The Le Moustier Adolescent:
A Description and Interpretation of its Craniodental Morphology

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Abstract: Although the fossilized remains of the Le Moustier adolescent have been known for almost a century, little has been written about them. In spite of war-time loss of most of the skeleton, parts of the skull, mandible, and upper and lower dentition did survive. For the first time, these non-postcranial elements are described in considerable detail. We also discuss the craniodental morphology of the Le Moustier adolescent in terms of the developmental emergence of Neanderthal characteristics and contrast these with Homo sapiens.

Introduction

From the very beginning, Neanderthals have both fascinated and frustrated paleoanthropologists. In spite of over 150 years of debate on just who Neanderthals are relative to ourselves, and to a wealth of known skeletal material, in some important ways we are still far from a consensus. Are Neanderthals their own species, *Homo neanderthalensis,* or just an archaic variant of ourselves, merely a subspecies at best? But although such diametrically opposed positions have persisted strongly through the decades, this does not also reflect a consistency of opposition. In spite of the clarity of King's (1964) case for recognizing the Feldhofer Grotto skull cap and bones as the remains of another species, *Homo neanderthalensis* (because it so obviously fell out of the range of variation of extant humans), it was Huxley's (1863) argument (that the very same specimen could be imagined as extending the range of human variation into the past) that attracted the greater numbers of sympathizers for well over a century. Why? In the last half-century at least, the answer lies in the extension of the dogmas of the evolutionary synthesis of the 1940s into the realm of human evolution. First is the notion that evolutionary change is a continually ongoing process of accumulating minuscule changes, driven by shifting means of expressed variability; and second, the attribution to humans and their ancestors of putative ranges of variability so extreme that diversification would essentially not be possible, largely because such variability would allow any hominid species at any point in time to occupy all available econiches (e.g. Mayr, 1950).

Because of these assumptions, the study of human fossils has largely been preoccupied with the discovery and demonstration of continuity between chronologically successive specimens, culminating in living humans. But such demonstrations are also dependent on the delineation of overlapping realms of seemingly similar ranges of morphological variability in time-successive forms. Thus "categories" of morphology are often perceived less in terms of the common denominator of a structure than in the degrees to which an anatomical region varies in the morphologies expressed in it. For example, the brow re-gions of Neanderthals and *Homo sapiens* are similar in that they can vary from one individual to the next in degrees of anterior protrusiveness and lateral thickening. Superficially this may seem to provide evidence of continuity between these two hominids – and, consequently that they are variants or morphs of the same species – but one can also similarly describe chimpanzees, gorillas, and even various species of New World monkey (see review by Schwartz, 1997). Within the range of individual variability, however, there is an underlying morphology that distinguishes the supraorbital configurations of chimpanzees, gorillas and those New World monkeys from one another, albeit to varying degrees.

In a series of papers (e.g. Schwartz, 1997; Schwartz & Tattersall, 1999, 2000s a,b,c; Schwartz et al., 1999), we stressed the importance of studying, whenever possible, the growth of features that are typically compared only after they are reached the adult stage. Although one's comparisons of fossil specimens are constrained by the vicissitudes of taphonomic processes and discovery, the typical use of adult specimens has, we believe, led to an artificial view of evolution and development that is reminiscent of Haeckel's biogenetic law (Schwartz & Tattersall, 2000 a). That is, the generally accepted procedure of lining up specimens chronologically in an evolutionary scala naturae leads to the incorrect perception that not only are evolutionary stages of morphs being illuminated, but so, too, are the developmental stages of morphologies.

Take, for instance, discussions of the "evolution of the human chin." When "the human chin" is seen merely as a bulge in the midline of the mandible, its supposed evolution may be traced from the flat and forwardly inclined symphyseal regions of some middle-late Pleistocene hominids (e.g. Arago 13), to symphyseal regions of other specimens that are either more vertical or appear to have a small "bulge" (e.g. Weimar-Ehringsdorf G, Regourdou), to yet others that have a more pronounced "bulge" and more symphyseal verticality (e.g. La Quina 9: Wolpoff, 1996). These variants are also seen as existing in the more chronologically and geographically restricted Krapina and Vindija specimens (ibid.). These claimed "trends" aside, however, the development of "the human chin" can only be appreciated when studying infants and juveniles. In this case, one sees that the symphyseal region of Neanderthals is initially flat and variably vertical, while that of *Homo sapiens* bears well-defined morphologies. In Neanderthals, differences in degree of verticality or flatness versus swelling of the symphyseal region emerge with growth of the individual. But in *Homo sapiens,* the specific morphologies of "the chin," which no adult Neanderthal has, emerge in the fetus and are retained to varying degrees of distinctiveness in the adult (Schwartz & Tattersall, 2000 a). Whatever symphyseal "bulge" an adult Neanderthal might

have, it is not evidence of an evolutionary trend toward the development of "the true chin," as in *Homo sapiens*. Clearly, as this example illustrates, it is inappropriate to conclude that a constructed sequence of fossils will reveal the evolutionary history of a feature. Equally clearly, it demonstrates the importance of understanding the development of any feature as an important part of the phylogenetic interpretation that one imposes upon it. It is, therefore, in this context that the Le Moustier individual, as an adolescent, takes on even greater significance for providing insight into the evolution of Neanderthals.

