Man and environment in the Palaeolithic
H. Ullrich (ed.), E.R.A.U.L. 62, 1995, Liège, pp. 97-110.

# Morphological evidence of adaptive characters in the genus *Homo*

**Alfred Czarnetzki***

**Abstract**
The fact that evolution took place within the genus *Homo* postulates special features on which the mechanisms of selection could act. Just through the last time a lot of publications are concerned with DNA substitutions through geochronological times (for example mitochondrial DNA) to reconstruct the phylogenetic tree of the species *Homo*. Unfortunately no comments are given on the adaptive character of these features.
Therefore the main attention of this paper is thrown on those characters that are:
1. responsable at the fossil remains,
2. provable at the next evolutionary step with special regard to the kind of their changes, and
3. able to make comparisons to features corresponding with features of known function in modern times.
By these conditions one can only reconstruct the way where evolution took place and which features are best adapted to their environment.
Inborn characters of behaviour in contrast to those which can be learned concerning the best adaptation to the social interactions of man within and between members of a group could be relevant, too. But these characters cannot be analysed in a stringed biological sence. That will mean that one cannot find a direct correlation between the behaviour and features that alter the morphology of the skeleton.
Therefore in this paper only morphological features of the human skeleton that can give some traceable informations about the adaptation to a special natural environment or activities will be analysed.

**Key words:** Adaptation, nasal index, specialization, Neandertal-man, climate, hydrodynamics

## Introduction

When reconstructing, for the genus *Homo*, the significance of morphological characters as criteria for assessing adaptation to relevant natural conditions, we have no alternative but to reason analogically from results obtained on extant populations (*Homo sapiens sapiens*). Invariably, of course, conclusions based on analogy run the risk of erroneous interpretation. First, it cannot be unreservedly assumed that just because structures are morphologically identical they therefore performed the same function. Nor should it be overlooked that influences deriving from the culturally conditioned technological or social environment, to the extent this is known, do not, or may not necessarily, act on recent humans the same way as they did on fossil representatives of the genus *Homo*. And lastly, when it comes to tracing the actual factors that influenced the course and direction of evolution, we cannot eliminate doubts that the available sources may prove too paltry to permit satisfactory reconstruction of past environments. For the "environment" concept naturally also encompasses changes in each environmental field (including the social environment) that have been wrought by human beings themselves. The stipulation must therefore be made, if error is to be kept to a minimum, that all conclusion-drawing should be kept within very narrow systematic bounds. For, in contrast to some erroneous interpretations of Darwinian theory (e.g. by Hawking 1988) concerning the mechanisms behind the evolution of animate nature, no serious scientist today doubts that organisms best adapted to the present (or altered)

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* Dr. Alfred Czarnetzki, Osteologische Sammlung an der Eberhard-Karls-Universität Tübingen, Postfach 1271, D-72074 Tübingen, Germany

environment have a better chance of surviving and increasing their numbers. Since therefore the occurrence of evolution is now uncontroversial, our first task - when constructing any phylogenetic line - must be to study and monitor altered characters for their adaptive value.

Analysis of DNA sequences (especially of mitochondrial DNA) for purposes of phylogenetic reconstruction has not yet succeeded in determining, with the necessary clarity, whether a particular DNA sequence has its fitness raised or lowered by variations in the respective biotope. This kind of analysis entails the further great disadvantage that such criteria as geochronology or isotope series are dismissed, that neither elimination from the gene pool nor negative selection are considered, and that a constantly operating substitution rate is quite arbitrarily postulated, despite all indications to the contrary. Nor can certain palaeontological data, such as the geochronological fixing of chimpanzee emergence at 9 million years, be completely ignored - that is, if plausible conclusions are to be reached. Ignoring these in favor of arguing solely from within a not-yet-established system inevitably throws out of kilter whatever conclusions are drawn - a danger that can be readily appreciated if we remember the reconstructed timepoint of splitting of the *Ophiidae,* the most recent group of reptiles to have emerged.

In contrast to genetic engineering research for purposes of reconstructing evolutionary processes, the method of investigating morphological structures, including their anatomical environment, is systematically tried-and-tested enough, though here too, as in any system, there is no royal road to avoiding erroneous conclusions not solely due to the limits placed on all human questioning. In addition, the method of directly comparing fossil-to-subfossil data with extant forms offers relatively greater certainty than is to be had from inferring past, independently uncheckable sequences of evolutionary processuality on the basis of present-day DNA processes. Furthermore, if comparison is performed within a species, reduced error probability over and against interspecific comparisons can be presumed.

When comparing adaptive features, absolute metric values cannot so far be presumed, since the latter's characteristics in this respect are still relatively unknown. To illustrate this point, consider, for example, that neither for a particularly large cranial length, nor for a particularly wide cranial base, nor for a steep face (with a closely correlated nasal height) is it possible to prove an advantage or disadvantage in specific natural biotopes. Probably the best known example is bodily height, so well known in fact as to render closer consideration here unnecessary. But numerous further examples could be readily supplied.

## Materials and methods

As the title suggests, our choice of material will be finds from the *Homo erectus* group, Neandertals and also fossil and extant *Homo sapiens sapiens* belong. Here we will be assuming that *Homo erectus* and *Homo sapiens neanderthalensis* in the Old World, just as is the case with *Homo sapiens sapiens,* is represented by a number of regional (i.e. African, Asian and European) variants - a finding established, with reasonable probability, above all by Bräuer (1994), though Rightmire (1990) had already earlier suggested as much.

Furthermore, recent anatomical preparations of joints (for studying microscopic morphological structures) were prepared in a special way for SEM studies aimed at analyzing the pressure-impulse transmitting structures.

To reconstruct cerebral organization, CT scans of fossil and recent skulls and heads were made and compared with extant specimens from clinical sources.

Available methods (for selective use) comprised, on the one hand, SEM studies, then CT scans, and finally, metric-morphological investigations. Also drawn on for analytic purposes were vegetational and climatological results, to the extent such were available or deemed useful (Frenzel et al. 1992).

## Results

Under natural conditions, a high degree of correlation is known to obtain between water vapor pressure (relative air humidity as a factor of temperature) and relative width of the body nasal cavity (Thomson Buxton's Rule, 1954) - showing a correlation coefficient of r = 0.82 (Weiner 1954). This means that neither temperature nor air humidity are alone decisive, nor the specific dimensions of the nose either, pace what is assumed in various publications in an effort to develop counter-arguments.

