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THE SUPRAINIAC FOSSA: THE QUESTION OF HOMOLOGY

ABSTRACT: The suprainiac fossa has been defined many ways, but can be most broadly defined as a depression above the inion whose expression is variable. It is ubiquitous in Neanderthals, and has often been considered a Neanderthal autapomorphy. Yet, similar depressions occur in some other hominids, including modern humans from the Upper Paleolithic. It has been argued that the suprainiac fossa of the Early Upper Paleolithic Europeans is not homologous to the form in Neanderthals. In this paper, the question of homology is examined. First, suprainiac fossa variation within Neanderthals is established; second, variation in modern humans, including Early Upper Paleolithic specimens is assessed and the question of the structural uniqueness of the Neanderthal suprainiac fossa is addressed. Finally, two developmental models for the suprainiac fossa are proposed to account for the fossa in juveniles and adults. The adult model suggests that the suprainiac fossa is related to the formation of posterior cranial superstructures and other aspects of cranial shape. This raises questions about the meaning of homology in this and other structures whose expression is mediated by remodelling.

KEY WORDS: Suprainiac fossa – Neanderthals – Early modern humans – Mladeč

INTRODUCTION

The suprainiac fossa is a variable depression above the inion. It is ubiquitous in Neanderthals, but similar depressions occur in some other fossil hominids (Haile-Selasie *et al.* 2004, Trinkaus 2004) as well as in modern humans. It gained attention among anatomists and paleoanthropologists as a Neanderthal feature (Hublin 1978a, 1978b, Santa Luca 1978) and the Neanderthal form of suprainiac fossa serves as the prototype for its definition. In Neanderthals, the fossa is generally elliptical in shape, usually transversely elongated, and is of variable depth. In many specimens, it has a rough, pocked surface. However in some Neanderthals and in other hominid groups, depressions above the inion occur which depart from this description. The issues discussed in this paper are whether these departures represent "true" suprainiac fossae, and whether suprainiac fossae homologous to those of Neanderthals occur in the Early Upper Paleolithic.

The suprainiac fossa has been used to support *both* sides of the debate over Neanderthal ancestry for modern humans, and therefore its occurrence in the Upper Paleolithic is of considerable interest. Some researchers have considered the suprainiac fossa to be uniquely derived in Neanderthals (Tattersall 1995, Santa Luca 1978), and have used it to support the hypothesis that Neanderthals belong to a phylogenetic lineage reproductively isolated from modern humans. For decades the suprainiac fossa has been considered a Neanderthal autapomorphy, either alone or combined with other elements of the occipital complex of traits that includes lambdoidal flattening, occipital bunning, a bilaterally arched nuchal torus, and the *"en bombe"* posterior cranial vault shape in *norma occipitalis* (Hublin 1978a, Santa Luca 1978). The suprainiac fossa and other Neanderthal features have been explained by the accretion theory that suggests that unique Neanderthal features became established by drift, through founder's effect, followed by long periods of low population growth, isolation, inbreeding, and further bottlenecks. According to this model, the suprainiac fossa is a neutral genetic trait, established by drift.

On the other side of the controversy, researchers have cited the incidence of the suprainiac fossa in Early Upper Paleolithic Europeans as support for the hypothesis of genetic continuity between Neanderthals and the Europeans that followed them in time. Declining, but significant, frequencies of the suprainiac fossa (and other Neanderthal non-metric traits) in the Upper Paleolithic record have been used to support the continuity hypothesis (Frayer 1993, 1997, Wolpoff 1999). Several scholars have pointed to the incidence of the fossa in non-Neanderthal groups to question the isolation of Neanderthals and/or reject the hypothesis that the Neanderthal suprainiac fossa is an autapomorphy. Using the incidence of the suprainiac fossa in Upper Paleolithic populations, they suggest that there was some genetic continuity between Neanderthals and their successors.

How can such opposing observations be understood? The problem is both one of definition and homology. While there is an occipital depression in the region above the inion in many Early Upper Paleolithic specimens, it is unclear whether such structures are "true" suprainiac fossae – whether they are morphologically equivalent to the suprainiac fossa of Neanderthals. Questions have also been raised about the homology of non-Neanderthal variants of the suprainiac fossa. In particular, these involve questions about whether the form of the suprainiac fossa most prevalent in Early Upper Paleolithic Europeans is homologous to the Neanderthal expression (*Figure 1*).

In 1991 I described differences between the common Upper Paleolithic variant and that found in the Neanderthals, but applied the term "suprainiac fossa" to both forms; since then Sládek (2000) has proposed the term "supranuchal fossa" to differentiate the Early Upper Paleolithic form from that found in the Neanderthals. The underlying assumption is that morphological differences between the suprainiac fossa and the supranuchal fossa indicate that the structures are not homologous. However, while it has been discussed in some detail (e.g., Hublin 1978a), there has been no systematic study of suprainiac fossa variation in modern humans compared to Neanderthals and the etiology of the suprainiac fossa remains unclear (Trinkaus 2004).

In this paper, the question of homology is examined in European Neanderthal and Early Upper Paleolithic remains, archaeological collections of modern humans, osteological collections and dissection room samples. First, suprainiac variation within Neanderthals is examined; second, variation in non-Neanderthals is assessed and the question of the structural uniqueness of the Neanderthal suprainiac fossa addressed. Of particular interest is whether Early Upper Paleolithic specimens from Mladeč only possess the supranuchal variant, or whether the Neanderthal form of the suprainiac fossa can be seen as well. Finally, developmental models for the suprainiac fossa are proposed to examine whether a single developmental homology could underlie all forms of suprainiac fossa expression.

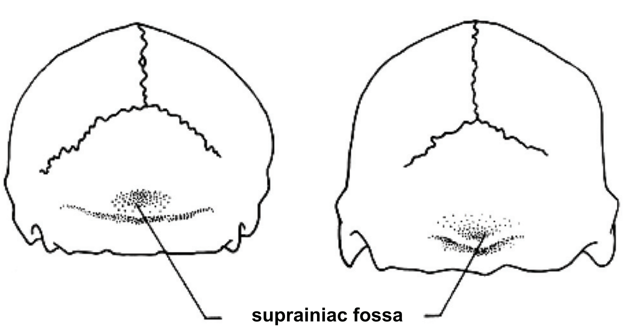

FIGURE 1. Two forms of the suprainiac fossa. In Neanderthals (left) the suprainiac fossa is usually a discrete, elliptical, depression above inion. In many modern humans (right) the fossa is V-shaped, less well delineated, and is associated with medial superior nuchal line development.

