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Further data about venous channels in South African Plio-Pleistocene hominids

Original data about venous channels in South African Plio-Pleistocene hominids are discussed. To assess possible changes in blood volume flow of fossil hominids, we test whether dimensions of three extracranial venous foramina were different between *Australopithecus africanus* and *Australopithecus (Paranthropus) robustus*. Moreover, providing further data about the small sample of South African Plio-Pleistocene hominids, we also attempt to re-analyse the incidence of divided hypoglossal canals and four emissary foramina in a very large sample of extant African apes representing all ages, species and subspecies, in *A. africanus* and in "robust australopithecines". Up to now, only very poor data on extracranial dimensions of venous foramina were available for fossil hominids. However, this topic provides interesting information about the modifications of volume flow during human evolution. Assuming that in fossil hominids, as in humans, dimensions of condylar and mastoid foramina, as well as those of jugular foramina, depended on volume flow through them, we conclude, first, that volume flow through internal jugular veins was comparable in South African australopithecines, extant chimpanzees and humans, and second, that, in comparison with the extant less-encephalized chimpanzees (presumably reflecting the ancestral condition), volume flow was higher through condylar veins in *A. (P.) robustus*. This increase was responsible for a significantly greater amount of blood drainage from the brain (and consequently an increased arterial blood supply). We support the view that encephalization was the prevailing functional explanation for volume flow increase through condylar veins in *A. (P.) robustus*, in comparison with its ancestor with its presumably more ape-like degree of encephalization.

Considering the incidence of emissary canals and foramina, significant differences between *A. africanus*, "robust australopithecines" and all the extant African ape species, were tested statistically. Concerning the condylar canal, we did not find differences between "robust australopithecines" and extant African apes. Concerning the incidence of divided hypoglossal canals, mastoid canals, parietal and occipital foramina, no difference was found between extant African apes, *A. africanus* and "robust australopithecines". High frequencies of either condylar or mastoid canals cannot be regarded as a "pongid condition". Moreover, we did not find convincing data to support the hypothesis that mastoid emissary veins (partly representing a putative "radiator" for cooling the brain) were selected in *A. africanus*, in comparison with "robust australopithecines".

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Introduction

Since the work of Schepers (1946) many studies have dealt with cranial venous patterns in Plio-Pleistocene hominids, investigating either natural endocasts or endocranial sulci and foramina. Saban (1978, 1983) studied the patterns of sulci on the sphenoid and temporal bones representing middle meningeal vessels. Referring to Schepers' (1946) description of *Australopithecus africanus* and Tobias' description of OH 5 (1967), Saban (1978, 1983) recognized, among australopithecines, two patterns of sulci representing middle meningeal veins and considered that they corresponded to distinct states of quantitative brain evolution. The *Australopithecus (Paranthropus) boisei* pattern was more complex and corresponded to a higher state of quantitative evolution (Saban, 1983). Later, Falk (1993: p. 94) considered that Saban's distinction was "questionable" and added: "hominid meningeal patterns should be reassessed with a view to identifying possible contributions from the orbit to the meningeal arteries of the

middle cranial fossa'. In his description of OH 5 (*Zinjanthropus boisei*), the type specimen of *A. (P.) boisei*, Tobias (1967: pp. 64–70) recognized a variant in the grooved pattern imprinted upon the endocranial surface of the skull representing the cranial venous sinuses. In this variant, an unusual and enlarged occipital/marginal (O/M) venous sinus, which runs close to the margin of the foramen magnum, is represented. Thus a variable venous quantity of blood by-passes the transverse/sigmoid sinuses. In *A. (P.) robustus/boisei*, the O/M sinus venous pattern is encountered in six out of seven (Kimbel, 1984), or ten out of ten (Falk *et al.*, 1995) specimens in which the area is preserved. Interestingly, the same variant occurs also in six out of six, or possibly seven out of seven, Hadar crania, usually classified as *Australopithecus afarensis* (Kimbel, 1984; Kimbel *et al.*, 1994). On the other hand, the O/M sinus venous pattern is lacking in all specimens of *A. africanus* (Kimbel, 1984; Conroy *et al.*, 1990) except the Taung child in which Tobias & Falk (1988) found “a dual pattern of cranial venous sinuses”, i.e., both O/M and transverse/sigmoid sinus venous patterns. The functional significance of the different variants observed for the venous system have been questioned (Kimbel, 1984, 1990; Brown *et al.*, 1993). Falk & Conroy (1983) suggested a functional interpretation of cephalic venous patterns related to alternative physiological and cranial architectural mechanisms. They considered (1983: p. 781) that, during the attainment of bipedalism, “an increasing cerebral venous drainage load” was placed upon the vertebral venous plexus. Interestingly, Falk (1986, 1990) extended her previous studies to the scoring of four emissary canals and foramina that contain the veins connecting the extracranial venous system to the blood sinuses and meningeal veins. She also questioned the etiology of divided hypoglossal canals and concluded that, for draining blood from the cranium, “robust australopithecines” retained “pongid-like frequencies for numerous features: relatively high frequency of multiple hypoglossal canals, relatively low frequency of mastoid foramina, and low frequency of parietal foramina” (Falk, 1986: p. 322). She added that “the posterior condyloid foramen, like the O/M sinus system, occurred in high frequencies in robust australopithecines because of epigenetic adaptations associated with selection for bipedalism in their ancestors” (*op. cit.*, p. 322). Concerning *A. africanus*, Falk (1986: p. 312) wrote: “The reduction in frequency of the condyloid foramen in gracile australopithecines is associated with increased frequencies of mastoid and occipital foramina over the robust condition.” To recapitulate, comparing frequencies of “three pathways” (i.e., the enlarged O/M sinus system, the condylar and divided hypoglossal canals), Falk (1986: p. 322) wrote that the “frequencies of these three pathways decrease between robust and gracile australopithecines. It is noteworthy that the former two occur in much higher frequencies in robust australopithecines than in pongids.” However, both size and distribution of cephalic veins belong to an evolving anatomical system that is closely associated with the evolution of many other elements such as encephalization.

This study has two aims. First, to assess possible changes in the magnitude of blood flow, we test whether dimensions of three extracranial venous foramina are different between *A. africanus* and *A. (P.) robustus*. Second, providing further data about the small sample of South African Plio-Pleistocene hominids, we attempt to re-analyse the incidence of divided hypoglossal canals and four emissary channels in a sample of 1154 extant African apes representing all ages, species and subspecies, in *A. africanus* and in “robust australopithecines”. Indeed, as Tobias (1994: p. 121) wrote: “More data on the ontogeny of the venous drainage patterns are needed, not only for hominids but also for other hominoids.”

In humans and African apes, the internal jugular vein is the main outlet of the blood from the skull. Its upper bulb represents a direct continuation of either the sigmoid and transverse sinuses or the O/M sinus complex (Matsushima *et al.*, 1983; Curé *et al.*, 1994). In addition to

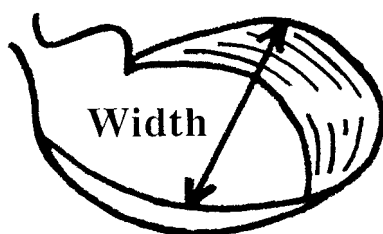


Figure 1. Width of the venous part of the jugular foramen.

this main venous outflow there are two important accessory ones, created by the condylar and mastoid emissary veins. Interestingly, [Solter & Paljan \(1973\)](#) examined the influence of the diameter of condylar and mastoid foramina on the dimensions of the venous portion of the jugular foramen on 300 macerated human skulls ranging from 11–88 years. They noted that the dimensions of the condylar and mastoid orifices were in inverse proportion to the dimensions of the venous part of the jugular foramina. Demonstrating that the dimensions of the condylar and mastoid orifices, as well as those of the venous part of the jugular foramina, depend on volume flow through them, they concluded (1973: p. 330) that “blood circulation through the jugular vein can (. . .) be compensated by auxiliary blood circulation on either the same or the opposite side of the skull”. Thus, to assess the magnitude of cephalic blood flow, we should score the different variants (sulci and foramina) but also keep in mind the problem of size of the different foramina. Moreover, dimensions of the endocranial grooves do not always necessarily indicate the capacity of sinuses. For example, [Streit \(1903\)](#) described weakly-impressed transverse grooves although the relevant sinuses were well developed.

Materials and methods

The anatomical terminology used here follows that of the International Code for Nomenclature ([Sobotta, 1977](#)). All fossil hominids were examined with a low-power binocular microscope.

All measurements (given in millimetres) were taken using an electronic digital caliper (accuracy: 0.03 mm), three determinations being made in each instance. The mean and standard deviation of each set of three readings were calculated. Since the jugular bulb is roughly cylindrical and passes through the jugular foramen in its postero–lateral part ([Lindblom, 1936](#)), we determined the width of this venous part of the jugular foramen ([Figure 1](#)). The extracranial diameters of condylar, mastoid, parietal and occipital canals were also determined. These measurements were taken in all the South African Plio-Pleistocene hominids in which one or more features were present ([Table 1](#)) and in chimpanzees including 16 specimens of known age of both sexes, within age limits of 3 months up to 39 years, from the Tai (Ivory Coast) forest. To compare our results to [Solter & Paljan’s \(1973\)](#) data in humans, the surface of these extracranial foramina was calculated from the formula for the area of a circle.