The nasal index of the Neandertal bony nose varies between values 59.04 - 66.06 (Gieseler

1974) while Heim (1981/82) calculated values of 53.7 to 60.0. But the nasal index, calculated by the given averages for the nasal hight (Na-Nsp) and bredth is 61.2. Transposed for the soft-tissue nose, index values cluster around approximately 104.6 - 112.68 (correlation of bony to soft-tissue nose r = 0.9157, Y = -38.9071 + 2.4309x), i.e. they fall within the same range as extremely broad-nosed representatives of the species *Homo sapiens sapiens.* Thus they are comparable to Tasmanians, Australians and Bushmen. On the other hand, we must not forget that, based on both prehistoric archaeological criteria and the faunal and floral studies set out below, the finds treated here must be assigned to a cold period. In any event, the sole Neandertal find so far that, based on data presented by Wetzel & Bosinski (1969) for the find bed (black Mousterian featuring pine, spruce, elm flora and cave bear, cave hyena, cave lion, red deer and cattle deer fauna) must be assigned to a warm phase within the Würm glaciation, is only represented by a diaphysis of the left Femur. However, the author's own studies have shown that all typical Neandertal features are present, i.e. the Femur diaphysis morphology clearly diverges from that of *Homo sapiens sapiens.* Finds from the Große Grotte (Wagner 1983) likewise indicate that the temperature drop associated with the Würm (Weichsel/Wisconsin) glaciation falls concurrently with *Homo sapiens sapiens'* first appearance within the Neandertal range. This means that, right down to late Neandertal times in central Europe (approx. 40-35 ka B.P.), subtropical-to-tropical conditions with especially pronounced air humidity levels generally prevailed.

All Early and Middle Pleistocene finds known to date of representatives of the genus *Homo* (but not belonging to the subspecies *Homo sapiens sapiens*) certainly derive, irrespective of the find site, from warm periods or from interstadials - which, as we know, can have the appearance of warm periods. This also applies, according to the data cited in the literature, to the recent finds from Atapuerca in Spain (Arsuaga et al. 1993), where skull 5 has an estimated nasal index of approx. 62.4 (for extant humans the corresponding figure is 112.8); or to the 1933 find from Steinheim/Murr (Fig. 1a,b), which has a CT-reconstructed nasal index of 64.51 (soft-tissue nose: 117.93). This places the Atapuerca skull as well as the Steinheim skull within the Neandertal variation band (see also Stringer 1993). To what extent the European finds from the Riß/Saale glacial do not belong in two warm spells within the latter, must still be regarded as an open question - despite the publication of de Lumley-Woodyear (1973). As known from the literature and examinations of the finds themselves, poor state of preservation has previously prevented nasal length and width from being accurately measured in any individuals whatsoever of the genus *Homo erectus.* CT scanning had earlier not been developed, so that the necessary corrections could not be worked out. Thus only approximative values are available for

Table 1. Bony nose parameters for various biotops (according to Wolpoff 1968).
N = North, C = Central, S = South, R = River, M = Mainland and some Palaeolithics (calculations by the author), Nea = Neandertals, Jp = Upper Palaeolithic people.

| | | Coast of New South Wales | | | Nea | Western Alaska | | | Jp |
|---|---|---|---|---|---|---|---|---|---|
| | | N | C | S | | R | R | M | |
| 1. | Nasal index | 58.40 | 53.88 | 55,49 | 61.34 | 44.92 | 44.28 | 43.46 | 47.60 |
| 2. | Surface of entry of the Apertura piriformis[1] | 13.91 | 13.63 | 13.43 | 19.12 | 13.14 | 13.01 | 12.81 | 14.196 |
| 3. | Surface of the Cavitas nasalis [1] | 135.54 | 138.67 | 136.52 | --- | 142.440 | 143.667 | 145.885 | --- |
| 4. | Size of the nasal surface [1,3] | 27.090 | 27.734 | 27.734 | --- | 28.488 | 28.733 | 29.117 | --- |
| 5. | Size of the Cavitas nasalis[1,2] | 144.664 | 140.520 | 138.060 | --- | 135.930 | 135.930 | 136.349 | --- |
| 6. | 4./5. x 100 | 18.729 | 19.737 | 19.777 | --- | 20.957 | 21.138 | 21.335 | --- |

Explanations:

1. Measurements 2 - 5 were calculated on the assumption that the bony nose approximately conforms to a geometrical prism. 2. Calculation was based on the following measuremts: nasal height, nasal width, and facial length (according to Martin 1928). 3. Measurement 4 assumes a 2 mm value for the epithelial cells' zone of influence on humidification or humidity retention.

these representatives. Considering the Old World *Homo erectus* hypodigm, we find an average nasal index of 60.607 with an absolute variation band that ranges from 50.7 (Choukoudien) to 75.38 (KNM-ER 3733). With reference to comparative-anatomical aspects, this essentially means an adaptation to hot and humid through moderate biotopes.

As is fairly evident from Table 1, the data selected by Wolpoff (1968) adhere very closely to Thomson/Buxton's Rule (1923), with the nasal index in the hot, humid climatic zones of Australia being significantly greater than in the cold, arid zones of Alaska. The index reacts so accurately that even the north-south gradient is clearly reflected by it. A similar phenomenon can also be observed within Europe. Here the nasal index of French Palaeolithics, who inhabited a more maritime climate, is a little larger (47.7) than that (47.5) of Upper Paleolithics of the Czech Republic, exposed as these were to a more continental climatic regime. No other nasal parameters offer such unambiguous testimony. However, in the case of a high nasal index - assuming heavily simplified but identical conditions - it is a fact that a relatively smaller amount of inhaled and exhaled air comes in contact with the epithelial cells of the nasal wall. The values for the Neandertal nasal index are significantly above those of the Australians (Tab. 1) and incidentally those of the "Hottentots" too (60.2). It can therefore be assumed, if one does not postulate completely divergent anatomical relationships for modern *Homo sapiens*, that the Neandertals must have been adapted to a hot, humid biotope - an assumption that receives more support from the stratigraphic finds than is the case with their attribution to cold climates.

In this regard, the physiology of breathing must be considered: this reacts to an ad hoc temperature drop of 20° by doubling the heart-stroke volume while, at the same time, the stroke volume increases and the pulse rate slows down. In particular, however, blood supply to the mucous tissues in the nose, mouth and pharynx increases to warm and moistere the inhaled air. Cooling of the arterial blood is therefore quite without significance: firstly, since it is implicated in the opposite function, i.e. warming the inhaled air; secondly, since it is directly channeled back from the capillaries into the venous blood circulation; and thirdly, since the A. carotis interna as well as the A. basilaris (the connection of the right and left A.