VARIATION IN THE NEANDERTHAL SUPRAINIAC FOSSA

Neanderthal variation for this study centres on the suprainiac fossae of the Krapina hominids, thirty four occipital bones from a single Early Neanderthal site (Caspari 2006). These were compared to other Neanderthals to assess suprainiac fossa variation according to three criteria: size and shape, external cortical structure (degree of "pocking"), and associated superstructures (e.g. the transverse occipital torus, or the expression of well developed superior nuchal lines). As discussed below, the shapes of the suprainiac fossa and associated superstructures are interrelated.

Size and shape

There is considerable variation in the size and shape of Neanderthal suprainiac fossae. Some are so large that they incorporate much of the occipital plane, as seen, for example, in Salzgitter-Lebenstedt (Hublin 1984) and La

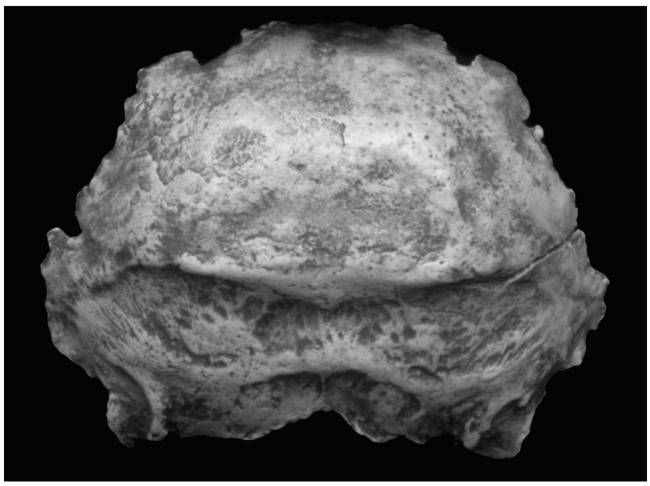

FIGURE 2. Large suprainiac fossa on the occipital from Saltzgitter-Lebenstedt. Photograph is of a cast in the collections of the Université de Bordeaux.

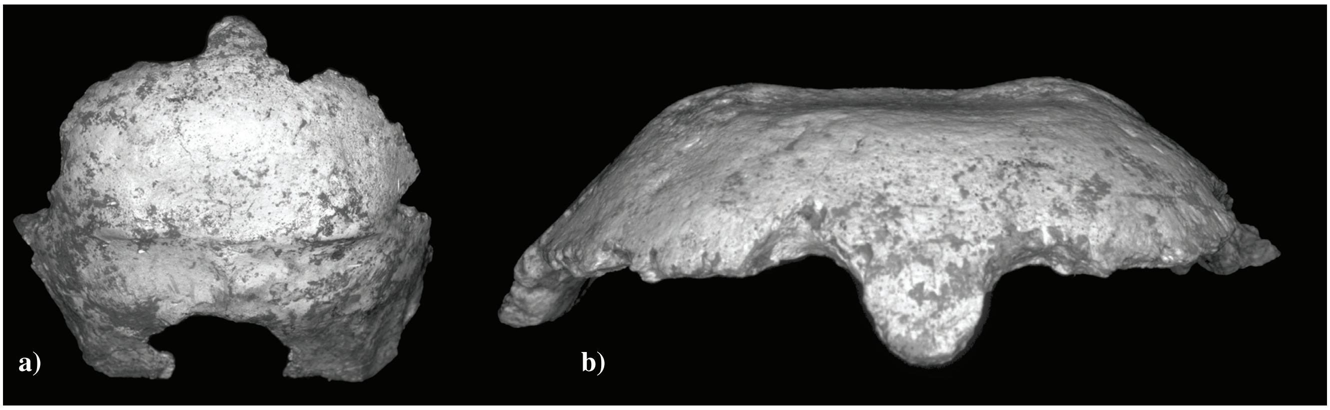

FIGURE 3. Posterior (a) and superior (b) views of the occipital from La Chaise (B–D). The suprainiac fossa is so large that it incorporates much of the occipital plane. Note how the suprainiac fossa informs the shape of the posterior cranial vault. (Photograph courtesy of Milford H. Wolpoff.)