The craniodental remains

The postmortem history of the Le Moustier adolescent is an unfortunate one. Although it was a virtually complete skeleton when discovered in 1908, wartime bombing in 1945 burned the museum and destroyed most of the postcranial skeleton. The skull and mandible, although severely damaged (especially in the face), survived in large part because they had been kept apart from the rest of the skeleton. In light of Stringer et al.'s (1984: 100) comment − "[a] new study of this fossil is required" − we provide here a description and then a discussion of the craniodental remains, both of which we hope will help to fill this lacuna.

Description

The preserved cranial remains now consist of a largely complete frontal; most of the left temporal bone with adjacent pierces of parietal, occipital and alisphenoid; most of the right temporal bone with large adjacent pieces of occipital; a right partial parietal bone to which a large piece of left parietal is glued; a fragment of the basiocciput and a piece of adjacent right occipital bone; a fragment of the sphenoid (the particular side is unclear); part of the palate with the left I^1 missing; most of the mandible, which is in two pieces and preserves all teeth but lacks the left coronoid process. There are various other bone fragments that are much less mineralized than these pieces, and would seem not to be associated with them.

The cranium is lightly built and its bone is quite thin; the cranial vault sutures are closed endocranially and the lateral vault sutures are closed inside and out. The basiocciput appears to have begun to close. The upper and lower molars would all have broken through the gum. As is indicated by a minimal development roots, the M^3s appear to have been in the process of erupting. The M_3s, at least, look impacted. The C_1 is impacted and lies beneath the root of I_2.

The frontal fragment quasi-articulates with the parietals behind. A series of marks on the frontal, the same coloring as the surrounding bone, may be cutmarks; most notably there are two long, parallel incisions that run obliquely and are cut at an opposite angle by shorter parallel incisions. In general shape, the cranium appears not to have been very long in profile. There is a moderate slope along the frontal that levels out well before bregma The top of the braincase is quite flat. Well above lambda, the back of the skull descends gently to reach its posteriormost extent just above the suprainiac depression. Viewed from above, the top of the skull is broad; in coronal section, the braincase is somewhat square, with relatively straight side walls that complement the somewhat flat top. The greatest width occurs far back, just behind the mastoid processes and quite far down on the side of the braincase.

The supraorbital tori are low, double-arched, and quite short superoinferiorly. They are thickest as they emerge from the glabellar region, and thin superoinferiorly towards the midline of the orbits; more laterally, they maintain a low, constant height. The tori are confluent across a very broad, swollen glabellar region. They curve smoothly backwards from the superior orbital margins, and the roofs of the orbits smoothly angle into them. Viewed from above, the anterior profile of the tori is concave; their axes angle back from midline. The superior orbital margins are rounded from side to side, indicating that the orbits would originally have been ovoid and not wide. The left frontal sinus is exposed. It extended posteriorly above the region of glabella and terminates laterally well before reaching the midline of the orbit. In its natural orientation, and in profile, the frontal shows a slight depression above and behind the supraorbital tori, especially laterally. Behind the depression, the bone rises obliquely. About midway to bregma, the plane of the frontal bone becomes more horizontal. Viewed from the front, there is a moderate lateral curvature across frontal plane. Postorbital constriction is minimal. There is only a slight scar, rather than a temporal ridge, which first rises from behind an apparently short frontal zygomatic process and then courses gently upward. Nasion is situated quite high up on glabella, and the peaked frontonasal sutural surface was quite tall superoinferiorly. It appears that the coronal suture, which is preserved in three places, was uniformly denticulate. Internally, the frontal crest is low and not very long, but well defined. The frontal lobes protruded quite far forward above the orbital cones.The palate is heavily reconstructed and reconstruction material obscures its upper surface. Underneath, it appears that the palate was shallow. Its preserved walls slope gently on all sides.

As preserved on the left side, the squamous portion of the temporal bone is long, but not high-rising (apparently reaching its highest point quite anteriorly). There is a distinct "corner" along the anterior extent of the squamosal suture. The inferior part of the alisphenoid is not angled, but instead curves in toward the basicranium; thus, a distinct infratemporal fossa is not formed. An indistinct parietal notch is preserved on the left side. The parietomastoid suture is relatively long, and somewhat horizontal. The lambdoid suture rises steeply from region of asterion, without an "anterior lambdoid" suture (Schwartz & Tattersall, 1996). The posterior root of the zygomatic arch originates well in front of a very small, compressed acoustic meatus; the arch is minimally laterally flared. The low, upwardly curving suprameatal crest is confluent with the supramastoid crest, which, in turn, continues the curve upwards. As preserved on the right side, there is a low, barely distinct vaginal process lying along the midline of a relatively short ectotympanic tube. The vaginal process peaks slightly

around an apparently thin styloid process (which left its impression on the vaginal process) that lay quite medial to the meatus. The vaginal process fades out well medial to the acoustic meatus. The relatively small stylomastoid foramen lies posteriorly, at the base of the preserved styloid pit. The ectotympanic tube is separated by a broad notch from the base of the mastoid process. The articular fossa is quite wide, relatively deep, and moderately long anteroposteriorly; it is bounded anteriorly by a low articular eminence and medially by a rather small, distinct medial articular tubercle. The postglenoid plate is wide mediolaterally and appressed to the ectotympanic tube.