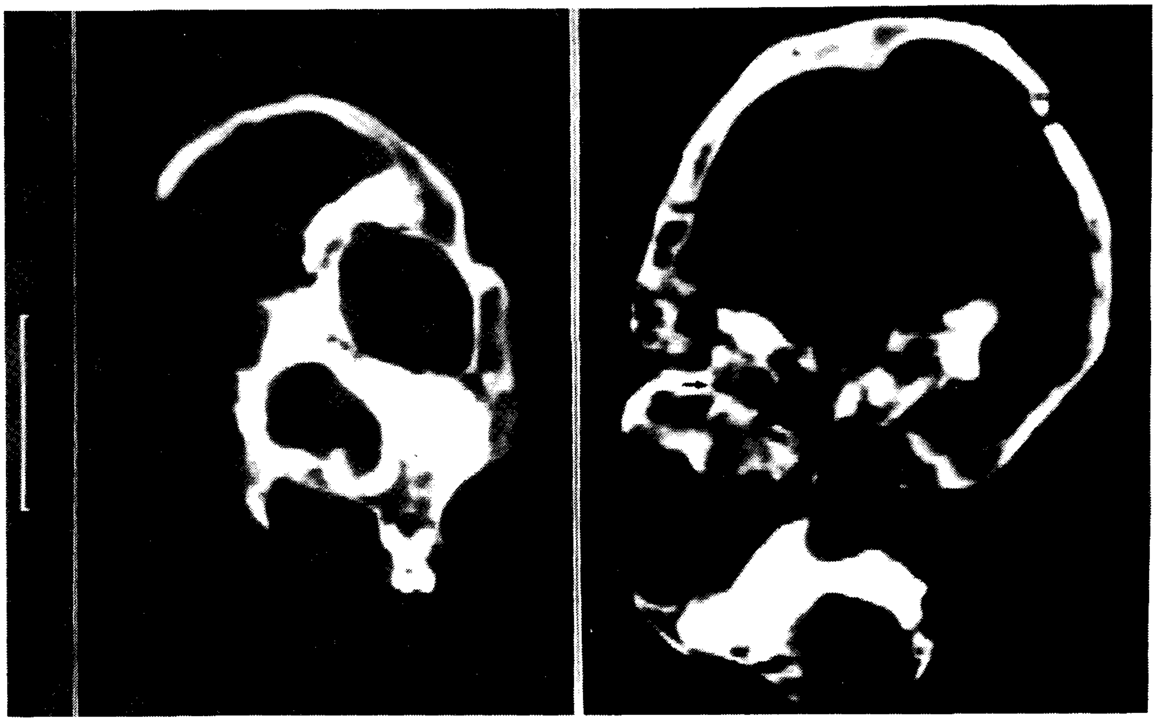


Fig. 1. CTs of the Steinheim-skull. The strong shadows are caused by rest of the sediments that are not allowed to be removed.
a: Axial cut at the level of Processus frontalis of Os zygomaticum with the wide space of the nasal cavity.
b: Horizontal cut at the level of Fossa mandibularis. The entrance of the Canalis caroticus is marked.

vertebralis) supplying the brain is excluded as a factor here (Fig. 3a,c), because its topographic siting posterior of the A. carotis externa, their distance from the nasal cavity ensures that it has no contact with the inflowing air and a cooling will be more evident only on its short way through the Sinus cavernosus. Also, as a result of the high flow speed of the blood (12 m/sec) and the poor temperature conductivity of the connective tissue leading to the pharyngeal cavity, including the connective tissue's own walls and the distance between the nasal cavity where the inhaled air is warmed too and the mentioned posititon of the artery in this part of the Larynx, the blood cannot be cooled down in this artery. As comparisons of the topographic relationships of the basal cranium of *Homo sapiens neanderthalensis* (Fig. 2) and *Homo sapiens sapiens* (Fig. 3c) show, the position of the Canalis caroticus is identical. Under no circumstances do they exceed the variation band found within the subspecies *Homo sapiens sapiens*. A high nasal index, under these conditions, is at a longterm disadvantage in cold-arid climates, since a reduced surface area is exposed to air passing through the nasal cavities - thus also making possible a reduction in turbulence (Tab. 1). For this reason, it cannot be demonstrated today under natural conditions in cold-arid biotopes.

Another example of adaptation, though till now it could not be as clearly conceptualized in its correlation to specific environmental circumstances as could the nasal index, is the size of the cancellous bone of joint extremities in relation to the pressures transmitted. Certainly, the assumption is warranted today that the size is directly proportional to the maximal physiologic pressures transmitted - which, following a proven hydrodynamic principle (Copf et al. 1989), with all it consequences concerning the thermodynamic and turbulence-induced forces (Fig. 4a-d), leads to a rapid reduction of the pressures generated within the space described. But what is so far lacking is sufficiently exact study of the correlation between size and pressure. The publication of Ruff et al. (1991) indicates that there is a direct correlation between the body weight and the dimensions of the Caput femoris while that of Trinkaus et al. (1994) make apparent that little change can be observed through different activity in this region in contrast to that of the cortical bone (diaphysis). For the time being, the only hypothesis which can be proposed, with any degree of plausibility, is that incidence of a large size/volume at the joint exremities indicates transmission of elevated pressures, and vice versa.

It is generally known that relatively large sizes are found in the subspecies *Homo sapiens neanderthalensis*. In the Erectus radiation, values are in conformity with the lower variation band of *Homo sapiens sapiens*. The lowest values are found in the subfamily closest to the genus *Homo*, the Australopithecinae (Tab. 2). According to general orthopedic guidelines, an average-sized *Homo sapiens sapiens'* Caput femoris can transmit pressures of up to at least 12.000 N. By way of comparison, the commensurate figures for *Homo sapiens neanderthalensis*, *Homo erectus* sp., and *Australopithecus* sp. are estimated at approx. 15.841 N, 11.172 N, and 5.836 N respectively. Thus the Neandertal joint is designed to handle considerably greater forces than is the case with Erectus or modern man. This fits in with the observation that the muscles bypassing (by a joint) the Articulatio coxae invariably leave sizeable muscle attachment patches (M. iliospoas, Mm. glutaei, gemelii, obturatores, etc.); on the other hand, the Mm. adductores can hardly - in contrast to *Homo sapiens sapiens* - be said to be overdeveloped, although they likewise bypass this joint. Since the Mm. vasti do not leave behind such pro-

Table 2. Size of the Femur extendig up to cancellous bone Cavitas medularis, measured in ccm ( x = Arithmetic mean, s = standard deviation, e = individual value).

| | x | s | e |
|---|---|---|---|
| Women, recent | 141.67 | 26.403 | --- |
| men, recent | 143.93 | 28.066 | --- |
| Neandertal | --- | --- | 190 |
| Spy | --- | --- | 220 |
| Trinil | --- | --- | 120 |
| KNM-ER 1481 | --- | -- | 134 |
| *Australopithecus africanus* | --- | --- | 70 |

minent muscle attachment sites as dc the Mm. adductores, only the relative curvature of the diaphysis, and the bending stresses concentrated there exclusively, can be said to point to the (relative to the Mm. adductores) very powerful Mm. vasti, as evidenced by their muscle attachment sites.

