The phylogenetic principles of mma;

A hypothetical biostratigrafic model

Czarnetzki, A.[1], Berens von Rautenfeld, D.[2], Samii, M.[3]

1) formerly: Dep. Paleanthropology and Osteology, Institute of Anthropology and Human Genetics, University of Tuebingen, Wilhelmstr. 27, D-72074 Tuebingen

2) Medizinische Hochschule Hannover, Inst. f. Funktionelle und Angewandte Anatomie, Carl-Neuberg-Str.1, 30625 Hannover

3) International Neuroscience Institute (INI), Rudolf-Pichlmayr-Straße 4, D-30625 Hannover

4)

When filling in our phylogenetic pedigree, no skeletal element can be omitted from consideration. The discovery of three relatively small fragments of the human skull[1], i.e. the skull fragments of the Neandertal from Neu-Warendorf [2] and the two erectoid hominids from Sarstedt [3] , impelled us to initiate a detailed examination of the course of the impressions of the Arteria meningea media (median meningeal artery = mma) and their characteristics within the hominidae. To this end, we examined 31 human cadavers by trepanning the braincase and studying the differences of the indentations between arteries and veins. Unfortunately the mma pattern, as found in the last full anatomical description of Dmanisi[4] or in *Homo ergaster* (i.e. KNM-ER3733) from eastern Africa (where it existed at 1.78 million years[5,6]), is rarely depicted in the literature. To be sure, different patterns in this artery (mma) have been described [7] and a summary[8 – 14] given of the papers published thus far. Brandt[7] could demonstrate that many of the latter [d.h. these papers] described only diffuse types of indentation patterns or else differences occurring in these patterns between fossil specimens. The literature mentions varying degrees of complexity in the impression patterns left by vessels, but omits to say what criteria were used when differentiating between the impressions of veins and arteries at the different phylogenetic developmental stages (or, for that matter, in their phylogenetic biostratigraphy). The differentiation between arteries and veins was only first insisted [15] on in 2003. Brunner mentioned that a “large amount of self-training and experience” is indispensable for differentiating as exactly as possible between veins and arteries. An overview was tabled on the extent of variation in the arterial pattern of specimens deriving from Eurasia and the northern part of Africa[11, 15].

We are now in a position to differentiate, for the first time, between the main branch of the mma that is impressed just after passing the foramen spinosum (including its size) and side branches. Based on our data, we could observe throughout the phylogenetic process not only the existence of different patterns [9,16,17,] but also a generally continuous change in the arterial pattern found in specimens from Eurasia. Precisely this arterial system and its main branches are very conservative on both species and subspecies levels, as is well known and well attested. In particular, we could observe changes in (i) the course, (ii) the size and (iii) the branching of the meningeal artery – unlike the internal carotid artery, it solely supplies the surface of the cerebrum (especially the parietal lobe) with arterial blood.

Thus, in the earliest phylogenetic representatives of the species *Pithecanthropus erectus*, we find that (i) the rear branch is the one that has the greatest size and features an individually variable number of smaller branches. This main branch, (ii) other than in modern humans, generally assumes a posterior course soon after passing the Foramen spinosum, as is depicted in Fig. 1, Stage 1. This pattern has been described[15] as an “Asian” one.

These changes can be useful for reconstructing the developmental stages of the parietal lobe. Our phylogenetic model is based not only on our own observations, including inter al. on fossil specimens like *Pithecanthropus* I (= Trinil 2) and *Pithecanthropus* II (= Sangiran 2), Smb4, OH9, Zhoukoudien 10, Steinheim and Reilingen, Salé and Arago, Vindija, Mladeč, Weimar-Ehringsdorf, 31anatomically modern humans (*H.s.s.*) and published data [8,9, 10, 11, 13, 15] . But it is based on a consideration of other schemes [10, 18] as well. A final point: the following description of the main branch and its tributaries is based (see fig. on the assumption of an anatomically modern brain.

Stage 1

represents the earliest phylogenetic pattern. Its main criteria are a) anterior convexity in the trajectory of the artery after passing the Foramen spinosum and b) branching off within the temporal lobe into a main posterior branch and a tiny anterior one. These posterior branches supply the main surface of the parietal lobe, while the anterior sidelines supply only a very small part and differ in having a significantly smaller size. (Holotype: Trinil 2). In

Stage 2

the artery initially turns, after passing the Foramen spinosum, in a posterior direction (anterior concavity). The point-by-point branching into tiny anterior and main posterior branch occurs within the area of the temporal lobe. The main branch runs to posterior, whereas, after further ramifications, the surface of the parietal lobe is almost entirely taken up with tiny branches running to anterior. The anterior branch supplies only a small (anterior) part of the surface of the parietal lobe and the posterior part of the frontal lobe. Between stages 1 and 2 a continuous transition is evident. (Holotype: Sangiran 2).