Besides measurements, we recorded five discrete traits: divided hypoglossal canal, condylar and mastoid canals, parietal and occipital foramina. In order to derive frequencies for bilateral features and to compare extant species with fossil hominids (where only one side is often present), we considered the trait present if it appeared on one or both sides of the cranium (individual sampling method, different from the side sampling method reported in [Braga,](#)

Table 1 South African Plio-Pleistocene hominids investigated

Specimen	Site	Estimated age at death
<i>A. africanus</i>		
MLD 37/38	Makapansgat	Mature
STS 5	Sterkfontein	Mature, same as Sts 6, i.e., 35 ± years (Mann, 1975)
STS 19	Sterkfontein	26 ± 3 years (Mann, 1975)
STS 25	Sterkfontein	Mature
STS 26	Sterkfontein	Mature
STS 58	Sterkfontein	Mature, same as STS 19 (Mann, 1975)
STW 53	Sterkfontein	Mature
STW 187a	Sterkfontein	—
TAUNG	Taung	6 ± 1 years (Mann, 1975)–3 years (Bromage, 1987)
<i>A. (P.) robustus</i>		
TM 1517	Kromdraai B	20 ± 1 years (Mann, 1975)–ca > 10.5 years (Bromage, 1987)
SKW 11	Swartkrans	Mature
SK 27	Swartkrans	8 ± 2 years (Mann, 1975)–5.5–6 years (Bromage, 1987)
SK 46	Swartkrans	34 ± 3 years (Mann, 1975)
SK 47	Swartkrans	13 ± 2 years (Mann, 1975)–7.5 years (Bromage, 1987)
SK 48	Swartkrans	20 ± 1 years (Mann, 1975)
SK 54	Swartkrans	Immature (Mann, 1975)
SK 83	Swartkrans	32 ± 2 years (Mann, 1975)
SK 859	Swartkrans	Immature

1995*b*: p. 146). In the case of fossil hominids, where only one side could be observed, this preserved side was used to represent the cranium. These traits were scored in all the South African Plio-Pleistocene hominids in which one or more features were recordable (Table 1). Concerning *A. (P.) boisei* specimens, we used data from the literature (Tobias, 1967; Leakey *et al.*, 1971; Day *et al.*, 1976; Falk, 1986; Brown *et al.*, 1993). In order to obtain a satisfactory picture of the variation of each trait in all the African apes, skulls of 1154 juvenile and adult individuals from the following species and subspecies were studied: 148 *Pan troglodytes verus*, 223 *Pan troglodytes troglodytes*, 215 *Pan troglodytes schweinfurthi*, 172 *Pan paniscus*, 235 *Gorilla gorilla gorilla*, 106 *Gorilla gorilla graueri* and 55 *Gorilla gorilla beringei*. Adults were distinguished from juveniles on the basis of third permanent molar eruption. Juveniles were all those without 3rd, 2nd or 1st molar eruption. Adults had, at least, one 3rd molar erupted and an incompletely or completely closed sphenoccipital synchondrosis. Ages and sexes of these specimens are listed in Table 2.

For probing the existence of canals, we used different flexible wires and horse hairs (1 and 3 mm in diameter). Pits, patent blind canals, and extracranial foramina too narrow to transmit these probes, were recorded as absent (method reported in Braga, 1995*b*: p. 146). Boyd (1930) was the first author to score systematically emissary foramina in very large skeletal series. In many cases, he found difficulty “in coming to a decision in regard to the bore of the canal, owing to its sinuosity, and also because sometimes the external aperture was quite large, while the lumen narrowed down considerably” (*op. cit.*, p. 108). In some cases, when a canal was “so sinuous that it was impossible to pass a probe”, Boyd (1930: pp. 108–109) acknowledged that “one is left in doubt as to whether there is a complete emissary foramen or not”. We should stress here the fact that, for extant species, the scoring procedures diverged between authors. For example, concerning the mastoid canal in humans, Boyd (1930) and Falk (1986) reported, respectively, a frequency of 68 and 90%. Falk (1986: p. 320) considered that the frequency reported by Boyd for the mastoid foramen was “probably low because Boyd scored a foramen

Table 2 Numbers, species, age-groups and sex of African ape skulls investigated

	Females		Males		Undetermined sex	
	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults
<i>P. t. verus</i>	14	45	9	57	7	16
<i>P. t. troglodytes</i>	34	82	34	34	16	23
<i>P. t. schweinfurthi</i>	29	23	27	34	39	63
<i>P. paniscus</i>	34	28	31	22	38	19
<i>G. g. gorilla</i>	36	63	34	84	9	9
<i>G. g. graueri</i>	8	34	4	36	19	5
<i>G. g. beringei</i>	5	14	7	20	6	3

as present if a wire would not pass through it". She added that her own result, according to her own scoring procedure (diverging from that of Boyd for the mastoid canal) was "probably more realistic" (*op. cit.*, p. 320). This example clearly demonstrates that, to compare extant species and fossil hominids, we must use the same scoring procedures. Concerning frequencies of emissary canals in humans, the more complete data from the literature (i.e., data including variation among human populations) are those reported in the important synthesis by Hauser & De Stefano (1989). For all the features studied, for both extant species and fossil hominids, we decided to use the same scoring procedure as the one reported by Hauser & De Stefano (1989: pp. 82, 115, 202) (known as the method of Berry & Berry, 1967). Emissary canals were recorded as present if a probe entered either in their external or internal openings (even if the probe could not be passed through). This method has the great advantage to be comparable with the scoring technique employed in many detailed descriptions of fossil hominids (i.e., the existence of an emissary canal is always deduced from the presence of extracranial or intracranial foramina). Indeed, as in many fossils, canals are filled with matrix; it is impossible to pass a wire through them. Consequently, to compare the incidence of emissary canals between extant species and Plio-Pleistocene hominids, the use of the same scoring procedures for both material is essential. If it is not the case, a scoring bias is introduced in the comparison. Moreover, we should add that when the individual count is used [the sampling method also used by Boyd (1930, 1934) and Falk (1986)], a scoring doubt encountered on one side of the skull is removed if the existence of a canal is conclusive on the opposite side.

To evaluate the differences in means between two groups, we used the *t*-test. In the case of two-sample *t*-tests (when the two groups were independent, i.e., each datum in one group was in no way associated with any specific datum in the other group) (differences between taxa), the equality of variances assumption was verified with the Levene's test. When the data occurred in pairs (when the two groups were dependent, i.e., each observation in the first group was in some way correlated with an observation in the second group) (differences between sides), we used paired-sample *t*-test. In addition to these *t*-tests, and because it is commonly recommended (Zar, 1984: p. 186) in the case of multiple means comparisons, if the analysis of variance (ANOVA) (in the present study: Model II or random effects model of ANOVA) first rejected a multisample hypothesis of equal means, we used a multiple comparison test (the Tukey procedure with unequal sample sizes is recommended; Miller, 1985). However, some authors do not recommend multiple comparison tests in Model II of ANOVA situations (Zar, 1984: p. 185). For dichotomous nominal scale data (i.e., observations recorded as present or absent), differences among two or more proportions (sex, age, side, specific and subspecific

Table 3 *t*-Tests for dependent samples (right/left) in *P. t. verus*, *P. t. schweinfurthi* and *Pan paniscus*

Right vs. left	Jugular width				Condylar canal				Mastoid canal			
	Juveniles		Adults		Juveniles		Adults		Juveniles		Adults	
	<i>n</i>	<i>P</i>	<i>n</i>	<i>P</i>	<i>n</i>	<i>P</i>	<i>n</i>	<i>P</i>	<i>n</i>	<i>P</i>	<i>n</i>	<i>P</i>
<i>P. t. verus</i>	13	0.6558	14	0.2372	4	0.3617	5	0.7909	0	*	0	*
<i>P. t. schweinfurthi</i>	7	0.1276	3	0.2065	6	0.6948	3	0.3754	3	0.4678	3	0.0075
<i>P. paniscus</i>	3	0.4449	6	0.3158	1	*	4	0.7817	0	*	3	0.9438

Marked differences are significant at $P < 0.05$ (**P* cannot be calculated).

differences), as well as associations of dichotomous variables, were assessed using the appropriate contingency table analysis: the Pearson Chi-square statistics or the Fisher's exact tests, if the contingency table has insufficiently large frequencies. Indeed, the proportions to be compared with each other was not the mean of a set of proportions; then, multisample testing procedures were not applied (Zar, 1984: p. 401). All these tests were performed using the STATISTICA software package. Although we prefer the one-tailed procedure in Fisher's exact tests, we provide and discuss the results of both procedures (one-tailed and two-tailed). Armitage & Berry (1994) consider that the one-tailed procedure of Fisher's exact tests is probably to be preferred. All the statistical techniques we employed in this study and their appropriateness are detailed in Zar (1984).

Results

Width of the venous part of the jugular foramen

Many investigators found that the human right jugular foramen was larger (Solter & Paljan, 1973; Lang & Weigel, 1983). On the contrary, in juvenile or adult chimpanzees, we never found significant differences between right and left sides (Table 3). Solter & Paljan (1973: p. 322) reported that, in humans, "the dimensions of the venous portion of the jugular foramen and those of the terminal part of sigmoid groove do not differ substantially with age". However, the youngest specimens of their sample were only 11 years so they could not estimate the size increase from infancy to childhood. Results for the width of the venous part of the jugular foramen in Tai chimpanzees are given in Table 4. This dimension increases from infancy to childhood, while it decreases after childhood.

Results for chimpanzees are given in Table 5. With two exceptions, we did not notice any significant difference between chimpanzee species and subspecies (*t*-tests). In juveniles, the left width of the venous part of the jugular foramen was significantly smaller in *P. t. schweinfurthi* than in either *P. t. verus* or *P. paniscus* (respectively, $P = 0.0422$ and $P = 0.0159$) (Table 5). Using the Tukey procedure (multiple comparison test), no significant difference between chimpanzee taxa appeared (Table 7).