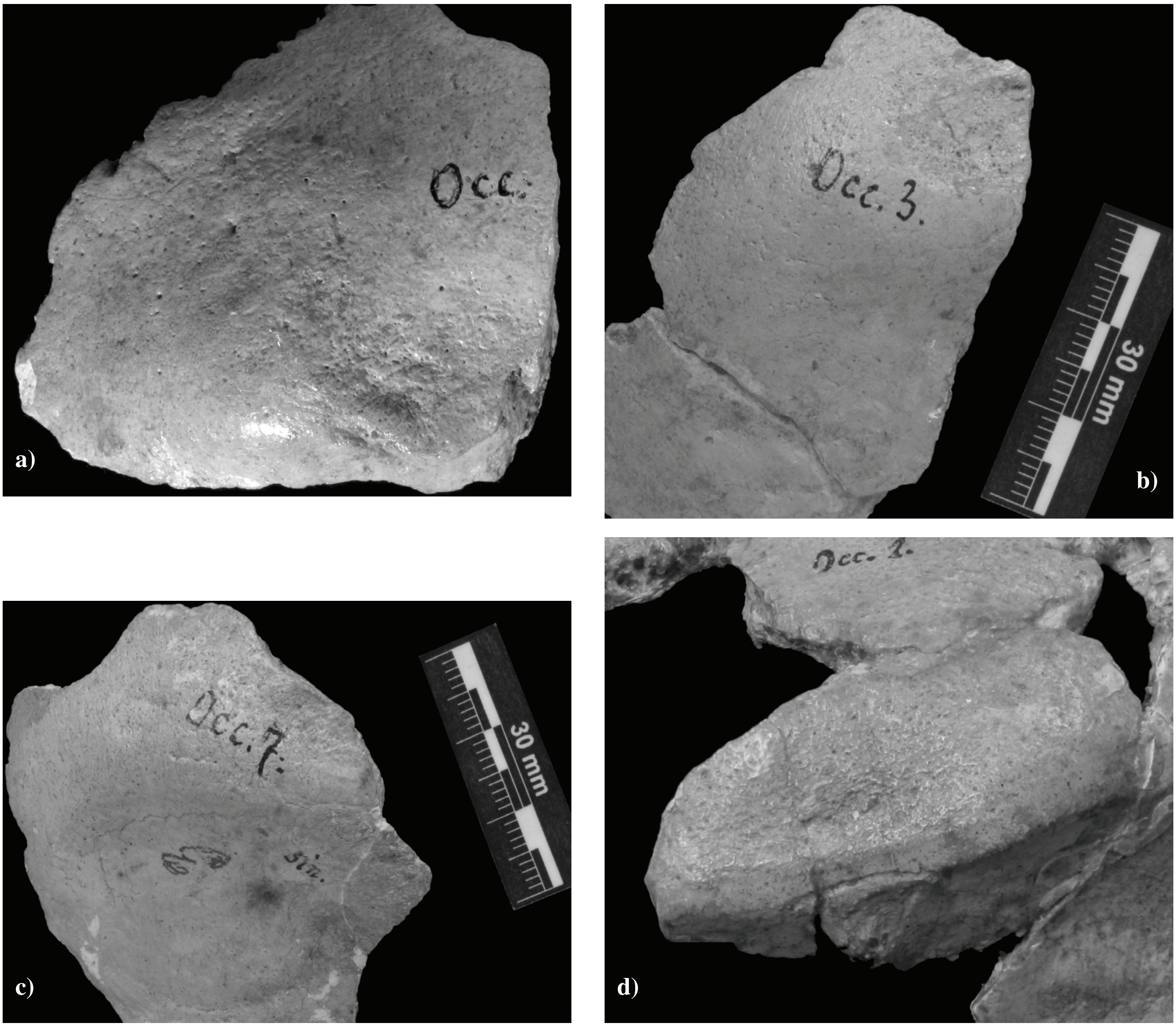

FIGURE 4. Suprainiac fossa variation at Krapina. Pictured are: Krapina 18.5 (a), Krapina 9 (b), Krapina 13 (c) and Krapina 5 (d). The fossae of Krapina 9 and 13 can be seen in the right superior corners of the specimens. Although incomplete, they are well delineated and contribute to the bilaterally arched nuchal torus. (Photographs of Krapina 9 and 13 courtesy of Luka Mjeda and the Croatian Natural History Museum.)

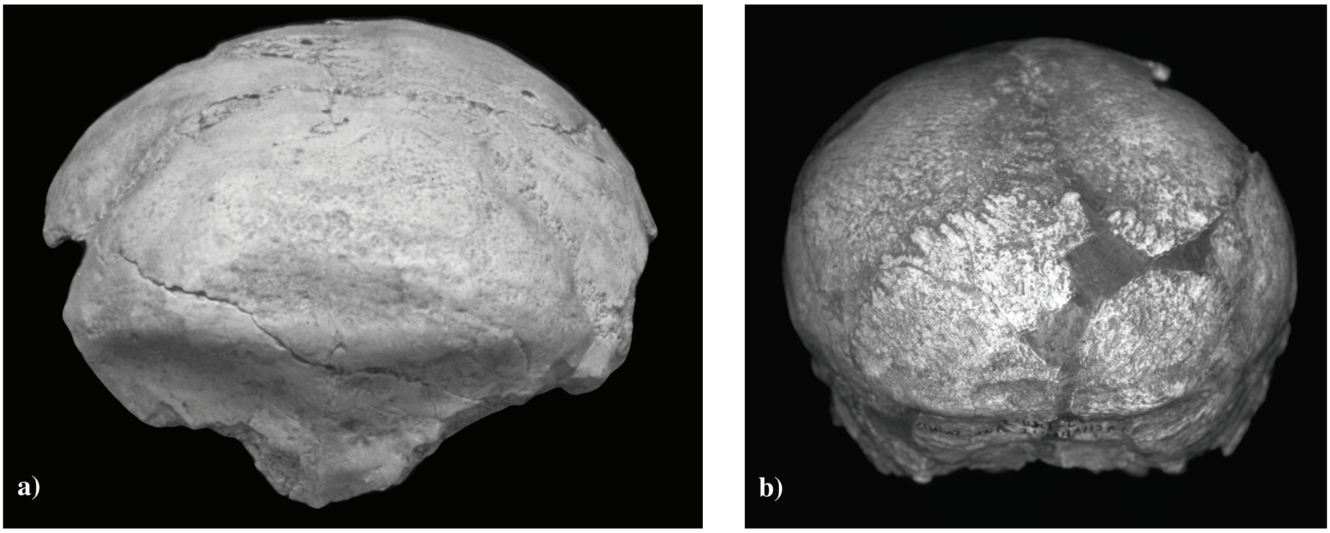

FIGURE 5. The occipital from Marillac (a) and a posterior view of the La Chapelle aux Saints cranium (b). Both exhibit broad, short, suprainiac fossae in contrast with those shown in the preceding figures. (Photograph of La Chapelle courtesy of Milford H. Wolpoff.)

Chaise (Bourgeois-Delaunay) (*Figures 2* and *3*). In La Chaise (*Figure 3*) the suprainiac fossa incorporates much of the occipital squama. The large depression is surrounded on all sides by thickened bone. This kind of suprainiac fossa may appear as a depression in the middle of a very broad, thick "torus" that can incorporate most, or all, of the posterior aspect of the occipital plane.

Other fossae are smaller *(Figure 4)*, confined to the region directly above the inion, and do not extend higher on the occipital plane. The common Neanderthal suprainiac fossa, exemplified by Krapina 5, is elliptical and more restricted than that of La Chaise. It generally occurs in the area between the bilateral arches of the Neanderthal nuchal torus.

Shapes of suprainiac fossae likewise vary (*Figure 5*). While the elliptical fossa is common, in some specimens it is round (e.g. Krapina 18.5 in *Figure 4*), and it can present in irregular shapes; in La Chapelle (*Figure 5*) it is "doubled" resembling a horizontal *Figure 8*.

Superstructures

The most important variable associated with suprainiac fossa variation is superstructure development, the expansion of the external table of the posterior occipital bone. Neanderthal suprainiac fossae are always expressed in conjunction with a nuchal torus or other development of thickened bone on the occipital plane. The nuchal torus is a thickening of the external table of the occipital bone

FIGURE 6. Two views of the juvenile Krapina 2, showing a well developed suprainiac fossa and nuchal torus. The surface of the suprainiac fossa is more pocked in juveniles than in adults.