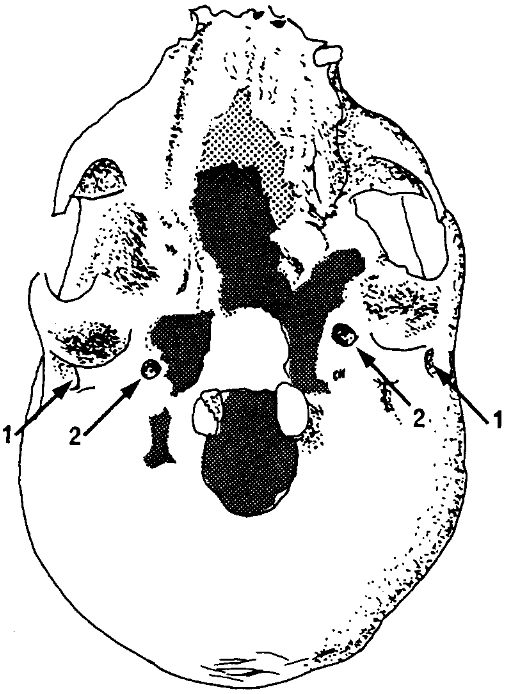


Fig. 2. Generalised redrawing of the basal view of the *Homo sapiens neanderthalensis* from La Chapelle aux Saints after Heim (1989). The position of the entrance of the Canalis caroticus (2) is exactly the same as in modern humans (1 = Porus accusticus externus, 2 = Canalis caroticus).

Naturally a similar line of argument holds for the Articulatio genu as well. In individuals of comparable Femur length, the mediolateral and dorsoventral extension likewise exceeds the dimensions found in *Homo erectus* and *Homo s. sapiens*. The dimensions found here confirm what, in any case, was apparent from the curvature of the Femur diaphysis, namely that an excessive (in relation to bodily height) pressure load can be assumed - involving, in the final analysis, the Mm. vasti as the principal tractional force.

Next, as third of the many characters that could be singled out, the organization of the cerebral cortex of the Cerebrum will be analysed. As is well known, the cytoarchitecture of the cerebral cortex (Substantia grisea) provides insight into how the respective functional units are demarcated, thus supplying a basis for comparative-anatomical study of the size proportions obtaining between the corresponding areas. It can be assumed that the contour and the length of the frontal part of the Os parietale directly match those of the Gyrus prae- and postcentralis. Thus it can be postulated, from a comparative-anatomical perspective, that the areas responsible for the sensomotoric functions associated with vocalization (from a purely muscular perspective) occupy the available portion quite independently of the development of Broca's language center. Thus, in respect of the shape of the Os parietale in *Homo erectus* sp., the area available for vocalization is correspondingly smaller than is the case in *Homo sapiens sapiens* - indeed, comparative-anatomical studies have invariably shown it to be localized in the distal part of the cerebral cortex which for example occupy 36.4% of the Gyrus praecentralis in monkeys and 41.7% in *Homo sapiens sapiens*. And this is in contrast to modern humans precisely the part, in *Homo erectus* sp. (Pithecanthropus I, 33.3 %), that is less developed relative to the horizontal part that controls the functions of the feet, trunk and hands.

The areas of the Lobus temporalis containing cytoarchitectonic fields 20-22, and also the adjacent cytoarchitectonic fields 38-42 and 52,are known to be specialized in cognitively differentiating sounds and noises registered by the auditory system. When these areas are overemphasized, with commensurate enlargement of the relevant parts of the cerebral cortex surface, increased performance levels can be assumed for there situated aptitudes. The external morphology of the Os parietale of *Homo s. neanderthalensis* - though not *Homo erectus* sp. - shows especially in this area just such an enlargement (Fig. 4 a,b). This is principally evidenced in those parts of the Os parietale that project laterally over the Proc. mastoideus, by virtue of which the Proc. mastoideus gives the impression of having been medially displaced. The same can be plausibly argued for the Polus occipitalis in respect of the visual cortex. Here too a widely extended Os occipitale - independently of the configuration of the Planum nuchale, as can be demonstrated e.g. for *Homo s. neanderthalensis* - is an indication that fields 17 and 18 dispose of a relatively greater area, meaning that both the number of cells and the possible neuronal linkages are commensurately augmented. Hence, optical perception has undergone appreciable amplification over and against what is normal for *Homo s. sapiens* Such then may apply for the classical Neandertals especially.