Results for South African Plio-Pleistocene hominids are given in Table 6. In *A. africanus*, we did not find a significant difference between right and left sides ($P = 0.8796$). If we compare this measurement (right side) between, first, STS 5 and STS 19, and second, the Taung child, we can notice a general increase. The estimated age is 6.5 ± 1 years (Mann, 1975) or 3.3 years (Bromage, 1987) for the Taung child, and 26 ± 3 years (Mann, 1975) for STS 19. So, from

Table 4 Width of the venous part of the jugular foramen for humans (data from Lang *et al.*, 1983) and known age Ta chimpanzees

	Humans				Chimpanzees			
	Mean	Min.	Max.	S.D.	Mean	Min.	Max.	S.D.
2-6 years								
Right	5.19	3.00	7.50	1.38	5.52	4.49	7.11	1.17
Left	6.04	4.00	14.50	2.77	5.04	4.07	6.49	1.10
8-12 years								
Right	7.67	5.50	9.50	1.37	6.45	5.90	7.28	0.59
Left	5.75	3.50	7.50	1.57	6.26	4.90	7.68	1.17
Adults								
Right	7.34	3.60	12.80	1.76	6.23	4.10	7.43	1.01
Left	6.78	4.30	11.50	1.39	5.80	4.39	6.41	0.68

these two specimens, we note that, from infancy to adulthood, the width of the venous part of the jugular foramen increased by 64%. If we compare the Taung child's measurement to that of STS 5, the increase is smaller, i.e., 39%. In order to minimize age influence, when we compared *A. africanus* and *A. (P.) robustus*, we did not include the Taung child in our sample. Doing the comparison (*t*-test) for the left side only (on the right side, *P* cannot be calculated), the *P*-value was 0.5193. Thus, we did not observe any significant difference between *A. africanus* and *A. (P.) robustus*. We also searched for differences (*t*-tests) between fossil hominids and chimpanzees. We found no significant difference between *A. africanus* and chimpanzees (Table 6). On the contrary, the left width of the venous part of the jugular foramen was significantly larger in *A. (P.) robustus* than in *P. paniscus* (*P*=0.0124). However, no difference was found between *A. (P.) robustus* and either *P. t. verus* (*P*=0.3036) or *P. t. schweinfurthi* (*P*=0.1617) (Table 6). Using the Tukey procedure (multiple comparison test), no significant difference appeared (Table 7).

Extracranial diameter of condylar and mastoid canals

The condylar foramen (f. condylaris), also called "condyloid foramen" (Boyd, 1930, 1934) or "posterior condyloid foramen" (Falk, 1986), is the posterior and outer opening of the condylar canal (canalis condylaris). It lies in the condylar fossa, behind either the occipital condyle or the jugular foramen. The condylar canal transmits the corresponding emissary vein (v. emissaria condylaris). Its inner aperture is situated at the end of the sigmoid sinus groove (sulcus sinus sigmoidei). The mastoid foramen (f. mastoideum) corresponds to the outer opening of the mastoid canal. This canal transmits the corresponding emissary vein (v. emissaria mastoidea), and in some cases, a small branch of the occipital artery (a. occipitalis).

With regard to the extracranial diameter of condylar and mastoid canals in humans, Solter & Paljan (1973: p. 329) considered that "relevant comparative data related to age and body side serve no practical purpose". On the contrary, Lang *et al.*'s (1983) results for humans showed that the extracranial diameter of the condylar canal was significantly higher in both sides with ageing. In human neonates, the mean values were 1 and 0.83 mm (minimum: 0.5; maximum: 1.0), respectively for the right and left sides. Between 15 and 17 years, these mean values were 3.63 and 4.0 mm, respectively (minimum: 2.5; maximum: 4.5). In chimpanzees, for the condylar canal, we never found significant differences between right and left sides.

Table 5 Width of the venous part of the jugular foramen, extracranial diameter of condylar and mastoid canals in juvenile and adult chimpanzees

	Jugular width						Condylar canal						Mastoid canal					
	Right		Left		Right		Left		Right		Left		Right		Left			
	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults		
MN	S.D.	MN	S.D.	MN	S.D.	MN	S.D.	MN	S.D.	MN	S.D.	MN	S.D.	MN	S.D.	MN	S.D.	
P. t. verus	5.78	1.01	5.86	1.12	5.65	1.21	6.29	0.92	1.55	0.37	1.68	0.72	1.71	0.23	1.61	0.77	—	—
P. t. schweinfurthi	4.68	0.98	4.91	0.47	4.20	0.54	5.40	0.91	0.87	0.23	0.85	0.08	0.79	0.28	1.53	1.07	1.07	0.45
P. paniscus	5.22	0.72	5.06	0.54	4.74	1.46	5.22	0.54	0.95	0.06	1.28	0.24	1.21	0	1.26	0.26	—	1.12
—————																		
Juveniles																		
Right						Left						Right						
N1	N2	P (Levene)	N1	N2	P (Levene)	N1	N2	P (Levene)	N1	N2	P (Levene)	N1	N2	P (Levene)	N1	N2	P (Levene)	
13	7	0.7849	13	7	0.0422	14	3	0.1860	14	3	0.1860	14	3	0.9359	14	3	0.9359	
13	3	0.2904	13	3	0.7529	14	6	0.0899	14	6	0.0899	14	6	0.3505	14	6	0.3505	
7	3	0.4364	7	3	0.0159	3	6	0.9055	3	6	0.9055	3	6	0.2118	3	6	0.2118	
—————																		
Adults																		
Right						Left						Right						
N1	N2	P (Levene)	N1	N2	P (Levene)	N1	N2	P (Levene)	N1	N2	P (Levene)	N1	N2	P (Levene)	N1	N2	P (Levene)	
4	6	0.4180	4	6	0.7314	5	3	0.1569	5	3	0.1569	5	3	0.4867	5	3	0.4867	
4	2	0.2248	4	2	0.1010	5	6	0.1382	5	6	0.1382	5	6	0.0144	5	6	0.0144	
6	2	0.1719	6	2	0.2365	3	6	0.1477	3	6	0.1477	3	6	0.0249	3	6	0.0249	
—————																		
Mastoid canal																		
1	3	0.2116	0	3	*	0	3	*	0	3	*	0	3	*	0	3	*	
3	0	*	3	1	0.2365	3	4	0.5167	3	4	0.5167	3	5	0.6671	3	5	0.6671	

Means (MN) and standard deviations (S.D.) are given in mm. In the t-tests for independent samples (between chimpanzee taxa), the equality of variances assumption was verified with the Levene's test. Marked differences are significant at $P < 0.05$ (*P cannot be calculated).

Table 6 Width of the venous part of the jugular foramen, extracranial surface (ES) and diameter (D) of condylar and mastoid canals in South African Plio-Pleistocene hominids