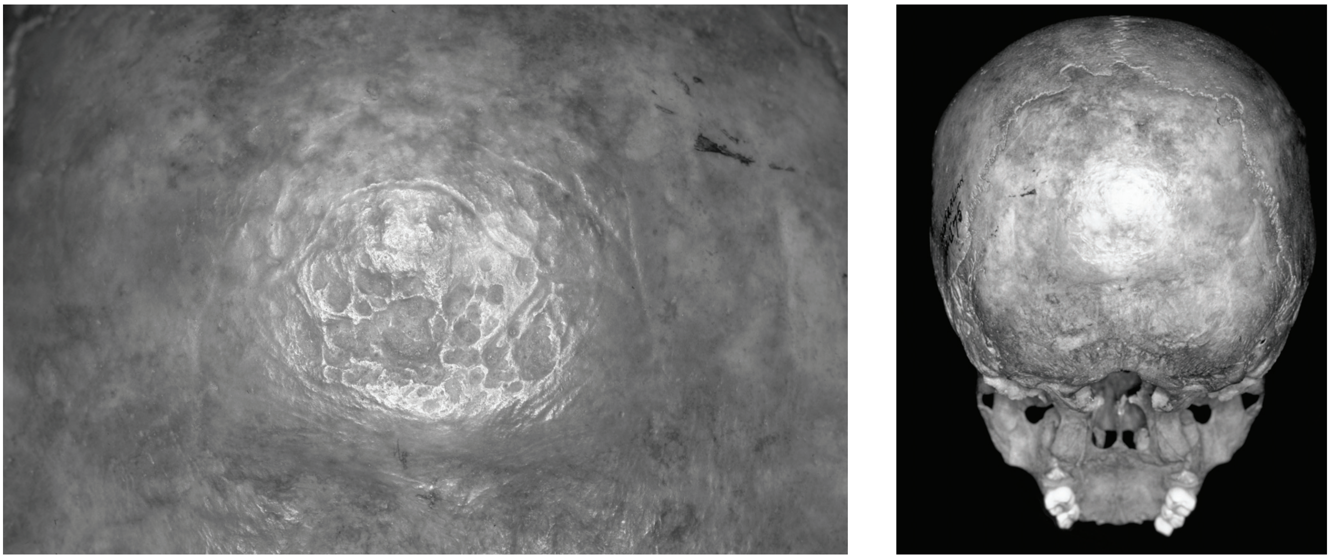

FIGURE 7. Suprainiac fossae of two modern children aged 3 (left) and 7 years.

above the superior nuchal line; although the torus often occurs between the superior and supreme nuchal lines, it is not necessarily defined by them. It differs from the nuchal lines and crests in that it is not directly related to muscle attachments (no muscles insert into the torus) (Sakka 1972). However, it probably functions as an adaptation to stress on the posterior cranial vault generated in part by the nuchal muscles (Caspari 1991, Demes 1977, 1985, Plhak 1983, 1986, Weidenreich 1940). The expression of the nuchal torus in Neanderthals is variable, although it is weakly developed compared to many other fossil hominids (Jelínek 1972, Zhang, Potts 1994). It is bilaterally arched, and generally poorly expressed laterally (Hublin 1978a, 1978b). In many specimens the upper margin is obscure; the torus tapers off superiorly without a discrete superior border. In other specimens, such as La Chaise in *Figure 3*, there is a broad general area of thickened bone on posterior aspect of the occipital plane. Whether or not this constitutes a "true" torus, Neanderthal suprainiac fossae occur in this area on the occipital plane where the external table is thicker than in other places on the occipital bone. The fossa represents an indentation in the midst of this thickened area, and thus contributes to the shape of the nuchal torus and to the entire posterior aspect of the posterior cranial vault. Sometimes, it excavates the superior margin of a "true" torus, (i.e. a "band" of bone) and thus contributes to the "typical" bilaterally arched Neanderthal nuchal torus. In other cases the fossa occurs in the middle of the thickened area, so that the "torus" surrounds the fossa on all sides. Even in children, the suprainiac fossa occurs in an area of thicker bone; by excavating the centre of it, the suprainiac fossa contributes to the formation of a bilaterally arched torus in these children (*Figure 6*).

In sum, the Neanderthal suprainiac fossa occurs in an area of thicker bone and contributes to the bilaterally arched nuchal torus development associated with Neanderthals.

Gross structure

The major variant in gross structure is the degree of porousness, or "pocking" on the ectocranial surface. The Krapina specimens were seriated and scored (placed into one of 3 categories) based on degree of pocking (Caspari 2006). At Krapina, there is an association between the degree of pocking and age at death; younger specimens are more heavily pocked than older individuals. *Figure 6* exemplifies this; the juveniles, represented here by Krapina 2, are considerably more pocked than adults at Krapina (*Figure 4*). There is also variation in degree of suprainiac fossa pocking in adults, which may also be a reflection of relative age.

NON-NEANDERTHAL VARIATION: IS THE NEANDERTHAL SUPRAINIAC FOSSA UNIQUE?

The suprainiac fossa is known to occur in non-Neanderthals; Trinkaus (2004), for example, has described the suprainiac fossa of Eyasi 1, and discussed its implications for the differentiation and diffusion of Middle Pleistocene regional patterns. Post-Neanderthal suprainiac fossae have also been described, addressing the phylogenetic issues discussed above (Frayer 1993, Wolpoff 1999). Post-Neanderthal suprainiac fossa variation was assessed for several modern human samples including 14 adults from Pod, a Bronze Age site near Bugonjo, Bosnia-Herzegovina, osteological and dissection room samples, and the Early Upper Paleolithic crania from Mladeč, Pavlov, Brno, and Předmostí (Caspari 1991). At issue is whether the Neanderthal variants discussed and figured in the previous section occur in the modern human samples.

Size and shape

The suprainiac fossae in modern humans fall into two categories; the first is similar to that seen in Neanderthals,