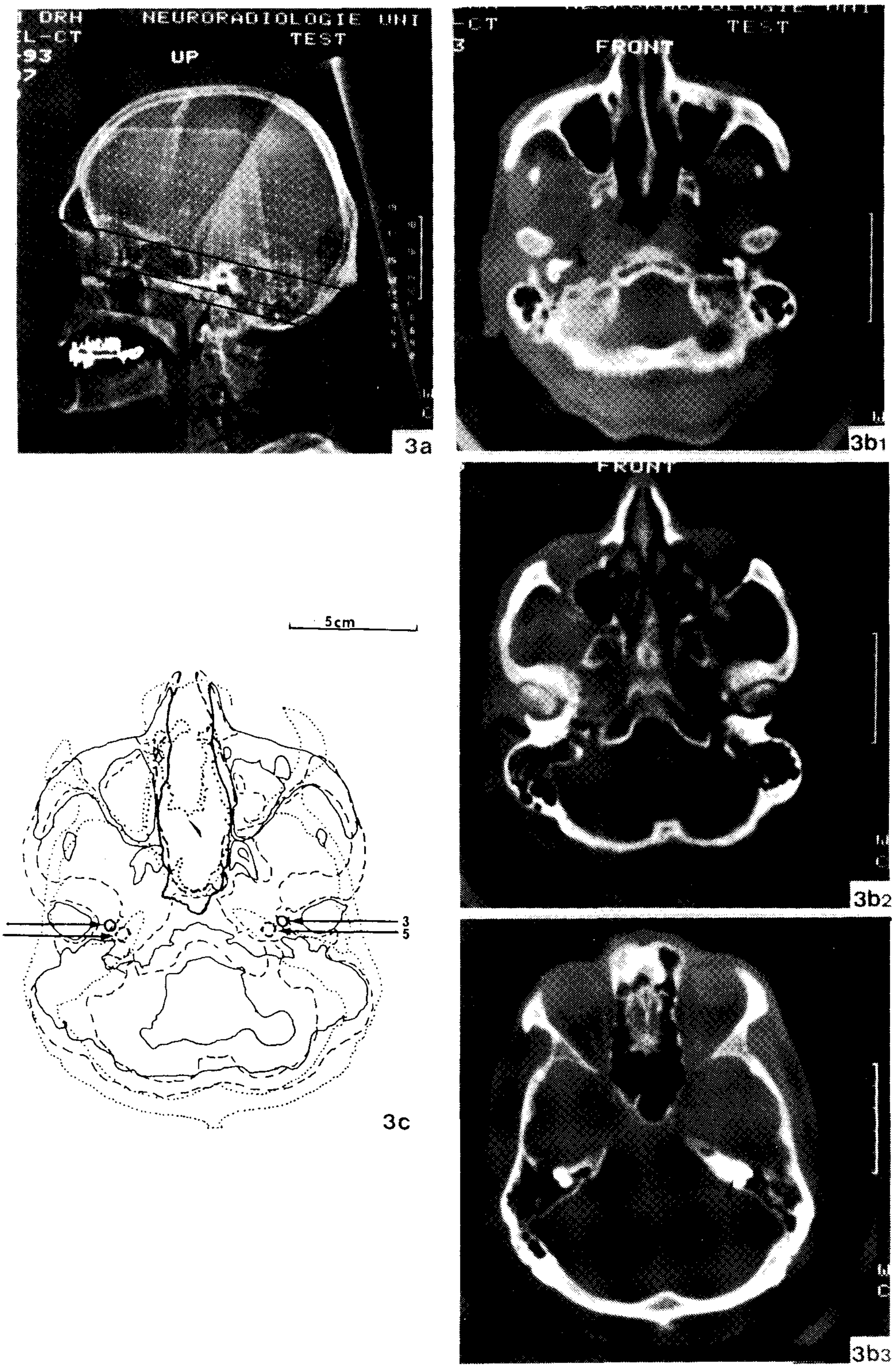
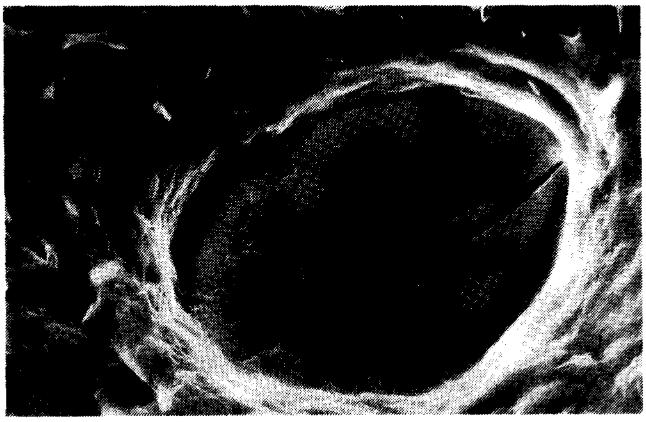


Fig. 3. Topogram and CT's at different levels of a modern man.
a. Topogram of a modern *Homo sapiens* head showing the different levels.
b. CT-scans on level 2 (b1), 5 (b2) and 10 (b3) of the larynx-pharynx-region showing the site of the Arteria carotis interna (➔) relative to the nasal cavity.
c. Superimposition of CTs level 3 (—), 5 (---) and 10 (...) with respect to the bony parts of fig. 1b and the position of the A. carotis interna relative to the bony region of the nasal cavity (marked stronger).



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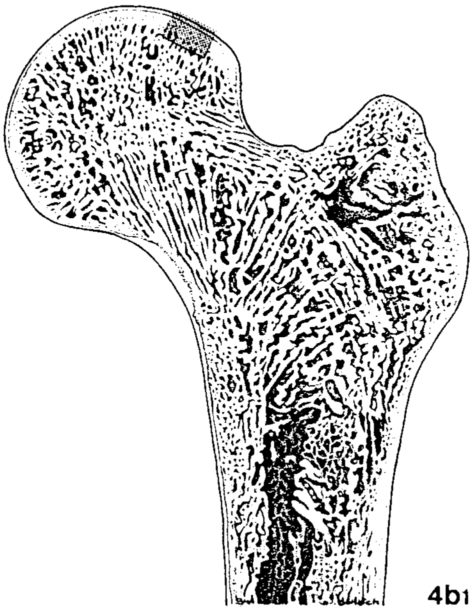

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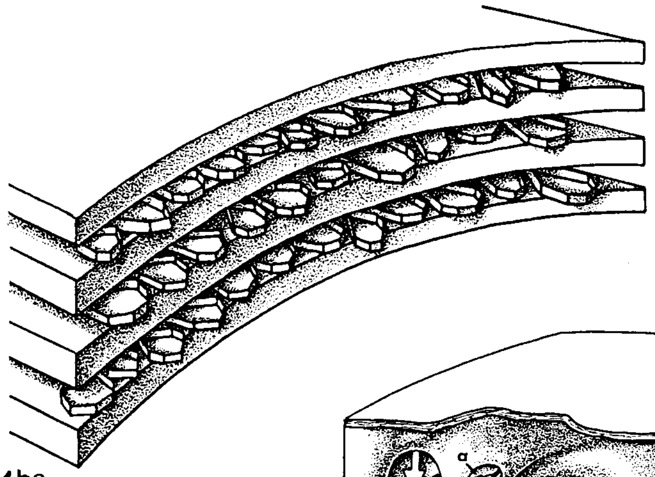

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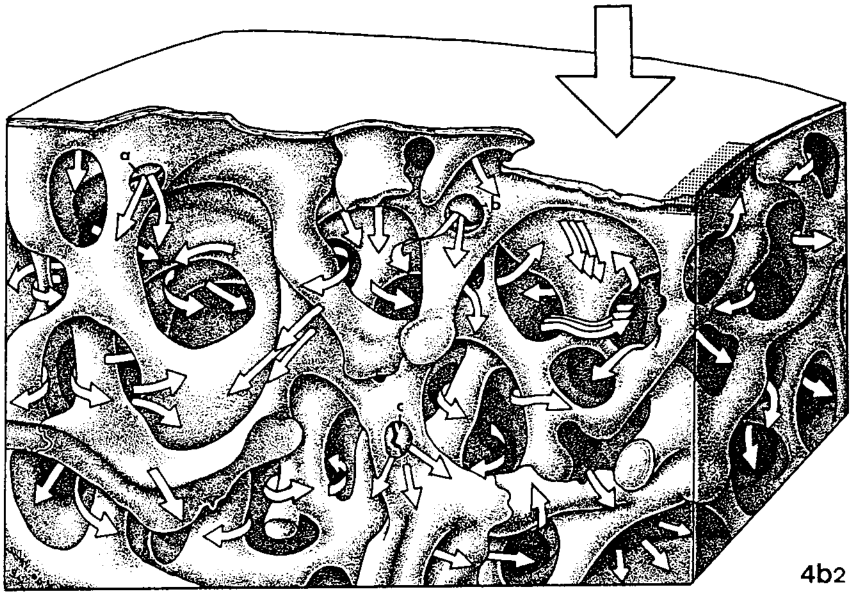