	Jugular width				Condylar canal				Mastoid canal																																																																																																																																																																			
	Right		Left		Right		Left		Right		Left																																																																																																																																																																	
	Mean	S.D.	Mean	S.D.	ES	D	ES	D	ES	D	ES	D																																																																																																																																																																
<i>A. africanus</i>																																																																																																																																																																												
STS 5	4.28	0.39	3.79	0.11	1.8	1.5	—	—	2.8	1.9	—	—																																																																																																																																																																
STS 19	5.05	0.16	5.93	0.11	—	—	—	—	3.1	2	—	—																																																																																																																																																																
STS 25	—	—	5.77	0.12	—	—	—	—	—	—	—	—																																																																																																																																																																
STS 26	—	—	—	—	2-1.1	1.6-1.2	2-1.1	1.6-1.2	—	—	—	—																																																																																																																																																																
TAUNG	3.08	0.13	—	—	—	—	—	—	—	—	—	—																																																																																																																																																																
<i>A. (P.) robustus</i>																																																																																																																																																																												
TM 1517	—	—	7.32	0.13	—	—	—	—	—	—	2	1.6																																																																																																																																																																
SKW 11	—	—	—	—	—	—	—	—	—	—	1.5	1.4																																																																																																																																																																
SK 27	—	—	—	—	6.2	2.8	—	—	—	—	—	—																																																																																																																																																																
SK 47	—	—	5.05	0.14	2.6	1.8	1.8	1.5	—	—	—	—																																																																																																																																																																
SK 48	—	—	—	—	6.2	2.8	3.1	2	—	—	—	—																																																																																																																																																																
SK 83	—	—	—	—	—	—	8-6.2	3.2-2.8	—	—	—	—																																																																																																																																																																
SK 859	—	—	—	—	—	—	0.8	1	—	—	—	—																																																																																																																																																																
<table border="1" style="width: 100%; border-collapse: collapse;"> <thead> <tr> <th rowspan="2"></th> <th colspan="3">Right</th> <th colspan="3">Left</th> </tr> <tr> <th>N1</th> <th>N2</th> <th><i>P</i> (Levene)</th> <th>N1</th> <th>N2</th> <th><i>P</i> (Levene)</th> </tr> </thead> <tbody> <tr> <td colspan="7">Jugular width</td> </tr> <tr> <td><i>P. t. verus</i> vs. <i>A. africanus</i></td> <td>14</td> <td>2</td> <td>0.3136</td> <td>14</td> <td>3</td> <td>0.5092</td> </tr> <tr> <td><i>P. paniscus</i> vs. <i>A. africanus</i></td> <td>6</td> <td>2</td> <td>0.9566</td> <td>6</td> <td>3</td> <td>0.0609</td> </tr> <tr> <td><i>P. t. schweinfurthi</i> vs. <i>A. africanus</i></td> <td>3</td> <td>2</td> <td>0.7966</td> <td>3</td> <td>3</td> <td>0.5005</td> </tr> <tr> <td><i>P. t. verus</i> vs. <i>A. (P.) robustus</i></td> <td>14</td> <td>0</td> <td>*</td> <td>14</td> <td>2</td> <td>0.3036</td> </tr> <tr> <td><i>A. africanus</i> vs. <i>A. (P.) robustus</i></td> <td>2</td> <td>0</td> <td>*</td> <td>3</td> <td>2</td> <td>0.5193</td> </tr> <tr> <td><i>A. (P.) robustus</i> vs. <i>P. paniscus</i></td> <td>0</td> <td>6</td> <td>*</td> <td>2</td> <td>6</td> <td>0.0124</td> </tr> <tr> <td><i>A. (P.) robustus</i> vs. <i>P. t. schweinfurthi</i></td> <td>0</td> <td>3</td> <td>*</td> <td>2</td> <td>3</td> <td>0.1617</td> </tr> <tr> <td colspan="7">Condylar canal</td> </tr> <tr> <td><i>A. (P.) robustus</i> vs. <i>P. t. schweinfurthi</i></td> <td>3</td> <td>3</td> <td>0.0277</td> <td>4</td> <td>3</td> <td>0.4639</td> </tr> <tr> <td><i>A. (P.) robustus</i> vs. <i>P. paniscus</i></td> <td>3</td> <td>6</td> <td>0.0466</td> <td>4</td> <td>4</td> <td>0.0219</td> </tr> <tr> <td><i>A. (P.) robustus</i> vs. <i>A. africanus</i></td> <td>3</td> <td>3</td> <td>0.0757</td> <td>4</td> <td>2</td> <td>0.0961</td> </tr> <tr> <td><i>A. (P.) robustus</i> vs. <i>P. t. verus</i></td> <td>3</td> <td>5</td> <td>0.8442</td> <td>4</td> <td>5</td> <td>0.8888</td> </tr> <tr> <td><i>P. t. verus</i> vs. <i>A. africanus</i></td> <td>5</td> <td>3</td> <td>0.2507</td> <td>5</td> <td>2</td> <td>0.0691</td> </tr> <tr> <td><i>A. africanus</i> vs. <i>P. t. schweinfurthi</i></td> <td>3</td> <td>3</td> <td>0.1493</td> <td>2</td> <td>3</td> <td>0.1227</td> </tr> <tr> <td><i>A. africanus</i> vs. <i>P. paniscus</i></td> <td>3</td> <td>6</td> <td>0.6896</td> <td>2</td> <td>4</td> <td>0.4726</td> </tr> <tr> <td colspan="7">Mastoid canal</td> </tr> <tr> <td><i>A. africanus</i> vs. <i>P. paniscus</i></td> <td>2</td> <td>4</td> <td>0.2083</td> <td>0</td> <td>5</td> <td>*</td> </tr> <tr> <td><i>A. africanus</i> vs. <i>P. t. schweinfurthi</i></td> <td>2</td> <td>3</td> <td>0.2555</td> <td>0</td> <td>3</td> <td>*</td> </tr> <tr> <td><i>A. (P.) robustus</i> vs. <i>P. t. schweinfurthi</i></td> <td>0</td> <td>3</td> <td>*</td> <td>2</td> <td>3</td> <td>0.3726</td> </tr> <tr> <td><i>A. (P.) robustus</i> vs. <i>P. paniscus</i></td> <td>0</td> <td>4</td> <td>*</td> <td>2</td> <td>5</td> <td>0.1626</td> </tr> </tbody> </table>														Right			Left			N1	N2	<i>P</i> (Levene)	N1	N2	<i>P</i> (Levene)	Jugular width							<i>P. t. verus</i> vs. <i>A. africanus</i>	14	2	0.3136	14	3	0.5092	<i>P. paniscus</i> vs. <i>A. africanus</i>	6	2	0.9566	6	3	0.0609	<i>P. t. schweinfurthi</i> vs. <i>A. africanus</i>	3	2	0.7966	3	3	0.5005	<i>P. t. verus</i> vs. <i>A. (P.) robustus</i>	14	0	*	14	2	0.3036	<i>A. africanus</i> vs. <i>A. (P.) robustus</i>	2	0	*	3	2	0.5193	<i>A. (P.) robustus</i> vs. <i>P. paniscus</i>	0	6	*	2	6	0.0124	<i>A. (P.) robustus</i> vs. <i>P. t. schweinfurthi</i>	0	3	*	2	3	0.1617	Condylar canal							<i>A. (P.) robustus</i> vs. <i>P. t. schweinfurthi</i>	3	3	0.0277	4	3	0.4639	<i>A. (P.) robustus</i> vs. <i>P. paniscus</i>	3	6	0.0466	4	4	0.0219	<i>A. (P.) robustus</i> vs. <i>A. africanus</i>	3	3	0.0757	4	2	0.0961	<i>A. (P.) robustus</i> vs. <i>P. t. verus</i>	3	5	0.8442	4	5	0.8888	<i>P. t. verus</i> vs. <i>A. africanus</i>	5	3	0.2507	5	2	0.0691	<i>A. africanus</i> vs. <i>P. t. schweinfurthi</i>	3	3	0.1493	2	3	0.1227	<i>A. africanus</i> vs. <i>P. paniscus</i>	3	6	0.6896	2	4	0.4726	Mastoid canal							<i>A. africanus</i> vs. <i>P. paniscus</i>	2	4	0.2083	0	5	*	<i>A. africanus</i> vs. <i>P. t. schweinfurthi</i>	2	3	0.2555	0	3	*	<i>A. (P.) robustus</i> vs. <i>P. t. schweinfurthi</i>	0	3	*	2	3	0.3726	<i>A. (P.) robustus</i> vs. <i>P. paniscus</i>	0	4	*	2	5	0.1626
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Measurements are given respectively in mm. In the *t*-tests for independent samples (between chimpanzee taxa and fossil hominids), the equality of variances assumption was verified with the Levene's test. Marked differences are significant at *P*<0.05 (**P* cannot be calculated).

Table 7 Multiple comparisons among the k population means: Tukey tests. s^2 is the error mean square from the analysis of variance

	Right		Left		Conclusion
	q	q(0.05)	q	q(0.05)	
Jugular width					
P. t. verus vs. A. africanus	2.39	3.958	2.73	4.232	k=5 $s^2=0.845$ DF=23 Accept H_0
P. t. verus vs. P. t. schweinfurthi	2.24	3.958	2.15	4.232	Accept H_0
P. t. verus vs. P. paniscus	2.46	3.958	3.37	4.232	Accept H_0
P. paniscus vs. A. africanus	0.74	3.958	0.13	4.232	Accept H_0
P. paniscus vs. P. t. schweinfurthi	0.32	3.958	0.39	4.232	Accept H_0
P. t. schweinfurthi vs. A. africanus	0.41	3.958	0.45	4.232	Accept H_0
P. t. verus vs. A. (P.) robustus	—	—	0.22	4.232	Accept H_0
A. africanus vs. A. (P.) robustus	—	—	1.72	4.232	Accept H_0
A. (P.) robustus vs. P. paniscus	—	—	1.81	4.232	Accept H_0
A. (P.) robustus vs. P. t. schweinfurthi	—	—	1.31	4.232	Accept H_0
Condylar canal					
A. (P.) robustus vs. P. t. schweinfurthi	6.11	4.367	2.16	4.453	k=5 $s^2=0.519$ DF=13 Accept H_0
A. (P.) robustus vs. P. paniscus	5.19	4.367	3.08	4.453	Accept H_0
A. (P.) robustus vs. A. africanus	3.93	4.367	2.20	4.453	Accept H_0
A. (P.) robustus vs. P. t. verus	3.33	4.367	2.22	4.453	Accept H_0
P. t. verus vs. P. t. schweinfurthi	3.50	4.367	0.22	4.453	Accept H_0
P. t. verus vs. P. paniscus	2.04	4.367	1.02	4.453	Accept H_0
P. t. verus vs. A. africanus	1.05	4.367	0.49	4.453	Accept H_0
A. africanus vs. P. t. schweinfurthi	2.19	4.367	0.28	4.453	Accept H_0
A. africanus vs. P. paniscus	0.65	4.367	0.32	4.453	Accept H_0
P. paniscus vs. P. t. schweinfurthi	1.87	4.367	0.69	4.453	Accept H_0
Mastoid canal					
A. africanus vs. P. paniscus	3.47	4.339	—	—	k=3 $s^2=0.147$ DF=7 —
A. africanus vs. P. t. schweinfurthi	2.22	4.339	—	—	—
P. t. schweinfurthi vs. P. paniscus	1.28	4.339	0.81	4.165	Accept H_0
A. (P.) robustus vs. P. t. schweinfurthi	—	—	2.18	4.165	Accept H_0
A. (P.) robustus vs. P. paniscus	—	—	1.68	4.165	Accept H_0

The critical value in this test is known as a "studentized range", abbreviated $q()$, and is dependent upon the significance level, the error DF for the analysis of variance, and k (the total number of means being tested).

On the contrary, for adult *P. t. schweinfurthi*, the right mastoid extracranial diameter was significantly larger than the left one ($P=0.0075$) (Table 3).

Results for chimpanzees are given in Table 5. With two exceptions, we did not notice any significant difference between the chimpanzee taxa (t -tests). In adults, the left extracranial diameter of the condylar canal was significantly smaller in *P. paniscus* than in either *P. t. schweinfurthi* or *P. t. verus* (respectively, $P=0.0249$; left, $P=0.0144$) (Table 5). Using the Tukey procedure (multiple comparison test), no significant difference between chimpanzee taxa appeared (Table 7).

