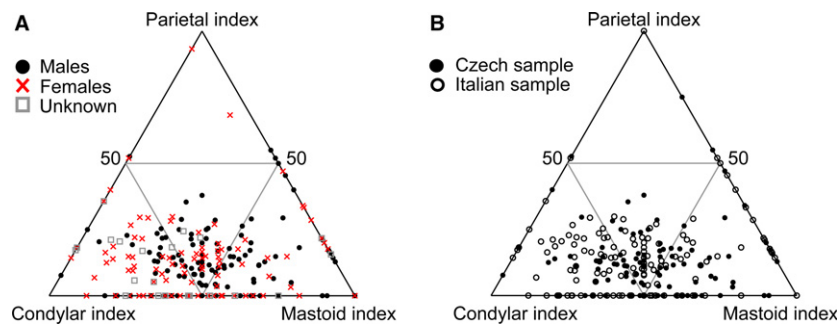


Fig. 7 Ternary plots for the three foramina indexes. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 14 Correlation between foramina indexes and cranial size (Spearman's rank correlation test)

	Parietal index		Condylar index		Mastoid index	
	ρ	P	ρ	P	ρ	P
Correlation between cranial size and foramina dimensions						
Mean size	0.114	0.070	−0.074	0.243	0.263	< 0.001***
Width-length index	0.033	0.600	−0.087	0.166	0.232	0.0001***
Height-length index	−0.078	0.206	0.034	0.586	−0.041	0.521
Height-width index	−0.096	0.124	0.119	0.062	−0.235	< 0.001***
Correlation between foramina dimensions						
Parietal index			−0.095	0.129	−0.023	0.709
Condylar index					−0.096	0.126
Mastoid index						

*** $P < 0.001$.

two distinct European populations, as well as in adult males and females. Endocranial vascular traces suggest that some macroanatomical features (such as the antero-posterior vascular distribution) may be influenced by geographic/genetic factors, while endocranial foramina (such as the mastoid channels) are also influenced by cranial morphology. Individual variation is nonetheless noticeable, producing distinct idiosyncratic combinations of features which suggest a multifactorial morphogenetic background and a marked independence among the traits. Information on these features is relevant to both anthropology and medicine. The functional implications of these morphological variations may involve endocranial thermal regulation, although experimental data in this regard are still lacking.

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