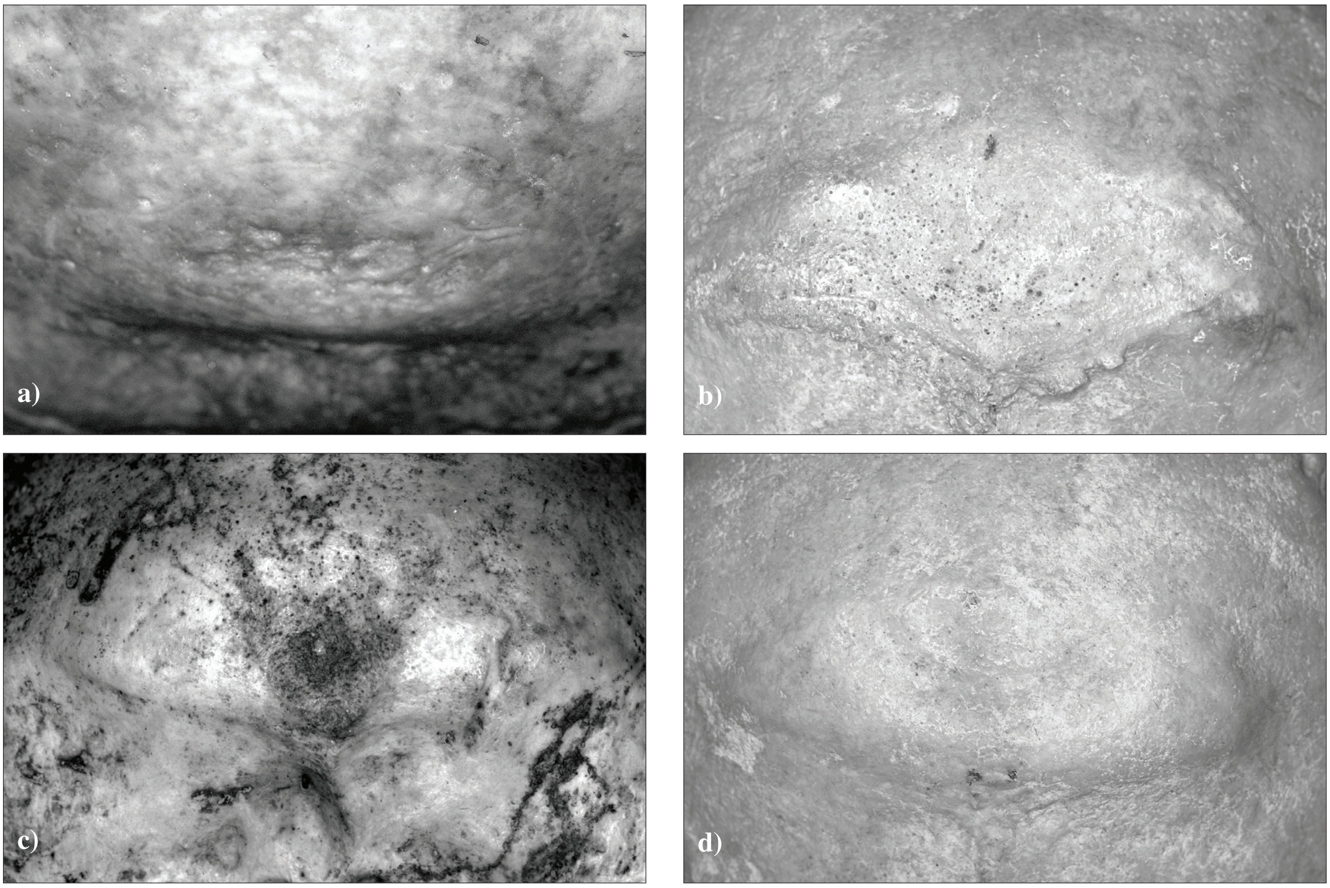

FIGURE 8. Examples of suprainiac fossa variation in adult modern (living) humans. The two crania above (a and b) are female, the two below are male (c and d).

but the other has a different form and is associated with well developed superior nuchal lines and external occipital protuberances, as discussed below. Following Sládek this form will be referred to as the supranuchal variety. *Figures 7* and *8* exemplify the first category expressed in juvenile and adult modern humans. The fossa is broad and transversely elliptical, resembling the fossa typically found in Neanderthals.

The supranuchal category is represented in *Figure 9*, which shows two crania from Pod with fossae common in robust individuals with strongly developed medial superior nuchal lines and external occipital protuberances. The suprainiac fossa shape differs from that typical of Neanderthals: its apex points inferiorly instead of superiorly, it is triangular in shape instead of elliptical, and its area is restricted, confined between the bilateral arches of the superior nuchal line.

Associated superstructures

The first category of suprainiac fossa described above resembles those of Neanderthals in their size, shape and gross structure (*Figures 7* and *8*). Like those of Neanderthals, these occur in areas of thicker bone on the occipital plane in both children and adults, which sometimes resemble a true nuchal torus.

The second form, the supranuchal variety, is clearly associated with superior nuchal line development and/or a well developed external occipital protuberance *(Figures 1* and *9)*, rather than with a nuchal torus (Caspari 1991). The superior nuchal line is not homologous to the nuchal torus; the latter is a buttress occurring above the superior nuchal line, a probable response to stress generated by second layer nuchal muscles (*semispinalis capitis*) which are very well developed in Neanderthals (Caspari 1991). The superior nuchal lines and external occipital protuberance of most Neanderthals are not well developed. In contrast, the well developed nuchal lines and external occipital protuberances seen in many modern humans are a response to stress generated by the first layer muscles and the *ligamentum nuchae*. The lines can be very thick, rugose and "torus-like," but they are the result of periosteal response to muscle action (especially the *trapezius* and the *ligamentum nuchae*, medially, and *sternocleidomastoid* laterally) causing bone formation directly under the muscle or ligament attachment. There is an area of resorption between the arches of the superior nuchal line in these cases, a depression, or fossa, above inion, whose shape is dictated by the morphology of the superior nuchal line. Similarly, there is frequently resorption above the external occipital protuberance, as shown in *Figure 9*.

Gross structure

As in Neanderthals, the suprainiac fossa is most pocked in children. *Figure 7* shows the suprainiac fossa in two modern children, aged 3 and 7 years, respectively. Both are markedly pocked. Some adult suprainiac fossae in modern humans exhibit pocking (*Figure 8*), although it is rarely as extensive as that found in children. Other adults exhibit no pocking at all: the surface of the suprainiac fossa is smooth. Like Neanderthals, this may be associated with age; all older adults observed have relatively smooth suprainiac fossa.

I have recognized two suprainiac fossa variants in modern humans, as described above. One form resembles those of Neanderthals; it shares the same gross morphology, it can be of similar size and shape and has the same superstructure correlates. The other, more common form is morphologically somewhat different, and is found in individuals with robust superior nuchal line development. There is no reason to question the homology hypothesis when the structures being compared are identical. For all criteria – form (shape), gross structure (degree of pocking), and associated structures – there are modern human suprainiac fossae that closely resemble the Neanderthal fossae, and these are likely homologous. However, questions remain about other variants of the suprainiac fossa. Is the variant most commonly associated with the superior nuchal lines of robust modern humans homologous to the Neanderthal suprainiac fossa? Exacerbating this issue is the fact that both forms can be found in the same population, including the early modern human sample from Mladeč.

THE QUESTION OF HOMOLOGY

Recognizing homology is an old but persistent problem. If a structure is identical in two closely related species, homology is usually assumed. In this case, structure and relationship are used to determine homology. If the morphology of a feature in two closely related species varies, the ontogeny of the feature is often examined to hypothesize homology. Testing the null hypothesis of homology for different suprainiac fossa forms therefore depends on development. In particular, given the variation in form, homology cannot be addressed unless the reason for the variation is understood. If all variations are caused by the same factors, I propose to treat them as homologous; if they are not, the null hypothesis may be challenged. Thus, testing hypotheses of development becomes an integral part of a test for homology.

Hypotheses of suprainiac fossa development

Trinkaus (2004: 28) recently expressed a general consensus that the suprainiac fossa "remains a morphological marker of unknown etiology." A few things, however, can be ruled out. The suprainiac fossa is not a site of muscle attachment. Dissection shows no muscle of consequence inserting in the suprainiac region. Only the epicranial aponeurosis is present, a structure so weak, supreme nuchal lines are rarely well developed. My experience is that in cadavers that exhibit suprainiac fossae, there is no indication of increased occipitofrontalis development, or more robust attachments in the suprainiac region.