Results for the extracranial diameter of the condylar canal in South African Plio-Pleistocene hominids are given in Table 6. We did not find a significant difference between right and left sides. In *A. (P.) robustus*, from infancy to adulthood, ageing results in an increase of size. In order to minimize age influence, when we compared the extracranial diameter of the condylar canal between *A. africanus* and *A. (P.) robustus*, we excluded SK 859, an immature specimen, from our sample. Doing the comparison separately for the left and right sides (t -tests), the P -values were 0.0961 and 0.0757, respectively (Table 6). Thus, using t -tests, we did not notice significant differences between *A. (P.) robustus* and *A. africanus*. We also searched for differences between fossil hominids and adult chimpanzees (t -tests) (Table 6). We found no significant difference between *A. africanus* and chimpanzees. On the contrary, the right extracranial diameter of the condylar canal was significantly larger in *A. (P.) robustus* than either in *P. t. schweinfurthi* ($P=0.0277$) or *P. paniscus* ($P=0.0466$). It was also significantly larger, on the left side, in *A. (P.) robustus* than *P. paniscus* ($P=0.0219$) (Table 6). Using the Tukey procedure (multiple comparison test), the same significant differences appeared, on the right side, first, between *A. (P.) robustus* and *P. t. schweinfurthi*, and second, between *A. (P.) robustus* and *P. paniscus* (Table 7). Thus, we noticed that the right extracranial diameter of the condylar canal was significantly larger in *A. (P.) robustus* than in two chimpanzee taxa (*P. t. schweinfurthi* and *P. paniscus*). Interestingly, no significant difference was noticed either between chimpanzee taxa or between *A. africanus* and chimpanzees.

Unfortunately, data about the size of the extracranial mastoid canal in chimpanzees (Table 5) and South African Plio-Pleistocene hominids (Table 6) are flimsy. We found no significant difference between fossil hominids and chimpanzees (Tables 5–7).

Extracranial diameter of parietal and occipital foramina

The parietal foramen (f. parietale) pierces the parietal bone near or in the sagittal suture in the obelion area. Boyd (1934: p. 115) includes under the term “parietal foramen” orifices located “not actually in the parietal bone, but in the apex of the occipital bone”. The parietal foramen normally transmits the corresponding emissary vein (v. emissaria parietalis), or Santorini’s vein, connecting the occipital veins with the superior sagittal sinus (sinus sagittalis superior). The occipital foramen (f. occipitale) pierces the occipital squama at or slightly above the inion but also near the posterior border of the foramen magnum. This foramen transmits the corresponding emissary vein (v. emissaria occipitalis), or vena obelionica.

In humans, the diameter of the right parietal foramen may attain 3–6 mm (Lang, 1979) but “usually does not exceed 1 mm” (Lindblom, 1936: p. 53). According to Lang & Brückner (1981), the human parietal foramen develops during the first year and its dimensions remain fairly constant during life. Data about the human occipital foramen are few. In 100 male adult middle Europeans, Hauser & De Stefano (1989) observed two small and three medium sized occipital foramina (respectively, a wire of 0.3 mm and 1 mm entered in them).

Table 8 Emissary foramina and divided hypoglossal canal in South African Plio-Pleistocene hominids

Specimen	Divided hypoglossal		Condylar		Mastoid		Parietal/Occipital	
	Right	Left	Right	Left	Right	Left	Parietal	Occipital
<i>A. africanus</i>								
MLD 37/38	—	—	—	—	— ²	— ²	0	1
STS 5	—	—	1 ²	—	1 (+?)	—	—	—
STS 19	s	s	0	0	1 (+?)	—	—	—
STS 25	—	—	—	—	—	—	0	0
STS 26	s	s	2 ²	2 ²	—	—	—	—
STS 58	—	—	—	—	—	—	0	—
STW 53 ¹	—	s ¹	—	0 ¹	—	—	—	—
STW 187a ¹	s ¹	s ¹	0 ¹	0 ¹	—	—	—	—
TAUNG	—	—	0 ²	—	—	—	—	—
<i>A. (P.) robustus</i>								
TM 1517a	—	—	—	—	—	1	—	—
SKW 11 ¹	—	—	—	—	—	1 ¹	—	—
SK 27	—	—	1	—	— ²	—	—	0
SK 46	—	—	—	—	—	— ²	—	—
SK 47	—	—	1	1	— ²	— ²	—	1 ²
SK 48	—	—	1	1 ²	—	—	—	—
SK 54	—	—	—	—	—	—	0	0
SK 83	—	—	— ²	2	—	—	—	—
SK 859	—	s	—	1 ²	—	—	—	0
<i>A. (P.) boisei</i>								
			data taken from the literature (1, 2, 3, 4, 5)					
KNM-ER 406	—	—	1 (1)	1 (1)	0 (2)	—	0 (2)	0 (2)
KNM-ER 407	s (3)	d (3)	—	1 (3) ²	0 (2)	0 (2)	0 (2)	x (2)
KNM-ER 417	—	—	—	—	—	1 (1)	—	—
KNM-CH 304	—	—	—	—	—	—	—	0 (2)
OH 5	s (4)	d (4)	1 (4)	1 (4)	0 (2)	0 (2)	—	—
KNM-ER 23,000	—	—	—	—	1 (5)	—	1 (5)	—

0, Absent; x, present; 1, one foramen present; 2, two foramina present; s, single hypoglossal canal; d, divided hypoglossal canal; ¹unpublished data; ²differing from Falk's (1986) study.

Numbers in parentheses correspond to the following references: (1) Leakey *et al.* (1971: pp. 179; 180); (2) Falk (1986: p. 316); (3) Day *et al.* (1976: p. 370); (4) Tobias (1967: p. 27); (5) Brown *et al.* (1993: pp. 146; 147).

We did not find a parietal foramen in South African Plio-Pleistocene hominids. On the contrary, we observed a 1.6 and 3.3 mm wide occipital foramen on, respectively, MLD 37/38 and SK 47 (Table 8). In both specimens, the occipital foramen was filled with matrix.

Incidence of divided hypoglossal canal

In a divided hypoglossal canal, one or several bony bridges divide it totally or partially. Besides the XIIth cranial nerve (n. hypoglossus), the undivided or divided hypoglossal canal contains a venous plexus and, frequently, the posterior meningeal artery (a. meningea posterior). When scoring this feature (method of Berry & Berry, 1967), the interobserver differences were low. Indeed, Marano (1984) reported the following high percentages of agreement: 93.2, 95.9 and 92.5.

Our observations on divided hypoglossal canal in South African Plio-Pleistocene hominids (Table 8) are congruent with Falk's (1986: p. 316) results. However, we were able to examine

two additional fossils from Sterkfontein: STW 53 and STW 187a. In both of them (respectively, on the left side and on both sides), the hypoglossal canal was single, Falk (1986) concluded that “robust australopithecines” may have retained the “pongid condition” for divided hypoglossal canals. However, concerning extant African apes, we should stress the fact that there is not a single “pongid condition”. There are multiple African ape conditions (Table 9), three of them falling within the human range (0–35.4%) reported by Hauser & De Stefano (1989: pp. 124–125, scoring method: Berry & Berry, 1967 or Dodo, 1974). This feature increases in frequency with age in humans (Hauser & De Stefano, 1989: p. 124) and in extant African apes, except in *G. g. gorilla* (Table 9). Interestingly, a low geographical variation was found among the different African ape subspecies (Braga, 1995a). Using the Fisher’s exact test, the difference between *A. africanus* and “robust australopithecines”, was not statistically significant (one-tailed and two-tailed $P=0.1429$).

Incidence of condylar foramen

Falk (1986: p. 314) scored the condylar foramen “conservatively” and acknowledged that her recorded frequencies may be “somewhat low”. Indeed, she scored this foramen as absent when the condylar fossa appeared “fused over with bone” and when an extra hole appeared “near” this “fused over area”. Boyd (1930: p. 108) found difficulty to score this canal “with a right-angled bend”. Berry & Berry (1967), Hauser & De Stefano (1989), as Boyd (1930, 1934), scored the condylar canal with a probe but did not draw our attention to extra holes appearing near a fused over area. Moreover, Hauser & De Stefano (1989: p. 115) scored, as condylar foramina, two or more separated apertures lying behind either the occipital condyle or the jugular foramen. We used this scoring procedure (method of Berry & Berry, 1967) for both African apes and fossil hominids. For this method, Marano (1984) reported the following percentages of agreement: 78.1, 82.6 and 92.5.

Our observations relative to the condylar foramen in South African Plio-Pleistocene hominids (Table 8) are not congruent with Falk’s (1986: p. 316) results, six points of difference being notable (Table 8). Concerning these six points, our observations are the following: (1) on the right side of STS 5, we observed only one 1.5 mm wide condylar foramen; (2) on both sides of STS 26, we observed two condylar foramina, the larger having a diameter of 1.6 mm, on the right, and 1.2 mm, on the left; (3) a careful examination of the Taung child’s right preserved condylar fossa revealed no foramen; (4) on the left side of SK 48, we observed a 2 mm wide condylar foramen; (5) considering its poor condition, we were not able to score the right side of SK 83; (6) on the left side of SK 859, we observed a 1 mm wide condylar foramen. Moreover, we were able to examine two additional fossils from Sterkfontein: STW 53 and STW 187a. In both of them, the condylar foramen was absent. Thus, instead of Falk’s calculated frequencies of 83% (5/6) and 25% (1/4) for, respectively, “robust australopithecines” and *A. africanus*, we found 100% (8/8) and 33% (2/6) (Table 8). For Falk’s (1986) results, using the Fisher’s exact test, the difference between *A. africanus* and “robust australopithecines” was not statistically significant (one-tailed $P=0.1190$; two-tailed $P=0.1905$). For the present study, using the same test, the difference was significant (one-tailed and two-tailed $P=0.0150$), the frequency for condylar canals being higher in “robust australopithecines”.

Concerning the African apes, we observed high frequencies of the condylar foramen in several *P. troglodytes* and *G. gorilla* subspecies (Table 9). These results contradict Falk’s (1986: p. 322) conclusion that “high frequency of the posterior condyloid foramen (if not the multiple hypoglossal canal) represent a condition that is derived compared with that of pongids”.