4b2

Fig. 4. a. Tensulae (tautly streched integuments) in the joint-near cancellous bone of the Caput femoris representing the hydrodynamic principle.

b. Schematic representation showing operational mode of the hydrodynamic system (redrawings by SEM-pictures).

b1: Overview of the distribution of the cancellous bone of the proximal part of the femur which is at all responsible for the hydrodynamic system.

b2: Section as indicated in fig. b1. The greater arrow indicates the main direction of the incomming impulse while the smaler one within the spongy bone indicates the dispersion of the power into all directions. Only 3 tensulae (a,b,c) are given instead of 30 per 1 cm$^2$.

b3: The structure of the subchondral corticalis (6 - 12 layers within 12μmm) with irregular pentagonid spaces naturaly filled with serous liquids.

## Discussion

Underlying the comments in this discussion section is the assumption that all fossil representative of the genus *Homo* are form variants - none of which, so the fossil record would suggest, is likely to have been long-lived, since the adaptive traits thrown up by the interplay of mutation and selection did not match well enough with the environment. This means that, when reconstructing the extent of their adaptability, i.e. their likelihood of undergoing further phylogenetic evolution, not all fossil finds or their special characters need be considered as representative.

Franciscus & Long (1991) note, among other things, that natural selection has not had any discernible influence on the nasal index. But here their conclusion is based, for one thing, on studies of recent populations (where clearly the influence of natural selection can be eliminated by technological and medical factors); for another, they have evidently overlooked the fact that the forerunners of modern *Homo s. sapiens* lived primarily in biotopes where the same background conditions for the nasal index invariably operated. For we are familiar with the fact that if mutations with a significantly lowered nasal index occur in a biotope where a positive selection advantage attaches to noses with a high index, a negative selection pressure will be brought to bear of the mutant resulting in the latter's eventual disappearance. Only the conquest of new biotopes, to which new variants featuring e.g. lowered nasal indices were adapted, could contribute to these new variants being preserved as they arose through mutation (positive selection). Evidently this did occur during the transition to modern *Homo sapiens* (speciation principle).

Franciscus & Trinkaus (1988), for example, interpret the chamaerhine nasal form of *Homo erectus* as an adaptation with the function of moistening air inhaled in cold, arid climatic regimes. However, in their analysis of nasal morphology from the perspective of its adaptability, measurements were used which, for one thing, cannot be employed to calculate nasal indices; for another, no correlation for them with specific climatological conditions has been proved. Thus this data and analysis platform cannot be expected to permit even approximately accurate estimates of selection advantage, or lack of such, for this character system (which is adaptive under natural conditions). It can be observed, in this connection, that the soft-tissue nose of the "Eskimos" is occasionally described as broad, despite the fact that the measured nasal index clearly places it among the Leptorhini.

According to the nasal index values of the Neandertals, the latter must have been adapted to the peripheries of hot, humid regions. Assuming here a certain flexibility, plus cultural and medical control over living conditions, in areas of diminished water vapor pressure, Neandertals might also have been found in subtropical to moderate biotopes. The prevalent find pattern has evidently led to commensurate conclusions about the extremely broad Neandertal Apertura piriformis. Thus Coon, for example, proposed the "radiator theory" (cited by Trinkaus & Shipman, 1993), while Franciscus & Trinkaus (1988), as described above, interpreted the high nasal index - evidently here drawing on Coon - as an adaptation to a cold, arid climate. But here they fail to consider that turbulence, in a nose with a low nasal index, inevitably far exceeds that encountered in a nose with a high index - thereby optimizing, in effect, warming-up and humidification functions. Finally, different authors (Demes 1987; Heim 1978; Hylander 1977; Rak 1986) have interpreted the broad Apertura among other features as simply a structure for optimizing pressure transmission during mastication. The above mentioned observations on the Condyli occipitales and the subchondral Corticalis must make us skeptical about accepting such an interpretation. None of these authors make any reference to the position of Thomson & Buxton (1923) - which has not so far been disproved.

What further tells against these (here only briefly touched on) interpretive attempts concerning the various form variants and relative size relationships of the Apertura piriformis, is the physiology of breathing as well as the topographic anatomy of the larynx-pharynx region (Fig. 1b,c). Indeed the physiological evidence is so clear that one has difficulty in grasping why it was, and evidently still is, possible for such interpretations to be advanced. But even the attempted interpretation of the bony lateral walls of the nasal cavity as structures for buttressing the masticatory forces is not tenable, whether looked at from the perspective of the functional-static or (especially) the abovementioned hydrodynamic components implicated in pressure-impulse transmission. For, as a consideration of the occipital region around the Condyli occipitales shows, the solid bone is relatively thin - especially at points exposed to particularly high stresses and strains. Indeed the subchondral Corticalis measures only 12 µmm at the Caput femoris. Only the cancellous bone structure of the Proc. alveolaris maxillaris and mandibularis permits us to conclude that these primarily constitute a complex hydrodynamic and elastomechanic (desmodontal fiber sheaves) system for rapidly reducing the pressures generated - which means that no pressure-impulse transmitting functions devolve upon the Proc. frontalis of the Maxilla and Os zygomaticum. Naturally this holds no less for the Torus supraorbitalis. In addition, the interpretation proposed by different authors (Demes 1987; Heim 1978; Hylander 1977; Rak 1986) - without here going into it further, with its various imponderables - would require that all chamaerhine-nosed representatives of the genus *Homo* generate greater masticatory pressures than is the case with leptorhine-nosed representatives of same. However, they do not raise this point at all.

As to the so-called pre-Neandertals from the Riß (= Saale) glaciation, even the relevant publication by de Lumley-Woodyear (1973) does not resolve, with acceptable clarity, the question of whether these finds are not to be assigned to a short-lived warm spell. One should recall here the difficulties arising over the interpretation of the finds from the Steinheim (Steinheim/Murr) sands, where much speaks for the assumption that e.g. woodland and steppe elephants shared the same biotope at the onset of a new cold spell - with woodland elephants, at least in part, still frequenting the area during summer, whereas steppe elephants would immigrate during winter only to withdraw in summer, and vice versa. This line of explanation readily explains - and not just for this find either - how forms diverging as greatly as these two come to be found in the same layers.