The suprainiac fossa is also unlikely to be a simple genetic marker, although it has been treated as such. The structure appears regularly and its systematic variation

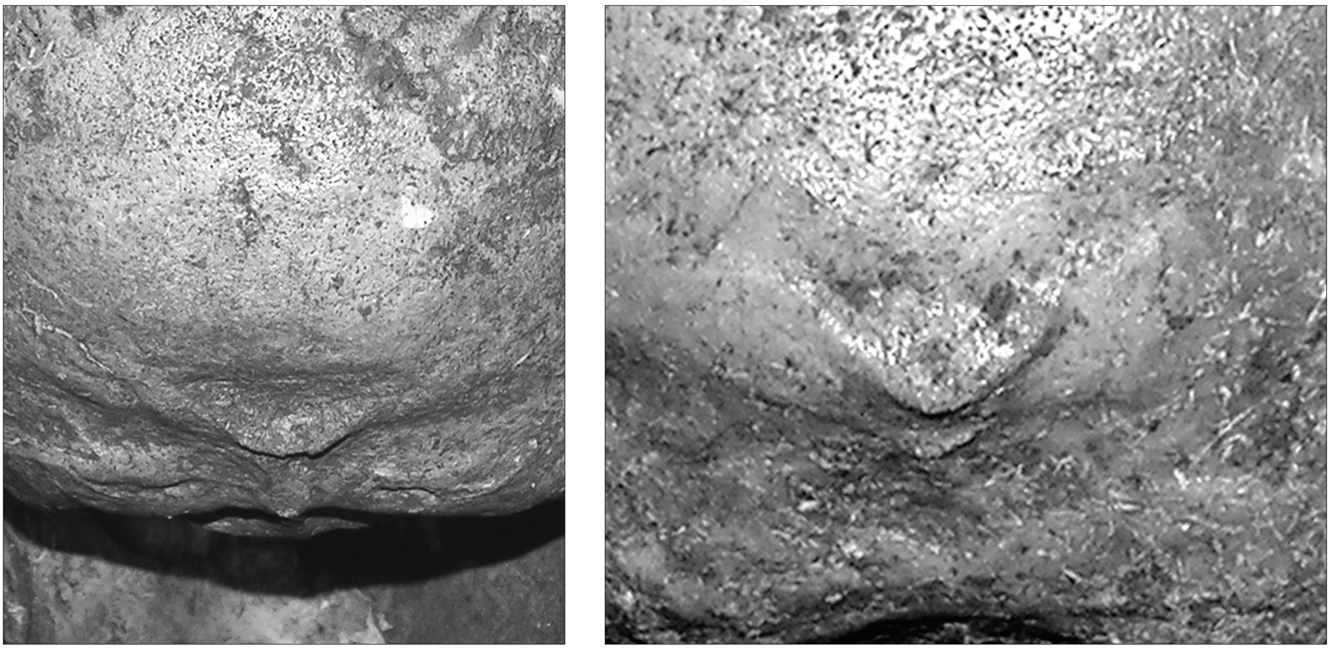

FIGURE 9. The supranuchal variety of suprainiac fossa shown on two specimens from Pod. This is a common expression in modern humans, associated with a well developed external occipital protuberance and/or the medial component of the superior nuchal line.

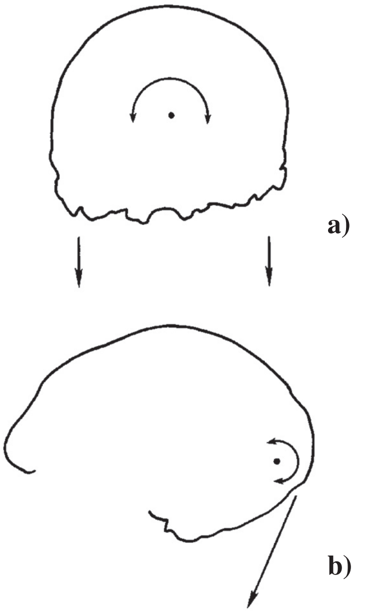

FIGURE 10. Forces generated by nuchal muscles cause bending around (at least) two axes. While the nuchal muscles cause bending around a coronal axis (below), the bilateral action of the major head extensors also create bending around a sagittal axis (above). While the torus resists both sets of stresses, the latter may account for the *configuration* of the torus (from Caspari, 1991).

associated with superstructure development suggests it is not simply a non-adaptive, neutral, genetic trait.

I hypothesize that the suprainiac fossa is best viewed as a consequence, or by-product, of the processes of cranial bone development and remodelling, on-going processes that initially occur in the foetal, infant and juvenile phases in the development of cranial shape. In adults, resorption above inion may also occur as a part of the remodelling process in the formation of cranial superstructures, whose development is mediated by mechanical stress. The suprainiac fossa is seen as a product of development, both ontogenetic remodelling and remodelling which occurs later in life as a result of different combinations of genetic factors and stress.

The suprainiac fossa is common and well expressed in infants and children (Heim 1982, pers. obs.). In infants and children the suprainiac fossa is a resorptive area that is a reflection of the developmental process that results in the occipital plane contour. As in all bone formation, this involves the remodelling process, a combination of deposition and resorption to achieve and maintain form. Similarities between the morphology of the suprainiac fossa and areas of developing foetal cranial bone in mammals suggest that the fossa may be a result of the processes that inform cranial shape. A number of researchers (e.g. Young, 1962, Hoyte 1966) have demonstrated ectocranial resorption in areas of maximum curvature in the developing crania of rats, rabbits and guinea pigs; this resorption results in the characteristic rounded cranial bones of the full term foetus. As best illustrated in Hoyte 1966, resorptive areas

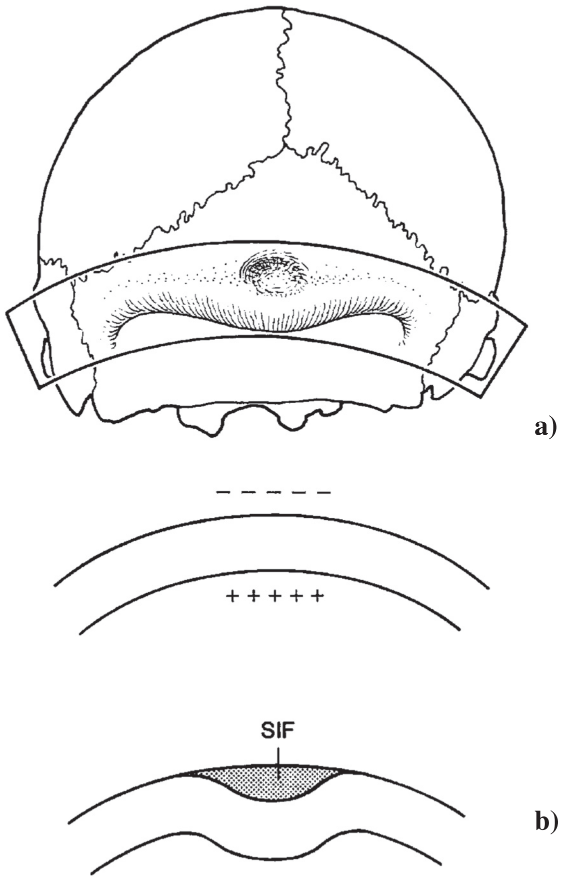

FIGURE 11. The nuchal torus can be represented as a bent beam (a), pulled laterally by the extensors around a fulcrum at the midline. A model of deposition inferiorly and resorption superiorly can explain the characteristic configuration of the Neanderthal torus (b). The structural curve at the midline forms where bending stresses are greatest. An alternative response would result in maximal development of the torus