Table 9 Relative frequencies (%) and absolute frequencies (n), for divided hypoglossal canal, condylar, mastoid, parietal and occipital foramina, on one or both sides

	Divided hypoglossal canal			Condylar foramen			Mastoid foramen			Parietal foramen			Occipital foramen		
	Juveniles	Adults	N	Juveniles	Adults	N	Juveniles	Adults	N	Juveniles	Adults	N	Juveniles	Adults	N
P. t. verus	15 33.3 (5)	100 40	(40)	14 85.7 (12)	99 86.9 (86)	15 26.7 (4)	18 33.3 (6)	14 7.1 (1)	97 19.6 (19)	15 0 (0)	98 0 (0)				
P. t. troglodytes	82 62.2 (51)	136 67.6 (92)	81 55.6 (45)	131 60.3 (79)	—	—	—	83 2.4 (2)	137 0 (0)	82 0 (0)	138 0.7 (1)				
P. t. schweinfurthi	81 50.6 (41)	107 63.6 (68)	80 61.2 (49)	92 87 (80)	9 44.4 (4)	7 71.4 (5)	86 3.5 (3)	114 5.3 (6)	87 2.3 (2)	115 0.9 (1)					
P. paniscus	99 27.3 (27)	61 34.4 (21)	99 79.8 (79)	59 93.2 (55)	13 69.2 (9)	19 89.5 (17)	102 2.9 (3)	64 3.1 (2)	102 0 (0)	66 1.5 (1)					
G. g. gorilla	79 82.3 (65)	155 81.9 (127)	78 65.4 (51)	147 86.4 (127)	—	—	—	79 22.8 (18)	154 16.2 (25)	79 25.3 (20)	155 4.5 (7)				
G. g. graueri	30 73.3 (22)	73 86.3 (63)	29 93.1 (27)	69 91.3 (63)	—	—	—	30 56.7 (17)	75 36 (27)	31 0 (0)	73 0 (0)				
G. g. beringei	18 94.4 (17)	37 100 (37)	18 66.7 (12)	37 86.5 (32)	—	—	—	18 11.1 (2)	37 8.1 (3)	18 5.6 (1)	36 2.8 (1)				

Moreover, Falk's (1986) African ape sample is of unknown origin. Geographical variation was not considered in Falk's (1986) determination of the condylar canal incidence in African apes (this was also the case for the other emissary canals and foramina). Furthermore, we should lay stress on our scoring technique. Indeed, to avoid the introduction of a bias in the comparisons, we used the same scoring procedure for both extant African apes and fossil hominids. We considered the condylar foramen as present even if filled with matrix (as occurred in fossil hominids) or even if it was difficult to pass a probe through it (as occurred in extant African apes). There are no significant differences between many extant African ape taxa and "robust australopithecines" (for example between adult *P. t. verus* and "robust australopithecines", $P=0.2742$). Thus, contrary to Falk's (1986: p. 322) statement, the condylar foramen does not "occur in much higher frequencies in robust australopithecines than in pongids".

Incidence of mastoid foramen

According to Hauser & De Stefano (1989: p. 201), mastoid foramina "are situated most frequently about 32 mm behind the dorsal margin of the external acoustic porus either on the temporal or in rare cases on the occipital bone, or in the suture between them". Boyd (1930: p. 108) found it difficult to score this foramen which may correspond to "a long, much curved bony canal, intimately associated with the posterior temporal diploic vein". Falk (1986) also acknowledged that it was difficult to score this feature with a probe. She scored mastoid foramina as present in fossils "if present either externally in the mastoid region or internally in or near the sigmoid sinus" (*op. cit.*, p. 314). For chimpanzees and gorillas, Falk (1986: p. 314) scored mastoid foramina only "on the basis of external presence". We used this same scoring procedure in extant African apes and fossil hominids, i.e., the method of Berry & Berry (1967) for which Marano (1984) reported the following percentages of agreement: 78.1, 82.7 and 92.5.

Our observations relative to the mastoid foramen in South African Plio-Pleistocene hominids (Table 8) are not congruent with Falk's (1986: p. 316) results, four points of difference being notable because, near the occipito-mastoid suture we found that the condition of the bone was not good enough to determine whether or not the mastoid foramen was present (Table 8). Thus, we excluded the following four specimens from the tabulation: (1) MLD 37/38, on both sides; (2) SK 27, on the right side; (3) SK 46, on the left side; (4) SK 47, on both sides. Moreover, we were able to examine SKW 11, an additional fossil from Swartkrans. This specimen clearly evinces a 1.4 mm wide left mastoid foramen. Thus, instead of Falk's calculated frequencies of 25% (2/8) and 40% (2/5) for respectively "robust australopithecines" and *A. africanus*, we found 57% (4/7) and 100% (2/2) (Table 8). For both results, using the Fisher's exact test, the difference between *A. africanus* and "robust australopithecines" was not statistically significant (Falk, 1986: one-tailed $P=0.5105$; two-tailed $P=0.6084$; present study: one-tailed $P=0.4167$; two-tailed $P=0.5000$).

A recent scoring of mastoid foramina in extant African apes (Table 9) showed that the incidence of this feature may be significantly different between taxa. For example, the incidence of the mastoid foramen was significantly higher in adult *P. paniscus* than in adult *P. t. verus* at the 0% level. There was no statistical difference between *A. africanus* and adults of either *P. paniscus* or *P. t. schweinfurthi* (respectively; one-tailed $P=0.8143$, two-tailed $P=1.0000$; one-tailed $P=0.5833$, two-tailed $P=1.000$). Moreover, there was no statistical difference between "robust australopithecines" and adults of either *P. paniscus* or *P. t. schweinfurthi* (respectively; one-tailed and two-tailed $P=0.1014$; one-tailed $P=0.5000$, two-tailed $P=1.000$). Thus, a low frequency of this feature cannot be regarded as a "pongid condition" (Falk, 1986: p. 322).

Incidence of parietal and occipital foramina

Boyd (1934) noted that the “strictly parietal foramina” were “always single” as the occipital ones. Braga (1995a) also noticed this pattern in African apes. When scoring the parietal foramen (method of Berry & Berry, 1967), the interobserver differences are low. Marano (1984) reported the following percentages of agreement: 95.8, 93.5 and 91.3.

We did not find any parietal foramen on South African Plio-Pleistocene hominids (Table 8), confirming Falk's (1986: p. 316) results. However, concerning KNM-ER 23000, an *A. (P.) boisei* specimen, Brown *et al.* (1993: p. 147) described “regularly spaced emissary foramina” at the level of the sagittal sinus groove, on the endocranial surface of the parietal bone. Thus, concerning the parietal foramen, we found a frequency of 25% (1/4) for “robust australopithecines” (Table 8). Using the Fisher's exact test, the difference between *A. africanus* and “robust australopithecines” was not statistically significant (Falk, 1986: one-tailed and two-tailed P cannot be calculated; present study: one-tailed $P=0.5714$, two-tailed $P=1.0000$). Our observations relative to the occipital foramen (Table 8) are not congruent with Falk's (1986: p. 316) results. Indeed, on SK 47, we observed a 3.3 mm wide occipital foramen, 37 mm behind the posterior border of the foramen magnum. This location seems to be close to that described by Falk (1986: p. 322) for an *A. (P.) boisei* specimen (KNM-ER 407), i.e., “lower on the occiput”. The occipital foramen present on MLD 37/38, an *A. africanus* specimen from Makapansgat, is located 10 mm below lambda. Thus, instead of Falk's calculated frequencies of 20% (1/5) for “robust australopithecines”, we found 29% (2/7) (Table 8). For both results, using the Fisher's exact test, the difference between *A. africanus* and *A. (P.) robustus* was not statistically significant (Falk, 1986: one-tailed $P=0.7222$; two-tailed $P=1$; present study: one-tailed $P=0.5833$; two-tailed $P=1$).

An interesting point about the incidence of parietal and occipital foramina in African apes (Table 8) is given by Cave (1994). Just as one of the present authors did (Braga, 1995a), he found “the presence of a foramen obelionicum in a considerable proportion (26%) of the gorilla crania” (*op. cit.*, pp. 42–43) either on the parietal or on the occipital bones.

Associations between discrete traits

We tested the associations between discrete traits in all the extant African ape species and subspecies, on each side. Details of the entire analyses are given in Table 10. Often, we were not able to reject the null hypothesis of random association. The five significant associations were the following: (1) between parietal and occipital foramina in *P. t. verus* ($P=0.0480$), *P. t. troglodytes* ($P=0.0035$) and *G. g. gorilla* ($P=0.0180$); (2) between the divided hypoglossal canal and mastoid foramen, on the left side, in *P. t. verus* ($P=0.0325$); (3) between the divided hypoglossal canal and condylar foramen, on the right side, in *G. g. graueri* ($P=0.0498$); (4) between parietal and mastoid foramina, on the right side, in *P. t. verus* ($P=0.0490$); (5) between parietal and condylar foramina, on the right side, in *G. g. graueri* ($P=0.0250$).