Examining the muscle attachment sites on the diaphysis of the Neandertal Femora, and bearing in mind the almost pure bending stresses located in this region of the diaphysis, we can conclude that the Mm. vasti - which, as is known, bypassed the Articulatio genu - were able (in contrast to the Mm. adductores) to generate significantly higher forces. What speaks for this interpretation is the massive articulation of the distal Femur and the proximal tibia, together with the commensurate hydrodynamic force-impulse transmission there situated. Owing to the relatively modest length of the diaphysis, little room was available for the insertion point of M. vasti - a disadvantage which required as compensation, along with other criteria, enlargement of the diaphysis girth. This form of adaptation can likewise, as is generally known, be exogenously induced by appropriate training, i.e. in contrast to the transverse extension of the Condyli femoris and the size of the Caput femoris. This supplies us, at the same time, with an explanation of e.g. the relatively powerful curvature of the Femur diaphysis that we find. Thus, despite their relatively short bodily height, the Neandertals stood out, anatomically speaking, from all other representatives of the genus *Homo* for overemphasized musculature due to pressures in the Articulatio coxae and genu; among modern populations, only individuals of over 180 cm show a comparable amount. The results of Ruff et al. (1991) and Trinkhaus et al. (1994) will mean that the size of the cancellous bone must be determined only by genetically controlled factors wich can not be altered by exogene factors. The bending stresses are similarly high, from the perspective of curvature severity, among Neolithic *Homo s.sapiens* populations of various periods and regions (Czarnetzki 1966). In contrast to Neandertals, the amount of curvature is, on average and as a rule, concentrated in the proximal third; moreover, and in contrast to the Neandertals, no continuous curvature is found - but rather a relatively straight distal diaphysis featuring a rapid transition from straight to curved. This in turn suggests that, in *Homo s. neanderthalensis*, the Mm. vasti insertion points should be differently localized on grounds of anatomical-topographic criteria, i.e. they belong further distal than is found in most anatomically modern populations. This permits a slightly divergent function to be inferred (with all due caution, to be sure) from the angle of insertion. But whether - apart from being a specialization for specific movements - this function suffices, in its variability, to postulate outright deviation from normal movement patterns, of the kind found in modern populations, cannot be resolved with a requisite degree of clarity. Somewhat more solidly based, on the other hand, is the suggestion that the Neandertal muscular-anatomical configuration, to the extent this can be reconstructed, developed to cope with extreme stressing of the lower extremity joints. Here the most prominent character is the straightening observed in the Articulatio coxae and genu, whereas adduction plays a relatively subordinate role (as compared with *Homo s. sapiens*). In any case, a preferred mode of locomotion, e.g. of the kind envisaged by Trinkaus & Shipman (1993), cannot be conclusively proven by this line of analysis. All that can be reliably concluded from the find material is a pronounced specialization in respect of certain movement patterns - where the ability to straighten these particular joints evidently assumed inordinate importance, as a result of encountering greater stresses than was, and is, the case in *Homo erectus* sp. and *Homo s.sapiens* respectively.

A far better known character is the curvature of the radius, pointing to a unique specialization of flexors, extensors and to a lesser extent rotators of the lower arm, in the sense that the muscle cross-section is visibly overemphasized - which cannot be observed even in *Homo erectus* sp. For all this substantial evidence, the methods of biomechanics have not yet succeeded in enabling the adaptive advantages of these characters to be analyzed with an accuracy sufficient to permit

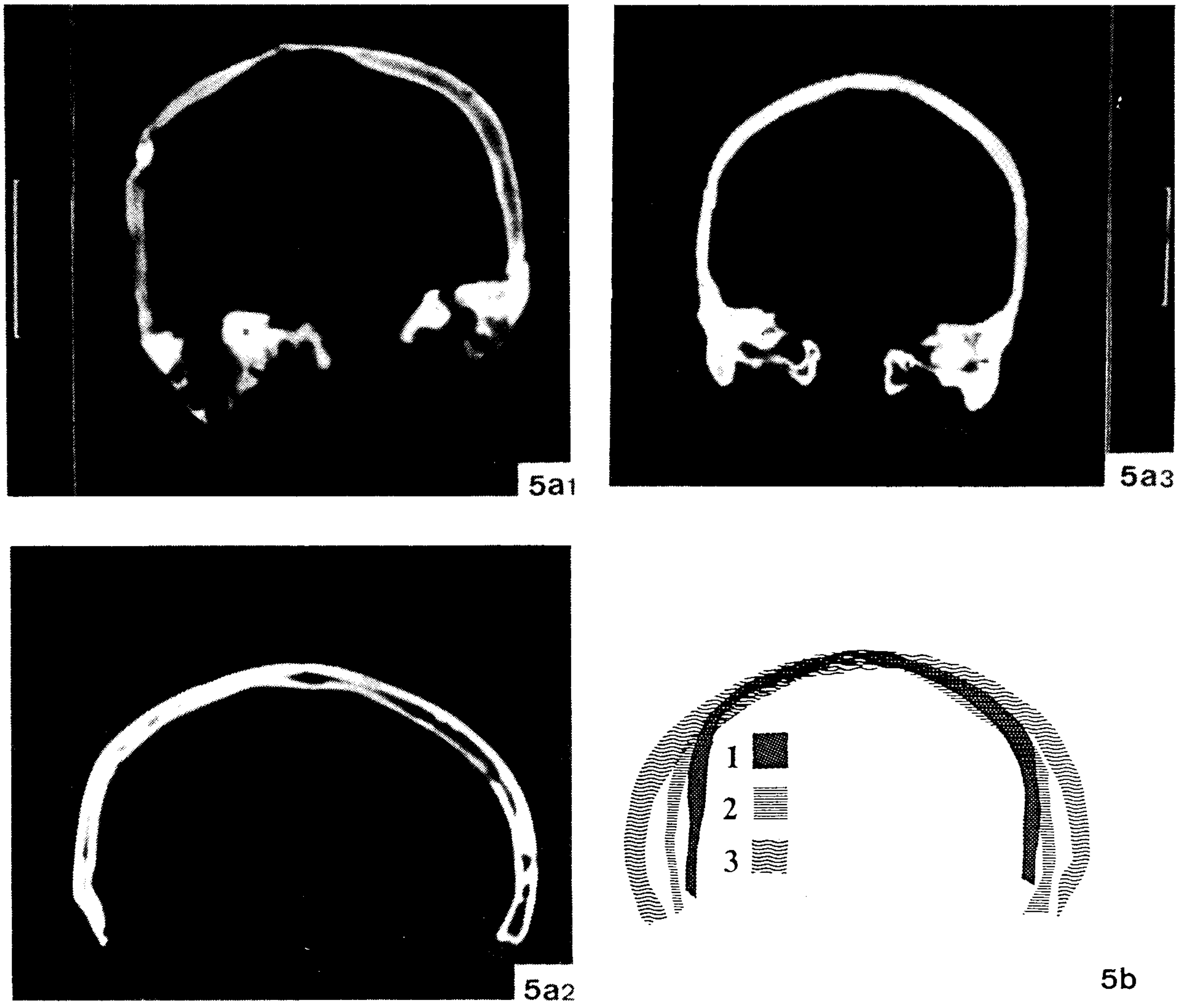

Fig. 5. a. CTs showing the differences between. 1. *Homo sapiens steinheimensis*, 2. *Homo sapiens neanderthalensis* and 3. *Homo sapiens sapiens*. Note the similarity in the vertical orientation of the lateral part of Os parietale between specimen 1. und 3. and the typical curvature of 2. especially on the left side which is positioned some more back than the right side.