in the developing cranial vaults were marked by Alzarin, and resemble the suprainiac fossa in both shape and structure. Depressions above inion are common in modern and Neanderthal children, and may be a reflection of this developmental process.

It is possible that the suprainiac fossa in adults is a retention of this juvenile trait. If so, there is probably a genetic basis for its retention and this may account for the high frequency of the suprainiac fossa in some populations. This would explain the "typical" suprainiac fossa described for Neanderthals and some modern humans above. However, it is unlikely to account for the morphologically different form of the fossa found in association with the superior nuchal lines of robust modern humans.

A second explanation is that the adult suprainiac fossa is a reflection of on-going remodelling processes associated with the development of superstructures and the maintenance of optimal cranial shape for mediating stress on the posterior cranial vault. This may account both for the "typical" suprainiac fossa found in Neanderthals and some modern humans associated with the nuchal torus

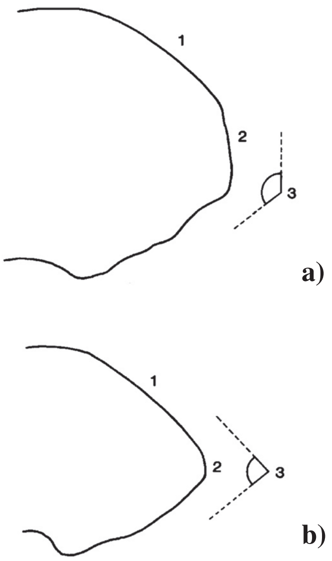

FIGURE 12. More and less optimal cranial shapes for minimizing strain engendered by nuchal muscles. The vertical orientation of the posterior cranial vault above acts to resist bending moments; stress is acting across a larger area, whose verticality increases its area moment of inertia and thereby its ability to resist stress without deformation. The suprainiac fossa can contribute toward more vertical orientation of the posterior vault (*Figure 3*) (from Caspari 1991).

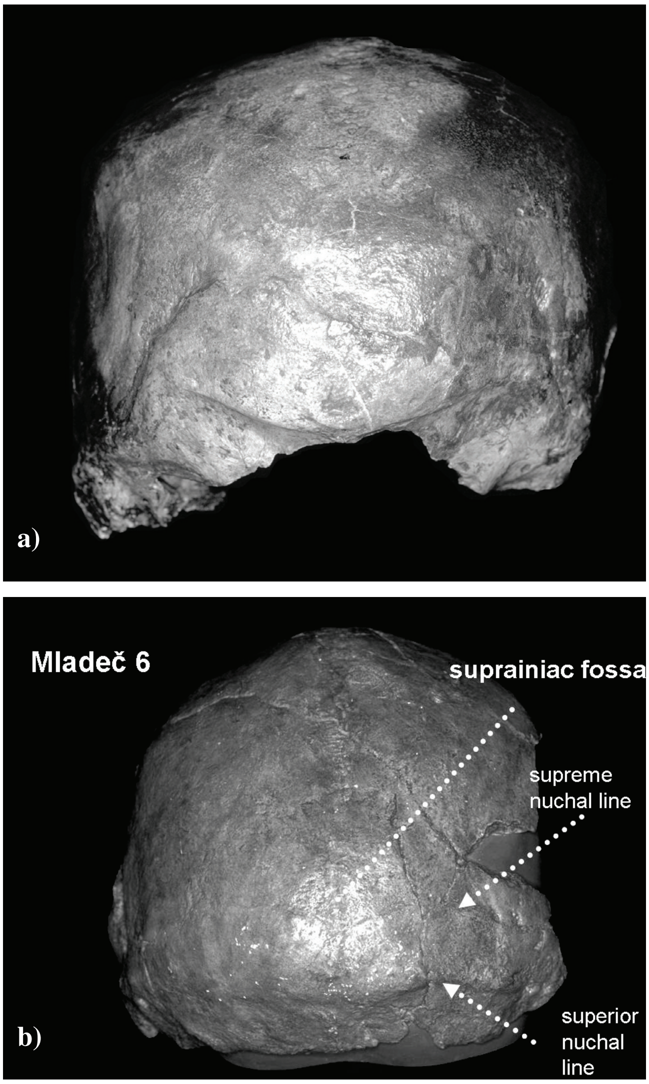

FIGURE 13. Occipital views of Mladeč 5 (a) and a cast of Mladeč 6 (b), with different patterns of superstructure and suprainiac fossa expression. Mladeč 5 exhibits a pronounced external occipital protuberance and superior nuchal line, while Mladeč 6 does not. Mladeč 6, however, does exhibit a faint suprainiac fossa above the nuchal torus.

(or area of thickened bone) and also for the form of the fossa associated with superior nuchal lines. In this case, different forms of the fossa are associated with different superstructures and different sets of mechanical influences and should not be considered homologous.

The two explanations for the expression of a Neanderthal-like suprainiac fossa in adults are not necessarily mutually exclusive: the retention of the juvenile condition and the remodelling explanation associated with skeletal adaptive response to strain may both occur. The common form of suprainiac fossa associated with the superior nuchal lines or external occipital protuberances of modern humans is likely caused by remodelling in adulthood associated with adaptation to strain. The stress on the posterior cranial vault may be different for Neanderthals and most modern humans because of different habitual activities and muscle use in conjunction with different cranial shapes. This could result in different superstructure development, and therefore different fossa expressions. Detailed below is the relationship between strain, superstructure development and suprainiac fossa formation.