Discussion

Extracranial dimensions of venous foramina

From his observations on extracranial dimensions of vascular foramina in fossil hominids, Weidenreich (1948) inferred the existence of functional relationships between “psychical functions” and volume flow:

Table 10 Associations between discrete traits

Pan paniscus									
Pan troglodytes verus					Pan paniscus				
Hyp. L	Cond. L	Mast. L	Par. L	Occ. L	Hyp. R	Cond. R	Mast. R	Par. R	Occ. R
—	0.2004	0.1954†	0.8457	0.7203*	—	0.4691*	—	0.5703*	0.8515*
0.7765	—	0.8125†	0.2002*	0.6197*	0.3241	—	—	0.7464*	0.9799*
0.0325†	0.8485†	—	0.0490*	0.4289†	†	—	—	†	†
0.3408	0.3695*	0.2330	—	0.0480*	0.6491*	0.3639*	—	—	0.0642*
0.5583*	0.6047*	0.5004†	0.0480*	—	0.8989*	0.8665*	0.0642*	—	—
Pan troglodytes troglodytes									
Hyp. L	Cond. L	Mast. L	Par. L	Occ. L	Hyp. R	Cond. R	Mast. R	Par. R	Occ. R
—	0.5961	0.7500†	0.9563*	0.9749*	—	0.5948	0.6667†	0.6235*	0.4218*
0.7901	—	†	0.9295*	0.9356*	0.1608	—	0.4000†	0.9612*	0.4907*
0.7500†	†	—	0.2500†	†	0.6667†	—	—	0.5556†	0.4048†
1.0000*	0.9090*	0.2500†	—	0.0035*	0.9088*	0.8547*	0.5556†	—	0.6245*
0.2417*	0.1974*	†	0.0035*	—	0.2412*	0.6212*	0.4048†	0.6245*	—
Gorilla gorilla gorilla									
Hyp. L	Cond. L	Mast. L	Par. L	Occ. L	Hyp. R	Cond. R	Mast. R	Par. R	Occ. R
—	0.9592	†	0.8109	0.7087*	—	0.0498	†	0.8594	†
0.7612	—	†	0.9689*	0.2828*	0.2187	—	†	0.0250*	†
†	†	—	†	†	†	—	—	†	†
0.4813	0.8422*	†	—	0.0180*	0.5897	0.6481*	†	—	†
0.9610*	0.2032*	†	0.0180*	—	†	†	†	†	—
Gorilla gorilla beringei									
Hyp. L	Cond. L	Mast. L	Par. L	Occ. L	Hyp. R	Cond. R	Mast. R	Par. R	Occ. R
—	0.6318†	†	0.5316†	0.5791†	—	—	—	—	—
0.2232†	—	0.7500†	0.4162†	0.3437†	0.2187	—	—	—	—
†	0.2000†	—	0.5000†	0.7500†	†	—	—	—	—
0.6060†	0.4887†	0.6000†	—	0.1402†	0.5897	0.6481*	†	—	—
0.6485†	0.5704†	0.8000†	0.1402†	—	†	†	†	†	—

*Yates' correction, †Fisher's exact test, ‡P cannot be calculated. Associations are significant at P<0.05.

“blood supply may play a decisive role in the differences between the psychical functions of notable brains and ordinary ones. If this is so, it may also be true for the difference between the brains of early hominids and those of modern man. Indeed, the holes and gaps of the bony case which lodges the brain and through which both arteries and veins pass are distinctly wider in modern man than in early hominids. There is a definite tendency for these ways of communication between the cranial cavity and the outside to widen in the course of evolution.” (*op. cit.*, p. 108)

Up to now, only very poor data about dimensions of cranial venous foramina were available for fossil hominids. Concerning the width of the venous part of the jugular foramen, we did not notice any significant difference between *A. africanus* and *A. (P.) robustus*. With one exception (*t*-tests), we did not find significant differences between chimpanzees and South African Plio-Pleistocene hominids. Moreover, in both chimpanzees and fossil hominids, the width of the venous part of the jugular foramen fell within the adult human range published by Lang *et al.* (1983). On the contrary, we noticed that the right extracranial diameter of the condylar canal was significantly larger in *A. (P.) robustus* than in two chimpanzee taxa (*P. t. schweinfurthi* and *P. paniscus*). Moreover, concerning the extracranial diameter of the condylar canal, we did not find a significant difference, first, between *A. africanus* and chimpanzees, and second, between chimpanzee taxa. Interestingly, for both condylar and mastoid canals, the means of the extracranial diameter in adult South African australopithecines were well below the adult human minimal means given by Solter & Paljan (1973: p. 329). Even though data about the extracranial diameter of the mastoid canal were flimsy, we found no significant difference between South African australopithecines and chimpanzees. Solter & Paljan (1973) demonstrated that the dimensions of condylar and mastoid extracranial foramina, as well as those of jugular foramina, depend on volume flow through them (i.e., a quantity of flow through a vessel per unit time). Assuming that a similar correlation occurred in fossil hominids, this means that volume flow through internal jugular veins was not higher or lower in South African australopithecines than in extant chimpanzees and humans. Moreover, volume flow through condylar emissary veins, first, was similar in all chimpanzees and *A. africanus*, and second, was higher in *A. (P.) robustus* than in either less-encephalized (as demonstrated by Hartwig-Scherer, 1993; McHenry, 1994; Kappelman, 1996) *P. t. schweinfurthi* and *P. paniscus*. The well-known relations between volume flow (or flow velocity) and resistance to flow (arising from the internal friction between the fluid layers and against the wall of the vessel), given by the Hagen–Poiseuille law (Schmidt & Thews, 1989), lead us to make further remarks. In their important textbook of physiology, Schmidt & Thews (1989: p. 484) wrote:

“volume flow and resistance to flow are directly and inversely proportional, respectively, to the fourth power of the radius. Therefore both of these variables are much more strongly affected by changes in vessel diameter than by changes in length, pressure difference or viscosity. For example, the volume flow in a vessel through which the flow is initially 1 ml s^{-1} will rise to 16 ml s^{-1} when the diameter of the vessel is doubled.”

Given the fundamentals of hemodynamics, since the right extracranial diameter of the condylar canal was significantly larger in *A. (P.) robustus* than in chimpanzees (*P. t. schweinfurthi* and *P. paniscus*), we should consider that volume flow was higher in even much greater proportions. Schmidt & Thews (1989: p. 484) wrote that “changes in radius of the vessels constitute the decisive mechanism for effective regulation of flow rate and pressure, whether local or large-scale adjustments of the circulatory system are required”. Hagens & Meyer (1990: p. 359) also emphasized the importance of vein size versus, for example, numbers of veins.

What is the functional significance of volume flow increase: (1) in condylar veins of *A. (P.) robustus* in comparison with less-encephalized chimpanzees, probably reflecting the ancestral condition for encephalization; (2) in both human condylar and mastoid veins in comparison with less-encephalized South African australopithecines (australopithecines dimensions well below the adult human minimal means)? Encephalization, “a between-species (or between-genera) higher order evolutionary phenomenon” (Jerison, 1990: p. 361), is the deviation from the expectations of allometry (brain size *vs.* body size). A higher level of encephalization increases the metabolic requirements for the brain (mainly the oxygen and glucose consumptions, as demonstrated by Abitbol, 1990: p. 344) and, consequently, volume flow of both the arterial blood supply and the venous outflow. Is the development of enlarged condylar emissary veins in *A. (P.) robustus* physiologically related to the encephalization? In this respect, Abitbol (1990: p. 344) wrote that “before encephalization could proceed”, the “cerebral blood flow had to be increased”. Very detailed studies from McHenry (1982, 1991, 1994) confirm that *A. (P.) robustus* was more encephalized than chimpanzees. Furthermore, McHenry (1991: pp. 451–452) wrote that “early *Homo erectus* was considerably larger than the South and East African ‘robust’ hominids so their larger endocranial volumes may be *relatively* closer to those of the ‘robust’ australopithecines”. McHenry (1994: p. 82) noted that the brain size increase from “*A. africanus* to the ‘robust’ australopithecines does not appear to be an artifact of body size increase but reflects progressive encephalization”. The only *A. (P.) robustus* endocranial cast available (SK 1585) also shows “a more human-like shape, size and disposition of the cerebellar lobes” (Holloway, 1972: p. 185). This result is congruent with Saban’s (1983) statement that the “robust” australopithecines’ middle meningeal pattern was more complex, compared with that of *A. africanus*, and corresponded to a higher level of quantitative evolution of the brain. Thus, even if secondary venous outflows, not detectable from the presence of distinct canals or foramina, could be present, we regard the higher encephalization quotient of *A. (P.) robustus*, in comparison with chimpanzees, as a good explanation for enlarged condylar emissary veins in South African “robust australopithecines”, in comparison with *P. paniscus* and *P. t. schweinfurthi* (Table 7). This hypothesis is reinforced by the absence of significant difference between *A. africanus* and all the chimpanzee taxa. Indeed, when we examine the encephalization quotient (based on Martin, 1983) provided by Kappelman (1996: p. 246) for extant chimpanzees (range: 1.42–1.89) and by McHenry (1994: p. 82) for *A. africanus* (1.62) and *A. (P.) robustus* (1.92), we can see that the value for “gracile” australopithecines falls within the range for extant chimpanzees. The encephalization quotient value for *A. (P.) robustus* is not far from the upper end of the range for extant chimpanzees. This could explain the absence of significant difference between *A. (P.) robustus* and *P. t. verus*.