Stage 3

is characterized by the artery curving on the surface of the temporal lobe; the curvature can be described as slight, first to anterior, then to posterior. Within this surface area, a tiny branch splits off and runs to the anterior surface of the parietal lobe, while, somewhat more posteriorly, the main branch heads in a superior and posterior direction. It supplies the main surface of the parietal lobe with fine branches running to anterior. (Holotype: Zhoukoudian 10). In

Stage 4

the anterior and posterior branches are nearly the same size and both of them – first the one, then shortly thereafter the other – split off from the main trunk of the mma. The posterior branch supports the blood supply to the surface of the parietal lobe from the rear, doing so from posterior to anterior, while the anterior branch supplies the surface of the precentral sulcus. (Holotypes: Reilingen, Salé, Arago). The

Stage 5

is distinguished from Stage 4 by the fact that an anterior branch has now become the main one. However, unlike in H.s.s., the course of this branch is posteriorly aligned, as too are all the other small branches diverging from the main branch. (Holotype: Vindija,). The latest developmental stage is reached with

Stage 6,

where the mma runs straight to anterior and along the coronal suture. In some specimens, it perforates the greater wing of the sphenoid at the sphenoparietal suture. The minor branches have split off within the surface of the parietal lobe and run to superior and posterior. Sometimes, very tiny branches split off posteriorly, close to the surface of the temporal pole.

(Holotype: in more than 1000 H.s.s. from prehistoric and historical times and in 31 modern cadavers).

The excellent state of preservation of bony substance in the two new specimens (Sst IV and V)[3] led to us undertaking a precise examination of their meningeal arterial system. The developmental stage of mma at Sst IV (a partially preserved left parietal bone) is nearly identical to that of Sangiran 2 and corresponds best to our Stage 2. Moreover, the overall similarity with *Pithecanthropus* I (i.e., Trinil 2) is only somewhat undermined by a well-developed sulcus of the sphenoparietal sinus, which superimposes (in part) the anterior arterial branch. In SstV (a completely preserved left temporal bone) the mma curves to posterior after passing the *Foramen spinosum*. This pattern is in exact agreement with Stage 1.

This places the two fragments (Sst IV and Sst V) biostratigraphically in the earliest stage of the human phylogeny (with especial reference to Asia).

Discussion

The first point is that this survey of a phylogenetic model is independent from any absolute dating of fossil hominids. Second, our results are based on a new method of differentiating between the impressions of veins and arteries and between the impressions of main and side branches. Some earlier results seem to conflict[17,19] with those presented here. A high degree of correlation[19] has been reported between the geometry of the neurocranium and the patterns of the mma in different groups of H.s.s. And it has been suggested that the differences among extinct hominids, as opposed to those within H.s.s., are related to the neurocranial geometry ("...low vault and posterior endocranial elongation[15,16]. These earlier results are only consistent with our observations regarding the pattern of the mma and the geometry of fossil hominid skulls. This do not, however, hold up with regard to the phylogenetic stage of the skulls – during our research, we were unable to observe any correlation between the geometry of the neurocranium and the phylogenetic stage. Our own observations, such as they were, led to a hypothetical phylogenetic model of the mma, as proposed in this paper.

This evolutionary model demonstrates – we believe convincingly and definitively – a clear developmental process for mma within the hominid phylogeny [20]. Our model finely discriminates differences between specific fossil specimens including in the area of individual variability.

Given that the chief function of the mma is to supply the surface of the parietal lobe with blood, as in the subspecies *H.s.s.*, any changes to the position of this artery during the phylogeny of the genus *Homo* might be expected to hint at further developments within the parietal lobe. This observation would signify, for instance, that the parietal lobe would shift to anterior during the phylogenetic process of the genus *Homo*. In tandem with this process, the frontal lobe would be shifted to anterior as well, thus reducing the flat frontal bone. In the specimen Sst IV, the negative of the central sulcus can be observed in the region where the anterior branch of the mma is positioned. This position is consistent with the supposition that the anterior branch of the mma will normally depend on that of the central sulcus or, in other words, the frontal part of the parietal lobe.

Therefore, examination of the course of the mma enables precise reconstruction of the phylogenetic stage of fossil skulls (and even of fragments from the parietal bone). But there is a proviso: careful attention must be paid to a) the differences between arteries and veins and b) arteries that develop in the context of meningitis. With a view to the present: finds from Africa, say, need to be examined, or re-examined, in light of the phylogenetic development of the mma. The data obtained might provide additional indications regarding a possible discrepancy or concordance, as the case may be, between morphology and developmental stage of the mma.

Abstract

This study has a presupposition: while each skeletal element may be of pivotal importance in reconstructing human phylogenesis, none is more so than the cranium. Based on the recovery of relatively small fragments of Ossa parietalia and temporalia antedating the Elster glaciation (MIS 13 – 17), the question arises as to whether certain criteria are met for assigning them to different stages in the phylogenetic development of the human line. The impressions of the Arteria meningea media were such as to require closer examination of their pathways, the size of their diverse branches, and also the specifics of the arterial impressions (as opposed to the venous ones). To this end, the casts of a total of 12 crania and/or their endcasts were assessed, as were also the schemata developed by a number of different authors [10, 11, 15]. In addition, 31 corpses of anatomically modern humans were dissected and examined. This led to the determination that it is essential to distinguish between arterial and venous impressions. This underscores[15] yet again that “a large amount of self-training and experience”, to quote one author, is indispensable when it comes to differentiating as exactly as possible between arteries and veins.