The mastoid process is more complete on the left, but its downward-pointing tip is broken. This process is not very long anteroposteriorly, and it does not appear to have projected very far. The broken right supramastoid process reveals many small air cells and only a few large ones, and it seems probable that it would have protruded beyond the occipitomastoid crest. The small, oblique supramastoid crest is level with the top of the acoustic meatus. The mastoid notch is fairly vertically oriented and appears to have been quite shallow, but moderately wide. This notch may have been bounded medially by a paramastoid crest. On the right side, there is an indication of a low occipitomastoid crest, while on the left side, the bone protrudes beyond the level of the occipitomastoid suture on each side.

The steeply rising lambdoid suture arcs smoothly across lambda; both it and the sagittal suture are minimally denticulate, and neither is segmented. A small ossicle in the right parietal lies very close lambda. The occipital plane is relatively small, and is somewhat wider than it is tall superoinferiorly. Like the parietals, the superior part of the occipital plane is fairly flat across from side to side; superoinferiorly, this plane begins to arc down and forward just above the suprainiac depression, which lies high on the occipital surface. Most of the suprainiac depression is preserved; it is wide and tall, with a generally elliptical shape and a shallowly concave, coarsely pitted surface. The superior nuchal line, which corresponds to the "occipital torus", is poorly defined. It is oriented more or less horizontally and is delineated below only by a very shallow infratoral sulcus.

The preserved fragment of cranial base includes most of the basiocciput and a portion of the lateral part of the occipital. The sphenooccipital synchondrosis was not fused. The basiocciput is broad from side to side, relatively thin, and its external surface quite flat. The damaged occipital condyle was situated quite anteriorly on what appears to have been a very wide, possibly long and ovoid foramen magnum. The postcondylar canal is not patent, but the condyloid canal is.

Internally, the petrosals are very wide. There is a well-developed arcuate eminence, and, as better preserved on the right side, more laterally another elevation of the superior surface. Also on the right side, there is evidence of a superior petrous sinus, while the subarcuate fossa is represented solely by a tiny depression. The sigmoid sinuses are short bilaterally, the transverse sinuses are quite long, and the superior sagittal sinus is quite indistinct.

The mandibular corpora are not very deep or thick.

Missing bone exposes the roots of all anterior teeth; the inferior surface is preserved. The front of the jaw is moderately broad and moderately arced from side to side. The symphyseal region is completely smooth and is essentially vertical anteriorly, curving only fractionally back to inferior border. As seen from below, the symphyseal region is uniformly thick anteroposteriorly. The wide and well-excavated digastric fossae face down; on the left side, a thick, blunt inferior tubercle lies under P_{1-2}. Anterior to this tubercle, and around the preserved symphyseal region, the inferior margin of the jaw is elevated. On both sides, there are two small mental foramina, one under P_1 and the other between P_{1-2}.

Internally, there is virtually no postincisal plane; the posterior symphyseal surface essentially vertical and bears no indication of genial tubercles or pits. The mylohyoid line is very oblique, and only moderately marked; the submandibular fossae are very shallow. On the left side, the broken mandibular foramen appears to have been compressed and oriented obliquely up and back. As seen on the right side, a very low pillar runs down the midline of coronoid process, which overhangs a well-defined preangular notch. The right gonial region is better preserved; the angle is a broadly open arc that curves smoothly into a posteriorly leaning posterior margin that is straight (reflected neither internally nor externally) and relatively smooth on both medial and lateral surfaces. There is no medial pterygoid tubercle, only a faint muscle scar in that region. The ramus itself is short superoinferiorly and relatively long anteroposteriorly, with a very long, shallow sigmoid notch that levels out posterior to the anteroposteriorly long and superiorly broadly blunt coronoid process and then runs horizontally to the base of the much lower condyle; thus the notch is lowest just in front of the condyle. The sigmoid notch crest runs to lateral to the midline of the condyle and terminates well below the articular surface.

The upper dentition is complete except for the left I^1. None of the teeth is greatly worn and the enamel on all is wrinkled to some extent. The reserved right I^1 crown is tall and very wide; wrinkling is manifested in longitudinal grooves on the lingual surface that run from the shallowly concave inferior portion to the tall, broad lingual swelling at base. The I^2s are narrow, very tall, and barrel shaped on their lingual surfaces, which bear distinct internal pits in front of tall lingual swellings; longitudinal grooves run from the lingual margin to the pit; the buccal surface arcs inward. The Cs are tall and rather narrow, with very long, steep distal slopes. Internally, each bears an almost free-standing, spike-like lingual tubercle; a stout keel with thin grooves on either side runs down to the tubercle from the mesially offset apex.