Falk & Conroy (1983) inferred that cranial venous blood flow changed in conjunction with adoption of a body position to an upright posture. They considered that the “establishment of a mechanism that would enable greater volumes of blood to be channeled to the vertebral plexus of veins in response to specific respiratory and postural conditions” (*op. cit.*, p. 321) could be done by increasing the frequencies of different emissary foramina and/or by enlarging the size of the emissary veins and O/M sinuses. If so, which proportion of blood flow increase, for which emissary vein, for which extant or fossil species in comparison with another one, may possibly be due to changes in postural and respiratory conditions? Indeed, the human blood venous outflow differs from that in quadrupeds because of hydrostatic pressure changes (see details in Falk & Conroy, 1983). However, Whiten (1990: p. 367) demonstrated that, in African apes, in comparison with quadrupeds, “the head is in an upright position on an upright trunk for much the greater part of the day”. Then, in African apes, the height of

the brain above the heart, responsible for the arterial pressure value, is closer to that of hominids than to that of quadrupeds. However, we acknowledge that hominids and African apes differ in the location of the foramen magnum and that, in this last group, the head and neck are not completely upright. Interestingly, [Berger & Tobias \(1996\)](#) demonstrated that a tibia recovered from Sterkfontein Member 4 (STW 514) evinced a “very chimpanzee-like morphology” while the closely associated *A. africanus* craniodental fossils suggested higher encephalization than *P. troglodytes* ([McHenry, 1982](#); [Tobias, 1994](#)). [Berger & Tobias \(1996: p. 347\)](#) considered that “*A. africanus* was extremely ape-like in its morphology, and possibly arboreally adapted”. Considering these findings but also [Clarke & Tobias’](#) recent discovery (1995), *A. africanus*, the earliest known South African australopithecine, combined a small level of encephalization ([Hartwig-Scherer, 1993: p. 32](#); [McHenry, 1994: p. 82](#)) and an ape-like limb morphology. Considering these recent findings, we suggest that encephalization was the prevailing functional explanation for volume flow increase in condylar veins of *A. (P.) robustus*, in comparison with chimpanzees, presumably reflecting the ancestral condition.

Obviously, since the ancestry of “robust” australopithecines and their phylogenetic relationships with early *Homo* have been the subject of important debate, it would be of great interest to assess the dimensions of vascular foramina in *A. (P.) boisei*, early *Homo* and *A. afarensis*.

Incidence of emissary foramina

[Falk \(1986: p. 320\)](#) included divided hypoglossal canals in her study on emissary foramina because this feature “appeared in three of four African black skulls exhibiting a robust australopithecine O/M sinus system”. [Braga \(1995*b*: p. 151\)](#) pointed that “the morphology of the hypoglossal canal (i.e., divided or not) is also associated with the development of the hypoglossal nerve and the occipital somites”. [Braga \(1995*b*\)](#) also referred to [O’Rahilly & Müller’s \(1984\)](#) description which demonstrates that there are two clearly separate hypoglossal roots in an early human embryo (approximately 33 days). [O’Rahilly & Müller \(1984: p. 215\)](#) considered that “this relationship may have a bearing on the divided hypoglossal canal”. Moreover, [Lang & Weigel \(1983\)](#) studied the sinuses and veins present in the region of the jugular foramen and hypoglossal canal. They did not mention any evidence to support the fact that divided hypoglossal canals are associated with a peculiar venous morphology. [Schmidt \(1975\)](#) clearly showed that the hypoglossal venous plexus, connecting or not with the vertebral plexus, can be found, either in a single, or in a divided hypoglossal canal. Furthermore, in humans, the hypoglossal venous plexus does not necessarily drain into the vertebral plexus. [Lang & Weigel \(1983: p. 52\)](#) reported that in only “5-76% of the cases, on the right side, the venous plexus of the hypoglossal canal drained not into the internal jugular vein, but instead proceeded below the base of the skull backwards to the vertebral plexus”. In most of 52 head-sections, [Lang & Weigel \(1983\)](#) noted that the hypoglossal venous plexus communicates, at different height, either with the inferior petrosal sinus, or directly with the internal jugular vein. Thus [Falk’s \(1986: p. 320\)](#) statement that “multiple hypoglossal canals permit blood to be delivered to the vertebral plexus of veins” is not supported by an anatomical study.

The incidence of emissary foramina in African apes, representing outgroups, was considered by [Falk \(1986: p. 321\)](#) as representing the “ancestral prebipedal hominoid condition”. However, to avoid misinterpretations, detailed comparisons with Plio-Pleistocene hominid features should be made, first, using the same scoring procedures, and second, using data from humans and all extant African ape species and subspecies, for all ages and sexes. Considering geographical variation in extant African apes, our new results about the incidence of condylar

foramina in a large sample contradict Falk's (1986: p. 322) conclusion that "high frequency of the posterior condyloid foramen (if not the multiple hypoglossal canal) represent a condition that is derived compared to that of pongids". Indeed, there are no differences between many African ape taxa and "robust australopithecines". Moreover, the parietal and occipital foramina can occur in relatively high frequencies in African apes (Cave, 1994; Braga, 1995a). Concerning the incidence of the mastoid foramen, no statistical difference was found between chimpanzees and *A. africanus* (this point was already emphasized by Whiten, 1990: p. 367) but also between "robust australopithecines" and *A. africanus*. Thus, a low frequency of this feature cannot be regarded as a "pongid condition".

Concerning the comparison of very small samples, Holloway (1990: p. 360) wrote: "what do differences between 25, 50, and 75% mean when the sample size for different hominid groups is less than five in many cases?" However, using statistics, this problem can be successfully approached. Indeed, Siegel & Castellan (1988: p. 103) consider that Fisher's exact test "is an extremely useful technique for analysing discrete data when the two independent samples are small". In the present report about the incidence of emissary foramina in *A. africanus*, "robust australopithecines" and all extant African ape species and subspecies, using appropriate general statistics (Siegel & Castellan, 1988; Armitage & Berry, 1994), we never found statistically convincing differences to support the idea: (1) first, that the "reduction in frequency of the condyloid foramen in gracile australopithecines is associated with increased frequencies of mastoid and occipital foramina over the robust condition" (Falk, 1986: p. 322); (2) second, that the condylar foramen "occurs much more frequently in robust australopithecines, as it does in *H. sapiens*, than it does in African pongids" (Falk, 1986: p. 322). For this later reason, we do not believe that high frequencies of condylar canal "occurred in high frequencies in robust australopithecines because of epigenetic adaptations associated with selection for bipedalism in their ancestors" (Falk, 1986: p. 322). If so, why do several chimpanzee taxa show comparable frequencies of condylar canal? Moreover, we noticed that the incidence of the condylar foramen varies from 60.3–93.2%, in adult African apes, and from 10.7–88.7%, in adult humans [scoring method of Berry & Berry (1967); Hauser & De Stefano, 1989: pp. 116–117]. As yet, concerning the incidence of divided hypoglossal canal but also of mastoid, parietal and occipital foramina, we did not find the slightest statistically convincing data to support a significant difference between *A. africanus* and "robust australopithecines". This finding is important in regard to Falk's "radiator" theory. Concerning a presumed "radiator for cooling the human brain", Falk (1990: p. 340) wrote: "the parietal and mastoid emissary veins that 'represent' this radiator increased in frequency during the course of evolution in the lineage leading from gracile australopithecines to *Homo sapiens*, but not in the robust australopithecines". Concerning the putative "lineage leading from gracile australopithecines to *Homo sapiens*", increased frequencies of parietal and mastoid emissary veins certainly do not characterize its earliest representatives. Moreover, concerning the mastoid and parietal foramina, as there are no statistical differences between "robust australopithecines" and *A. africanus*, the former did not lack the network of the corresponding mastoid and parietal emissary veins (representing the "radiator") more than the later. Thus, "robust australopithecines" did not lack the "cooling benefits" provided by this "radiator" more than *A. africanus*, as Falk (1990: p. 343) stated when she wrote that the "combination of thermal stress associated with a savanna mosaic environment and changed hydrostatic vascular pressures associated with bipedalism triggered multiple thermoregulatory adaptations in gracile australopithecines, including selection for the radiator network of veins"). By inferring such "thermoregulatory adaptations" in *A. africanus*, Falk (1990: p. 343) stated that the

“radiator” already existed at this time (even if not as developed as in *H. sapiens*). The detailed data presented here are very important as they contradict one of the major groundworks of Falk’s “radiator” theory, i.e., we do not see how “thermoregulatory adaptation”, inferred from the presence of emissary foramina, were different between *A. africanus* and “robust australopithecines”. However, we acknowledge the existence of vascular arrangements for cooling the spinal cord and spinal ganglia in humans. Indeed, on the basis of anatomical facts, [Zenker & Kubik \(1996: p. 11\)](#) considered that cooling effects brought about by “the extensive close contacts of spinal dura and spinal ganglia with the cooler blood of the internal vertebral venous plexus” were important.

Conclusions

This study has yielded the following results: up to now, only very poor data on extracranial dimensions of venous foramina were available for fossil hominids. Assuming that in fossil hominids, as in humans, dimensions of condylar and mastoid foramina, as well as those of jugular foramina, depended on the volume flow through them, we conclude, first, that volume flow through internal jugular veins was comparable in South African australopithecines, extant chimpanzees and humans, and second, that, in comparison with extant less-encephalized chimpanzees (presumably reflecting the ancestral condition), volume flow was higher through condylar veins in *A. (P.) robustus*. This enlargement was responsible for a significantly greater amount of blood drainage from the brain (and consequently an increased arterial blood supply). We support the view that encephalization was the prevailing functional explanation for volume flow increase through condylar veins in *A. (P.) robustus*, in comparison with its ancestor with its presumably more ape-like degree of encephalization.

Considering the incidence of emissary canals and foramina, significant differences between *A. africanus*, “robust australopithecines” and all the extant African apes, were statistically tested. Concerning the condylar canal, we found a significant (i.e., statistical) difference between “robust australopithecines” and *A. africanus*, the frequency being higher in the former group. However, we did not find differences between “robust australopithecines” and extant African apes. Concerning the incidence of divided hypoglossal canals, mastoid canals, parietal and occipital foramina, no difference was found between extant African apes, *A. africanus* and “robust australopithecines”. Thus, high frequencies of either condylar or mastoid canals cannot be regarded as a “pongid condition”. Moreover, we did not find convincing data to support the hypothesis that mastoid emissary veins (partly representing a putative “radiator” for cooling the brain) were selected as “thermoregulatory adaptations” in *A. africanus*, in comparison with “robust australopithecines”.

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