In light of the above, we were able to demonstrate (indeed this was our principal result) that the main branch of the Arteria meningea media in early human finds progressed continuously through time from posterior to anterior. In consequence, the side branches are aligned. Based on this progressive displacement, it was possible to distinguish six (6) stages of phylogenetic development, although no exact timeline could be assigned for any stage. Nor was this displacement from posterior to anterior an isolated occurrence: the Sulcus centralis too progresses in an anterior direction, thus displacing the Lobus frontalis in such a way that the Os frontale now stands upright.

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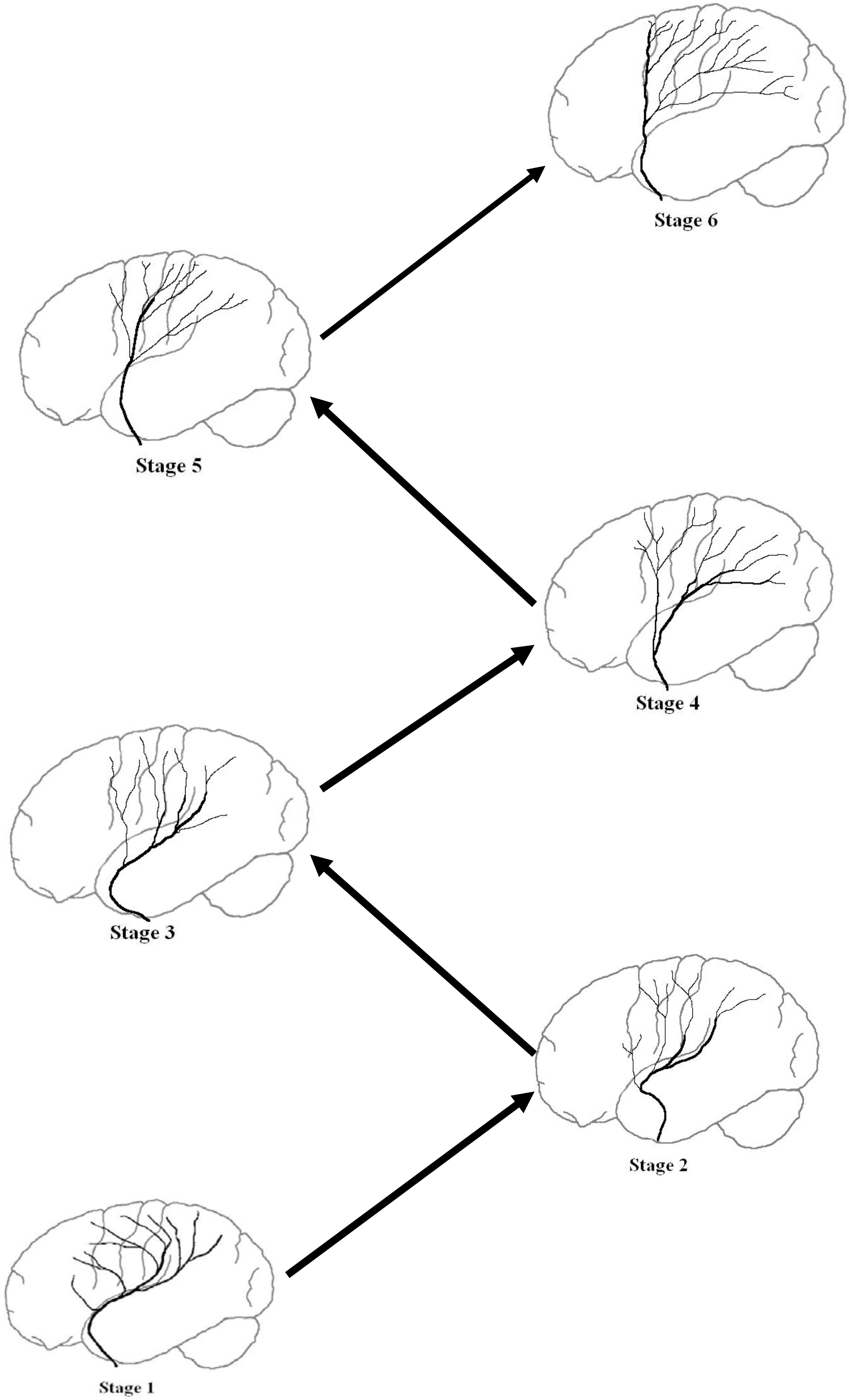
Stage 6
Stage 5
Stage 4
Stage 3
Stage 2
Stage 1