The upper P^1s are slightly smaller mesiodistally than the P^2s. Each has a well-developed paracone and a shorter, slightly mesially positioned protocone. A stout mesial crest between these two cusps encloses a small anterior fovea. A thicker distal crest encloses a slightly larger fovea; this crest swells distal part of the tooth somewhat on P^2. Also on P^2, the notch between the internal surfaces of the protocone and paracone is wider than it is on P^1.

On the left side, the upper molars increase in size M^1–M^3;

on the right side, the M^2 and M^3 are subequal in size. On the M^{1-2}s, the postprotocrista is stouter than the preprotocrista; the latter runs mesially around the face of the paracone. Especially on M^{1-2}, the base of the protocone is expansive buccally and intrudes on the deep, truncated trigon basin. All upper molars bear distinct a hypocone, which is most swollen distolingually on the M^1 and decreases in size M^1-M^3. Enamel wrinkling increases from M^1-M^3. Both M^1s bear a distinct pit on the mesial surface of the protocone. The molar metacones, which lie close to the larger paracones, decrease in size distally from M^1-M^3.

Except for the retained left dc_1, the lower teeth are not very worn. As in the upper teeth, the enamel of all lower teeth is wrinkled to some extent, with the incisors and the right canine being grooved lingually. All incisors are tall crowned and bear a vertical keel along the midline that terminates in a small lingual swelling at the base. The lower right canine is tall crowned, with a short, steep distal slope, and it bears a broader lingual pillar than do the incisors. The left lower canine is impacted at an angle below and overlapping the left I_2 root. The P_1 is smaller than the P_2; both have somewhat swollen buccal sides. On P_1, a stout crest runs from the moderately tall protoconid to a much shorter, peaked lingual swelling. A thick crest runs mesially from the apex of the protoconid to the base of a lingual swelling from which, as is better seen on the left, it is separated by a groove; this crest encircles a thin, deep fovea. Also on P_1, a stouter distal crest courses from the protoconid to become confluent with the lingual swelling and enclose a larger posterior fovea. The lower P_2s are narrower mesially than they are distally; the protoconid and the almost subequal metaconid lie close together, and a mesially arcing, short, stout crest between these cusps encloses a small anterior fovea. The distal part of P_2 is much larger, with a strong, relatively long crest running distally from the protoconid and turning back to meet the metaconid. In the distolingual corner of the crown, this crest is distended into an entoconid, and centrally it expands into a cusplike structure. The distal structure is more talonid basin- than posterior fovea-like.

The lower molars are essentially subequal in size. All bear a distinct, buccolingually broad trigonid basin that lies anterior to the widely separated protoconid and metaconid. All lower molars bear distinct a hypoconulid, which lies just buccal to the midline of the tooth, and a long, relatively wide talonid basin. On all, a stout crest runs mesially from the hypoconid into the center of the talonid basin. In occlusal view, the lower molars crowns are quite rounded, especially distally, giving a generally ovoid shape to the teeth. Enamel wrinkling increases in complexity M_1-M_3.

Discussion

Since the Le Moustier individual has historically been identified as "Neanderthal", the question that arises is: On what is this determination based? An obvious answer is that the site, Le Moustier, is the type site for the Mousterian, and "Mousterian" is typically used synonymously with "Neanderthal," at least in Western Europe.

But, since it is becoming clear that not all specimens identified as Neanderthal are associated with a clear-cut Mousterian technology (in fact, not all specimens are associated with tools at all), and technology is not relevant to a systematic analysis based on morphology, we must turn to the latter.

Among the craniodental features that have been suggested as "defining" Neanderthal are: cranial bone thicker; cranial vault long and low; face relatively large and puffy; nasal bones markedly projecting; snout and jaws anteriorly displaced (indicated in the mandible by a retromolar space between M_3 and the ascending ramus); supraorbital torus double-arched and arcuately continuous across glabella; frontal sinuses expanded laterally throughout the supraorbital torus; nasal aperture extraordinarily large and nasal cavity expansive; chin poorly developed or lacking altogether; occipital torus uniformly thick (not segmented or medially elevated), horizontally oriented, and well-delineated above and below; suprainiac depression pitted and circumscribed by a raised margin; occipitomastoid crest at least as prominent as mastoid process; anterior mastoid tubercle present; vaginal and mastoid processes not in contact; styloid process medially emplaced; medial pterygoid tubercle large; sigmoid notch deepest posterior to its midpoint; and sigmoid notch crest laterally terminating on mandibular condyle (e.g. Howells, 1973 a, b; Hublin, 1978; Rak, 1998; Rak et al., 1994; Santa Luca, 1978; Stringer & Andrews, 1988; Stringer et al., 1984; Vandermeersch, 1981).

