

out panting mediation could also be a factor releasing a thermal constraint on brain size, since nonpanting bipedal primates must have obtained more freedom for their behavior than panting quadrupedal animals. Nasal heat loss without panting, however, was no longer sufficient and another means of selective brain cooling developed in primates. It requires copious sweating from the face, scalp, and neck. Cool venous blood from the head skin is then collected not only by the cavernous sinus but also by other dural sinuses via both emissary and diploic veins. We can imagine the human brain, under hyperthermic conditions, as being profusely perfused with the cool venous blood.

The two subsequent evolutionary adaptations of the brain cooling system in *Homo* lineage might concern deep body temperatures, which became relatively low and brain-trunk temperature differences, which reached rather high value in humans (Narebski 1985). Low body temperature may be advantageous because it augments the safety margin between normal and maximum tolerable body temperature (Narebski 1985). According to Schmidt-Nielsen (1983), however, the safety margin remains uniformly at about 6°C, irrespective of the level of normal body temperature in different groups of warm-blooded vertebrates. On the other hand, the big difference between normal brain and trunk temperature should be advantageous because in mild hyperthermia brain temperature is likely to remain constant with little effort from the system for selective brain cooling. Along this line, the lowered body temperature could be an adaptation for attaining the high brain-trunk temperature difference.

In summary, the evolution of the brain cooling system in hominids must have resulted in multiple changes leading to the dramatic increase in brain size in the genus *Homo*.

## Venous drainage of the brain

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Several aspects of Falk's target article warrant comment: I am not personally convinced that an increased frequency of the enlarged occipital-marginal intracranial venous sinus system is as typical of "robust" australopithecines and *Australopithecus afarensis* as has been suggested here and elsewhere. Enlarged occipital-marginal venous sinuses are certainly not present in Omo L388-y6 (Holloway 1981a), now generally accepted to be a juvenile "robust" australopithecine and in some specimens these sinuses are clearly only enlarged unilaterally (SK 859, SK 1585, and KNM ER 407, see Kimbel 1984). Moreover, the sigmoid sinuses in the "black skull" KNM WT 17000, seem, in my opinion, to be easily as large as they are in larger brained "gracile" australopithecines such as Sts 5. I cannot imagine where more blood could have come from to enlarge the occipital sinuses in KNM WT 17000, especially in such a small-brained hominid. I suggest in fact that they were most likely absent in this important early *Paranthropus* specimen, which is presumed to be ancestral to later specimens of *p. boisei*.

I believe the suggestion that blood in an enlarged occipital-marginal sinus system drains preferentially into the vertebral venous plexus rather than into the internal jugular veins is incorrect. Both the transverse sinus-sigmoid sinus system and the occipital-marginal sinus systems deliver blood to the jugular bulb. Indeed, in any case the vertebral venous plexus has a major communication with the jugular bulb, as does the marginal sinus that courses in the dura at the level of the foramen magnum (see Matsushima *et al.* [1983], Figures 4 and 6). As all of these venous channels communicate extracranially at the jugular bulb, no "exclusive" drainage route to the thorax can be

predicted from the pattern of sinuses in the cranial cavity. These facts alone are sufficient to refute the physiological advantages ascribed to different groups of early hominids hypothesized on the basis of bony grooves observed in their posterior cranial fossae. I would argue further that in any case, physiological advantages are not likely to be unilateral in specimens with only one enlarged occipital marginal sinus.

Further support for my view comes from the following: The vertebral venous sinus system consists of extraspinal and intraspinal portions (Breschet 1819) but only the extraspinal portion is a major drainage route from the brain in man (Zouaoui & Hidden 1989). The extraspinal portion must anastomose with veins that drain into the external jugular vein. Shenkin *et al.* (1948) have in fact demonstrated that up to 22% of the blood in the external jugular veins is derived from blood travelling to the brain in the internal carotid artery. Blood within the extraspinal portion of the vertebral venous plexus may then easily pass into the external jugular veins, as may blood leaving the cranium via emissary veins.

The vertebral venous plexus acts as a reservoir for venous blood returning from the head during *transient* shifts in intrathoracic pressure that occur, for example, while lifting heavy objects or while straining. Blood passes into it primarily from the jugular bulb (Matsushima *et al.* 1983), the posterior condylar emissary veins (Braun & Tournarde 1977; Zouaoui & Hidden 1989) the basilar plexus anteriorly and sometimes even the inferior petrosal vein via the hypoglossal canal (Shiu *et al.* 1968). The system has a limited capacity and blood from it must eventually return to the thorax and heart via the azygos system of veins. That the internal jugular veins in primates are more important than the vertebral venous plexus and azygos system for returning blood to the heart is evidenced by the fact that the combined diameter of both internal jugular veins always far exceeds that of the azygos vein.

I believe that increased numbers of diploic or emissary foramina in hominids probably relate to a greater mass of vault bone with an increased arterial blood supply from the meningeal vessels, which then requires an increased venous drainage system. I do share the view, however, that heat regulation of the brain is vitally important and that some contribution to brain cooling in modern humans occurs through countercurrent heat exchange along the internal jugular and internal carotid arteries as well as in the cavernous sinus and through cooler venous blood running close to the surface of the brain in the venous sinuses (Cabanac 1986). Unfortunately, nakedness and the ability to sweat profusely, which I believe were likely to have been the most important adaptations to temperature regulation among early hominids, are not preserved in the fossil record.

## Heat stress as a factor in the preadaptive approach to the origin of the human brain

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Falk has proposed the following scenario for the evolution of the brain that eventually led to *Homo sapiens*:

bipedalism → development of a radiator → opportunity for brain expansion (→ means "results in").

The lack of a radiator resulted in the lack of brain expansion according to Falk's research findings. Both results, in my opinion, constitute a sound achievement.

The possibility of brain expansion, however, is not equivalent to the brain expansion itself. Using Falk's example: Having a big radiator does not necessarily mean that we must connect it to a big engine. It could cool a small engine as well. To transfer the