b. Graphic representation of the outline of the Os parietale drawn from the Bregma to Porion. 1 = Steinheim skull (dark), 2 = modern *Homo sapiens* (light), 3 = Monte Circeo skull (rippled). The section dubbed a handles (in all probability, based on comparative-anatomical studies) the function of the oral-pharyngeal area and the mimetic musculature.

inference of special physical movement and handling syndromes, such as may diverge from those of *Homo erectus* sp. and *Homo s.sapiens*. Thus the deeper point of referring to these methods here is only to focus our attention, somewhat more than previously, on the task of reconstructing the Neandertals' environment; also, and in particular, on elucidating the factors contributing to the selection advantage of this specialized form (which, after all, lasted upward of approx. 60,000 Ky).

On the basis of comparative-anatomical findings, enlargement of the cerebral cortex in the proximity of the vertical component of the Gyrus prae- and postcentralis might mean that *Homo erectus* sp., by comparison with *Homo s. sapiens*, exhibited a less differentiated sensorimotor performance in both the laryngeal-pharyngeal area and the mimetic musculature. This supposition receives excellent backing from studies by Lieberman, who has postulated for this species a reduced vocalization capacity. But nowhere has a particular specialization been isolated that conceivably points to a special adaptation in the inhabited biotopes. It must be remembered, as a general point, that not all traits available for study today need necessarily have possessed an adaptive character in their natural environment. Some traits, in fact, are known that are exposed neither to positive nor to negative selection pressures (neutral mutants). As a result, these traits remain unaltered in the gene pool until such time as the selection factors undergo change. The changes to the Lobus frontalis and parietalis in the proximity of the Gyrus prae- and postcentralis could perhaps have been significant in the development of social communication. But on no account are we entitled to conclude that these changes caused the emergence of social structures, since very complicated social structures are also known among representatives of lower systematic units. Because human social behavior is primarily associated with cytoarchitectonic fields 9, 10, 11 and 47 - and correlations with demonstrable natural factors neither have been, nor can be, demonstrated (on grounds of mutual exclusivity) - this aptitude is only accessible to blurred reconstruction and has therefore been omitted from the present treatment.

The prospect is different, though, when one recalls the size proportions of the Substantia grisea in classical Neandertals. Here we find, in contrast to *Homo s. sapiens*, an enlargement of the areas previously mentioned. This raises the question of whether the relatively large size of the Neandertal braincase is not primarily due to overemphasis and specialization of the functions assigned to the described and observed sites. It is a fair conclusion that, in this domain, the Neandertals were more highly specialized than modern populations; they were therefore definitely superior to these in recognizing sounds and noises and in optically registering information entering through the eye.

While the observed enlargement of certain areas and the concomitant optimizing of the corresponding aptitudes can hardly be questioned, it is far more difficult to elucidate the advantages of this developmental trend. Assuming the correctness of the received opinion that the classical Neandertals were big-game hunters, it makes sense to suppose that a generously developed area for cognitive-visual recognition would be exceptionally useful. The relatively large eye socket - indicating a relatively large eyeball - may conceivably have contributed, via an enlarged cornea and increased enlargement of the pupilla, to greater overall sensitivity to light in Neandertals, endowing them with excellent vision under dark or gloomy conditions. The possibility therefore cannot be categorically excluded that the relatively enlarged acoustic-cognitive brain areas were of similar advantage to big-game hunters, especially for discerning fine sound differences and concluding back correctly to their perpetrator.

## Review

With reference to nasal function and the correlation between vapor pressure levels and soft-tissue nasal indices, together with the high correlation between the indices of the soft-tissue and the bony nose, it could be clearly shown that all representatives of the genus *Homo*, down to the end of the Eem interglacial, must have lived in climatic zones characterized by high vapor pressure levels (high temperature coupled with high humidity). As a result, there was no selection disadvantage for this trait in contrast to a low nasal index. The classical Neandertals must likewise have been adapted to a hot, humid climate - a finding that breaks in fact with received opinion. Only for the Würm (Weichsel = Wisconsin) glacial, evidently as the result of new mutants appearing, can representatives of the genus *Homo* with a lower nasal index be documented in appropriate environments.

Recent results concerning pressure-impulse transmission via the joints point to the conclusion that increased joint size permitted greater pressures to be transmitted. Analysis of the joint extremities of classical Neandertals, also of the insertion attachment sites of the requisite muscle groups on the Femur, Radius and Ulna, leads us to expect - by comparison with *Homo erectus* sp. and *Homo s. sapiens* - a high degree of specialization with respect to stressing of the Articulatio coxae and genu (due to straightening mechanisms) and to exceptionally powerfully developed flexors and extensors in the Articulatio carporadialis. Indeed this power development exceeds any levels observable in representatives of the species *Homo erectus* sp. or in modern *Homo sapiens* (even with special training).

Lastly, close differentiation of the areas of the cerebral cortex, as opposed to a purely global assessment of the overall size of the cerebrum (including the cerebellum), permits us to conclude that the aptitudes situated in the corresponding areas were highly specialized. From this we may further conclude (with all merited caution) that the cognitive-acoustic and the cognitive-visual aptitudes of the classical Neandertals can, in contrast to *Homo s. sapiens,* be expected to be overemphasized. This finding cannot be extended with the same confidence to the *Homo erectus* sp. of the early and early Middle Pleistocene - since, in both cases, the corresponding cerebral cortex fields are relatively less developed than is the case in *Homo s. sapiens.* In view of the relatively large orbitae, it can be concluded (again with the necessary caution) that the eye sockets were also correspondingly large. All in all, this points to a cerebral specialization, possibly implicated in sustaining, over sizeable periods of time, the natural and cultural environment of the Neandertals. After all, he can be proven to have existed rather longer than to date modern man.

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