With regard to general cranial shape and bone thickness, this is recognized as being variable in Neanderthals (see review and citiations by Schwartz & Tattersall, in press) Since the Le Moustier individual was a subadult, its thin cranial bone does not add to the picture. Further, regardless of whether there would have been significant changes in overall shape with growth (a possibility we regard as remote), its apparently not very long cranium can be accommodated in with the range of variation known for adult Neanderthals [cf. Krapina, Amud, Guattari (Monte Circeo)]. Since Neanderthal children (e.g. Roc de Marsal, La Quina 5, Engis) had relatively low crania, and thus differed from the typically quite rounded configuration seen in the juveniles of extant anthropoids (Schwartz, 1997), it is reasonable to suggest that "low cranial profile", as seen in the Le Moustier individual, is derived for Neanderthals. Although the height of the crania of adult Neanderthals may vary (cf. Krapina C and La Chapelle-aux-Saints) (e.g. Wolpoff, 1996), it is not unreasonable to consider the entire range variation as being consistent, especially since it appears that the state, "low cranium", characterizes known juveniles. If, however, one were able to describe some Neanderthal crania as relatively "rounded", this configuration would have resulted from an alteration of the low cranium of the juvenile – in which case, this would certainly be a derived state, especially in comparison to most anthropoids.

It is unfortunate that the facial skeleton of the Le Moustier cranium is now missing, and that there was never a reliable reconstruction of the whole skull (Boule & Vallois, 1957), because the development of a "puffy" face (due to extreme

expansion of the maxillary sinuses) does emerge as a potential apomorphy of Neanderthals (cf. Arsuaga et al., 1993, 1997; Trinkaus & Howells, 1979). It is also impossible to assess directly the degree of anterior displacement of the snout. But since the lower facial region of specimens of young Neanderthals is not projecting, and the mandible of the Le Moustier adolescent is not fully grown in all dimensions (as demonstrated by the incomplete eruption of the M_3s and the concomitant absence of a retromolar space), it is likely that the snout of this adolescent Neanderthal had not achieved the degree of anterior facial displacement that is so uniquely developed in adult Neanderthals.

The feature "large" face describes not only Neanderthals, but also most middle-late Pleistocene European and Near Eastern specimens attributed to *Homo* (ibid.; Wolpoff, 1996). Thus this characteristic does not uniquely distinguish the former taxon alone. Further, lack of the lower face of the Le Moustier adolescent makes impossible an assessment of the size and shape of the nasal aperture as well as of nasal cavity structures. Although "large" nasal aperture also describes other middle-late Pleistocene hominids (e.g. from Sima de los Huesos and Steinheim), and is thus potentially apomorphic for a larger-than-Neanderthal clade (Schwartz & Tattersall, 1999; Schwartz et al., 1999), the presence of a well-developed medial projection of the wall of the nasal cavity just behind the aperture appears to be a viable Neanderthal apomorphy, as does the invasion into the nasal cavity of the medial walls of the maxillary sinuses (Schwartz & Tattersall, 1999, 2000 b, in press; Schwartz et al., 1999). The intrusion into the Neanderthal nasal cavity of these various structures obviates the description of this cavity as "expansive."

The configuration of the supraorbital region has been taken to be one of the most distinctive features of Neanderthals (e.g. Stringer et al., 1984), while the range of variation in its expression has led others (e.g. Wolpoff, 1996 and references therein) to see it as "transitional" towards *Homo sapiens*. In general, specimens from Europe and the Near East that have broadly been accepted as "Neanderthal" can be described as having a "double-arched" torus that is continuous across glabella, while extant *Homo sapiens*, and Holocene and some late Pleistocene specimens of *Homo*, have a "bipartite" brow (e.g. Stringer et al., 1984). In detail, supraorbital thickening in Neanderthals is continuous across the orbit with the torus tapering laterally. The configuration in *Homo sapiens*, however, consists of a medial portion (including glabella) that is "wing-" or "butterfly"-shaped, and is distinguished at the region of the infraorbital notch/foramen from a flattened and more inclined lateral portion (Schwartz & Tattersall, 2000 a, b, 2002). Where diminution of supraorbital distension has been the focal point of comparison, then specimens such as those from Vindija with thinner tori than is typical of Neanderthals, and some *Homo sapiens* with a greatly enlarged supraorbital region, have been seen as variations that grade into one another (e.g. Wolpoff, 1996 and references therein). If, on the other hand, the development of Neanderthal and *Homo sapiens* supraorbital regions is taken into consideration, the differences between these hominids become clear (Schwartz & Tattersall, 2000 b).

The common condition among juvenile extant anthropoid primates is for the supraorbital region to be unadorned, with taxon-specific morphology later emerging upon this essentially blank substrate (Schwartz, 1997). Thus, the bar-like torus of the baboon-mandrill clade, the anteriorly and superiorly projecting torus of the African apes, the projecting rims of hylobatids, the orbit-rimming mounds of the orangutan, and the glabellar "butterfly" with platelike lateral parts of *Homo sapiens*, take on their particular morphology with growth (ibid.). Cranial remains of juveniles in the human fossil record are scarce. Fortunately, there are a few well-preserved skulls of Neanderthal children aged 3–4 years old, and they demonstrate that this hominid also lacked any supraorbital embellishment at this stage of growth (Schwartz & Tattersall, 2000 b). By the age of 5 years or older, as witnessed in the La Quina Neanderthal child, the area from the gently bulbous glabellar region to more than midway along the superior orbital margins has begun to swell out as a continuous feature (Schwartz & Tattersall, 2000 b).