The size and form of the suprainiac fossa is related to the bilateral expression of the Neanderthal torus, and I view it as related to nuchal torus formation in Neanderthals. The bilaterally arched configuration of the Neanderthal torus may occur as a consequence of bending around a sagittal axis (*Figure 10*). The nuchal torus can be pictured as a bent beam, pulled on the sides by the major extensors around a fulcrum at the midline. The dipping of the torus at the midline opposes and minimizes the bending stresses that are greatest in the iniac region (*Figure 11*). An alternative response to the increased stress at the midline could be increased deposition of bone at the midline (as seen in *Homo erectus*). The increased deposition, however, renders the cranial shape less optimal for bending around the *coronal axis* (*Figure 12*); it both decreases the angle between nuchal and occipital planes and also the area moment of inertia at the midline. In effect, this makes the occiput pointier, the shape that engenders resorption in the foetal development of cranial bone (Young 1962, Hoyte 1966). The alternative construction includes a bilateral torus and suprainiac fossa, an area of resorption which decreases the curvature of the posterior vault at the midline. The suprainiac fossa contributes to the structural curve of the torus, resisting stress at the midline *and* flattens the back of the skull, creating a more vertical contour to the posterior aspect of the occipital plane. This contour minimizes strain on the posterior cranial vault (Caspari 1991, 2006).

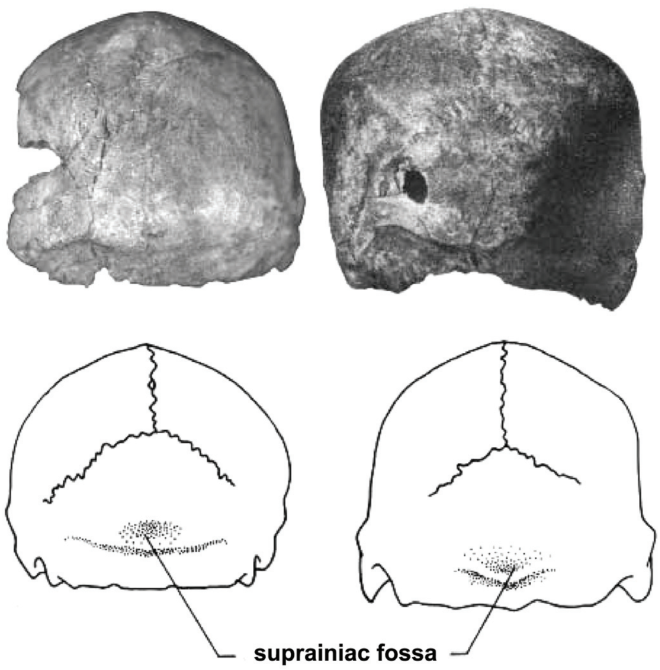

FIGURE 14. Mladeč 5 (right) and a cast of 6 in occipital view. Below them is a diagram showing the suprainiac fossa differences, comparing a Neanderthal (left) and the common Early Upper Paleolithic character state. Mladeč 6 has a weakly expressed suprainiac fossa similar to the Neanderthal condition, while Mladeč 5 lacks a Neanderthal-like suprainiac fossa. The Neanderthal suprainiac fossa is not homologous to the supranuchal variety of the fossa common in the European Upper Paleolithic. Nevertheless, both forms can be found in the Mladeč males.

Therefore it is reasonable to hypothesize that the suprainiac fossa forms in adults for much the same reason that it occurs in infants – to maintain optimal shape of the posterior cranial vault. Therefore, the adult form may not simply represent the retention of the juvenile condition. If true, the suprainiac fossa is the consequence of development; different forms of it may be associated with different developmental processes and are therefore not homologous. The Neanderthal form of the suprainiac fossa occurs in all Neanderthals and some modern humans (*Figures 7* and *8*). In infants and children this form is a consequence of attaining normal, rounded, cranial shape, a process that involves resorption of highly bossed regions of the cranial vault. In adults, the same morphology may reflect the repetition of this remodelling process with the development of cranial superstructures. The form of the suprainiac fossa associated with the superior nuchal line or external occipital protuberance of robust adult individuals is a product of the development of the rugose nuchal line, and may be explained by a bent-beam model of deposition and resorption. However, since the superior nuchal line is not homologous to the Neanderthal bilateral nuchal torus, the suprainiac fossa associated with its development is not homologous to the Neanderthal suprainiac fossa, even if a bent beam model explains both structures.

THE EXPRESSION OF THE SUPRAINIAC FOSSA IN THE MLADEČ MALES

The male crania from the Quarry Cave at Mladeč are pivotal to both the discussion of suprainiac fossa homology and to the question of Neanderthal ancestry for modern Europeans (Jelínek 1983). Mladeč 5 and 6 are both robust males, as is common in the Aurignacian and Gravettian associated males in Moravia. Yet they exhibit very different nuchal morphology. While Mladeč 5 has strong medial development of the superior nuchal line and external occipital protuberance, Mladeč 6 has a weakly developed superior nuchal line. However, unlike Mladeč 5, Mladeč 6 has a well developed nuchal torus. The two crania have different expressions of the suprainiac fossa as well. As shown in *Figure 13*, Mladeč 5 does *not* have a Neanderthal-like suprainiac fossa; while there is some resorption medially above the external occipital protuberance, this is the supranuchal variety of suprainiac fossa, and is not homologous to the Neanderthal fossa. On the other hand, Mladeč 6 has a small elliptical resorptive surface between the arches of the nuchal torus. Because the torus in Mladeč 6 is considerably taller than those of Neanderthals, the suprainiac fossa occurs well above the superior nuchal line, and well above inion. Nevertheless, it is associated with nuchal torus development and has the same morphology as the Neanderthal fossa and I consider it homologous to the Neanderthal structure (*Figure 14*).

CONCLUSIONS

Neanderthal suprainiac fossae are not autapomorphies: homologous forms are found in modern humans and in non-Neanderthal fossils. However, not all suprainiac fossae in modern humans are homologous. Suprainiac fossae of all kinds are associated with cranial development, whether ontogenetic or the development associated with the formation of superstructures, and may reflect the adaptive response to mechanical stresses that mediate both processes.

It is likely that the common form of the suprainiac fossa associated with robust modern humans, sometimes called the supranuchal fossa, is caused by remodelling in adulthood associated with adaptation to strain which results in rugose superior nuchal lines. However, there are two hypotheses for the expression of a Neanderthal-like suprainiac fossa in adults, both Neanderthals and modern, which are not necessarily mutually exclusive. First, it may be the retention of the juvenile condition; the suprainiac fossa is frequently found in infants and children, and I suggest it is a consequence of the process by which normal cranial shape is achieved. Second, the adult fossa may be caused by remodelling factors associated with skeletal adaptive response to strain incurred in adulthood. Like cranial development in infants, it affects points of maximum curvature, and is closely tied to torus formation. The form of the suprainiac fossa associated with robust morphology (the supranuchal fossa) is more common in modern humans and differs from the "typical" Neanderthal fossa although it is also the result of remodelling. Since the result is different superstructure development, and therefore different fossa expression, the two forms of the suprainiac fossa cannot be considered homologous.

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