As seen in the Le Moustier adolescent, the continuous glabellar-supraorbital swelling has become uniformly more pronounced, even to expanding the supero-inferior height of the lateral extremities of the brow. Given the latter aspect of supraorbital development, it is likely that the adult morphology the Le Moustier adolescent would have achieved would probably have been similar to Guattari 1, Gibraltar 1, La Ferrassie 1, and La Chapelle-aux-Saints: i.e. the brow would have been relatively tall supero-inferiorly throughout its length, with some tapering laterally. The generally thinner and less-common brow configuration, as seen in Vindija Neanderthal specimens, is more reminiscent of the phase of development represented by the La Quina child, and thus probably reflects a more hypostotic (and/or neotenic) growth pattern in these Croatian individuals than is typical of other known Neanderthals.

With regard to frontal sinus enlargement, our study of virtually every known Neanderthal specimen (Schwartz & Tattersall, 2002) reveals that one cannot characterize Neanderthals as uniformly presenting a laterally, or superiorly, expanded sinus. In parallel with what one finds in *Homo sapiens*, Neanderthals are quite variable in this regard. Consequently, while we can assume that frontal sinus enlargement in the Le Moustier adolescent may have continued farther than we now see, this information would not contribute to a definition of "Neanderthal" on the basis of apormophy.

The occipital region has been the focus of some discussion of the delineation of specifically Neanderthal traits. With regard to the configuration "occipitomastoid crest at least as prominent as mastoid process", we have elsewhere suggested that this is an invalid character because of lack of comparability among published studies in the identification of this structure. Even a loose translation of "occipito-mastoid crest" (a crest that lies medial to the mastoid notch, but not as far medially as Waldeyer's crest) does not make this a relatively constantly expressed feature

(Schwartz & Tattersall, 1996). For consistency's sake, an occipitomastoid crest should only be defined as a structure that lies along the occipitomastoid suture. A crest medial to this suture would be a paramastoid crest. These definitions aside, Neanderthals are not characterized by pronounced development of any one crest.

The characterization of other features – "occipital toru" uniformly thick (not segmented or medially elevated), horizontally oriented, and well-delineated above and below; suprainiac depression pitted and circumscribed by a raised margin" (see references cited above) – has unfortunately not been entirely accurate. To begin with, Neanderthals do not have a true occipital "torus" in the sense that a torus is a barlike extension of bone. Instead, a "feature" in this region emerges as the result of the nuchal plane undercutting the occipital plane and thus offsetting posteriorly to some extent the "juncture" between these two planes. This "juncture" essentially corresponds to the superior nuchal line (Schwartz & Tattersall, 2002). The undercutting of the occipital by the nuchal plane creates an "infratoral sulcus" that defines, by default, an essentially horizontal "structure" that is variably straight and of variable width across the occipital plane. The suprainiac depression, which is of variable size and symmetry among Neanderthals, defines the upper boundary of this pseudotorus, but only to the extent the depression is expanded laterally (ibid.). Although we have found that suprainiac depressions are indeed pitted to some extent, they are not circumscribed by a raised margin (ibid.). Consequently, neither the inferior border nor the shorter superior border of the occipital "torus" is crisply delineated.

With regard to the Le Moustier adolescent, the occipital "torus" is poorly defined inferiorly, being delineated below only by a very shallow infratoral sulcus. The suprainiac depression, however, is rather large, with a coarsely pitted surface. This apparent "reverse" of the configurations typical of adult Neanderthals is also seen in some Neanderthal children (e.g. from Engis, Teshik Tash), but not in all (e.g. from Roc de Marsal, La Quina) (Schwartz & Tattersall, 2002). Thus, while the degree to which the suprainiac depression is excavated and expansive may vary among children, adolescents (represented by Le Moustier), and adults, it is apparent, whether or not the cause is bone resorption (Caspari cited in Wolpoff, 1996: 659), that this feature is present from a very early stage onward in Neanderthals. In contrast to this is the situation in *Homo sapiens*, in which, in infants, children, adolescents, and adults, the details of a Neanderthal-like suprainiac depression do not develop (Schwartz, 1995). This is not to say that the occasional adult specimen does not have a "depression" in the midline of the occiput. Rather, that the position (generally in the region delineated below by the downwardly peaked and sometimes prominent external occipital protuberance) and morphology (typically small, rimmed or circumscribed at least inferiorly if not throughout, and perhaps sclerotic) of an occipital depression in *Homo sapiens* is not comparable to the Neanderthal suprainiac depression. The so-called suprainiac fossa seen in a few specimens of late Pleistocene *Homo sapiens* (most notably from Mladeč and Předmostí) (e.g. Wolpoff, 1996)

is spatially and morphologically recognizable as the occipital (supra-external occipital protuberance) depression of other *Homo sapiens* and should not be "homologized" with the differently and uniquely configured, and consistently present, suprainiac depression of Neanderthals.

A *"Homo sapiens"*-type occipital depression, with its attendant morphologies, is also found in other hominid specimens, most notably the Petralona skull (Schwartz & Tattersall, 2002). Given this shared feature, it could be either a synapomorphy or independently achieved autapomorphies of *Homo sapiens* and these other hominids. If, as has been suggested (e.g. Arsuaga et al, 1993, 1997; Santa Luca, 1978), the Petralona individual and other middle Pleistocene hominids (e.g. from Sima de los Huesos, Kabwe, Arago, Bodo) can be united with Neanderthals in a larger clade, the conclusion would be that this feature was independently derived.

A configuration resembling the Neanderthal suprainiac-"toral" region is seen in the Steinheim cranium: the "torus" (region of the superior nuchal line) is undercut by the nuchal plane and, although weathered, the surface above inion hints strongly at the presence of a suprainiac depression. Given the apparent synapomorphies seen in this specimen and fully apomorphic Neanderthals, it seems that the configuration of the occipital would be another shared derived feature uniting Steinheim with Neanderthals as sister taxa (Schwartz & Tattersall, 1996).

As we have detailed elsewhere (Schwartz & Tattersall, 1996), the presence of a mastoid tubercle is not represented consistently enough in Neanderthals to be considered apomorphic of them. Thus, the absence of such a feature in the Le Moustier individual, although of interest in terms of documenting variation in Neanderthals, is phylogenetically irrelevant. On the other hand, the character states "lack of contact between the vaginal and mastoid processes" and "medial position of the styloid process" are so widespread among hominids that they are surely primitive within the clade (ibid.). As such, the similarly configured Le Moustier individual would be plesiomorphic in these character states. The presence of a low and barely distinct vaginal process is consistent with the young age of the individual. But also, given the apparent youth of this individual, the disposition of the vaginal process suggests that it probably would not have become markedly larger with growth or have extended much farther laterally toward the acoustic meatus. These considerations, in concert with the fact that this process lies along the midline of the ectotympanic tube, indicate that it would not have come into contact with the mastoid process in adulthood.

With specific regard to the mandible, the symphyseal region of the Le Moustier individual, although that of an adolescent, is clearly distinguished from that of *Homo sapiens* (Schwartz & Tattersall, 2000 a; Zollikofer et al., 1995). As seen in the preserved symphyseal region of Neanderthal mandibles, including those of children, in inferior aspect, it is uniformly thick from front to back. The symphyseal region of *Homo sapiens* of all ages, however, is the thickest part of the corpus (ibid.). In further contrast, the anterior face of the Le Moustier symphyseal region is completely smooth and lacks any morphology of note, as

is typical of all younger Neanderthals as well as adults. In adult *Homo sapiens,* the symphyseal region bears a variably pronounced midline keel that fans out inferiorly into a variably swollen and triangular feature that is variably wide along the inferior margin; the lateral "termini" of this swelling may be thickened or "tubercle"-like, and on either side of the midline keel there are variably depressed fossae (see review by Schwartz & Tattersall, 2000 a). But this range of individual variability in adult *Homo sapiens* derives through normal processes of bone deposition and resorption from a much more consistent and blatantly expressed configuration that is seen early in the fetus: strongly everted symphyseal margins that are confluent with everted inferior margins, with deep fossae on either side of the midline (ibid.). The single midline keel emerges with fusion of the symphysis, and postnatal growth brings a softening of these crisply defined features. As to which represent the apomorphic character states, we suggest they are those developed in *Homo sapiens*. The configurations seen in the Le Moustier adolescent, because they are widespread among specimens assigned to the genus *Homo,* would appear to be primitive retentions in Neanderthals (Schwartz & Tattersall, 2002).

With the obvious exception of the Le Moustier adolescent, the character "medial pterygoid tubercle large" is otherwise ubiquitous among specimens of, and clearly distinctive of, Neanderthals (Rak et al., 1995; Schwartz and Tattersall, 2002). One might suggest that the presence of only a scar in this region in the Le Moustier mandible is due to the individual's relatively young age, but a large medial pterygoid tubercle is seen in Neanderthal children, including the 18 month old from Amud (Rak et al.,1994). As for Neanderthals having the deepest point of the sigmoid notch lying posterior to its midpoint and the sigmoid notch crest terminating laterally on the mandibular condyle, the Le Moustier individual does fit this description.

Conclusions

Although the features we listed earlier are typically cited as being distinctive of Neanderthals, a closer look at their development and distribution among specimens, and even the accuracy of cited configurations, yields a list of fewer potential Neanderthal apomorphies. Nevertheless, regardless of their absolute number, because they do appear to be derived character states they certainly distinguish a hominid we should refer to as *Homo neanderthalensis*. Since some of these apomorphies are also present in the preserved elements of the Le Moustier adolescent, they can satisfy the question we posed at the beginning of our discussion: Why is Le Moustier a Neanderthal? Unfortunately, without evidence from the facial skeleton, we are left with very few potential Neanderthal apomorphies. One apparent derived feature is the undercutting of the occipital by the nuchal plane with a distinct infratoral sulcus delineating a true and well-developed suprainiac depression above. The development of any form of a suprainiac depression is not confined to Neanderthals alone, however. Witness the Steinheim specimen, which seems to have had a weakly developed depression. "Double-arched" brows

with smoothly rolled anterior surfaces would also appear to describe the Steinheim specimen as well as Neanderthals, but the emergence of this characteristic in the Le Moustier adolescent at least suggests that it belonged to this clade. Two other features, also found in the Le Moustier adolescent, that can be considered Neanderthal apomorphies – deepest point of sigmoid notch lying close to mandibular condyle and sigmoid notch crest terminating laterally on the condyle – lend themselves to a general discussion of how we might interpret potential apomorphies of a taxon that are not present in every single specimen that would otherwise be associated with that taxon.

First, strictly speaking, neither of these mandibular features is found in every specimen identified as "Neanderthal". Witness the Tabun II mandible, which has the Neanderthal configurations on one side, and the so-called *Homo sapiens* configurations (sigmoid notch deepest in its midline, and sigmoid notch crest terminating centrally on the condyle) on the opposite side (cf. Rak, 1998; Schwartz & Tattersall, 2000 a). Does this mean that the Tabun II mandible is not that of a Neanderthal? Or that this lack of uniform representation of proposed apomorphies of all specimens assigned to a taxon or morph demonstrates the inapplicability of seeking to delineate derived features?

Given the nature of biology, we would have to say "no". Why should we expect that all specimens assigned to a taxon will have all apomorphies that apparently define that taxon? This might be what is hoped for. But there is the by now well-known fact that all multicellular organisms share most of their basic regulatory genes and related molecules. As such, it is possible to suggest a mechanism by why organisms of obviously disparate phylogenetic propinquity can develop what appear to be the same features: by chance, the same cascade of molecular communication was initiated (e.g. Schwartz, 1999). As we all know, in general, the more closely related organisms are, the more features they will have in common due to their longer history of shared ancestry. On a developmental level, we might also think of this degree of commonality as reflecting the inheritance of similar transduction signaling pathways leading to similar morphologies. To pursue this further, the more closely related the organisms, the more detailed will be their versions of basic morphologies (e.g. not just a molar, but a molar with a specific cusp pattern), and, consequently, the more they will share the levels of signaling pathways that go beyond the development of the basic morphology of a structure to its taxically more specific and less widely shared details (Schwartz, 2001).

Given the hierarchical nature of the features shared by closely related taxa, and, thus, the levels of morphology-specifying, gene-communication pathways, one must think in terms of the consequences of mutations affecting the regulatory control of development that have profound effects. Such mutations lead to differences that would be apomorphic at the level of small clades and species, and to those that produce within-species, individual variation of a feature (e.g., see argument on *cis*-regulation by Stern, 2000). Thus, when it comes to details of morphology such as "termination of sigmoid notch crest on the condyle" or "deepest point of the sigmoid notch", we are addressing

levels of gene regulation that would not be so substantially different that, on occasion, the "instructions" to form one version would be inadvertently altered to produce the other. As for these particular mandibular "traits", while it is convenient to discuss them separately, developmentally they are surely integrated. Theoretically, and realistically, other morphologies (indeed the vast majority) of a "slightly different" individual would remain unaltered.

If we were to apply this perspective to the Le Moustier individual, we would be less inclined to see its non-development of a medial pterygoid tubercle as indicating, on the one hand, that this reflects gene flow between Neanderthal and "anatomically modern" morphs of the same species, or other similar justifications of why Neanderthals and *Homo sapiens* are merely variants of the same species. On the other hand, we might conclude that it is impossible reliably to delineate potentially apomorphic features. Within the hierarchical context of development, the Le Moustier adolescent still bears in its preserved parts hallmark features of *Homo neanderthalensis,* a species whose recognition as an independent entity can no longer be ignored.

Summary

A detailed description of the preserved craniodental morphology of the Le Moustier adolescent lends itself to a discussion of the development of characteristics specific to Neanderthals, in contrast to *Homo sapiens,* as well as of characteristics seen in Neanderthals that are either primitive retentions or indicative of a relationship between Neanderthals and middle-late Pleistocene, non-*Homo sapiens,* hominids. Among features that emerge as apomorphically Neanderthal are the development of a continuous, "double-arched", anteriorly smoothly rounded supraorbital tori, the deepest point of the sigmoid notch lying close to the mandibular condyle, the sigmoid notch crest terminating laterally on the condyle, and marked undercutting of the occipital by the nuchal plane that creates an infratoral depression in conjunction with a well-defined and surficially pitted suprainiac depression. Less pronounced versions of the latter two cranial features are seen the Steinheim skull, suggesting a sister-group relationship between the hominid this specimen represents and Neanderthals. An essentially featureless, broad, and anteroposteriorly thin, external mandibular symphyseal region describes a wider array of middle-late Pleistocene hominids than Neanderthal, thereby emphasizing the uniquely configured symphyseal region of *Homo sapiens.* The absence of a defined medial pterygoid tubercle, another potential Neanderthal apomorphy, can be understood in terms of the regulation of development, and is consistent with the observation that the occasional specimen does not bear every detail of the taxon it represents.

Acknowledgements

References

ARSUAGA, J.-L., MARTINEZ, I., GRACIA, A., CARRETERO J.-M. & CARBONELL, E. (1993): Three new human skulls from the Sima de los Huesos Middle Pleistocene site in Sierra de Atapuerca, Spain. *Nature* 362, 534–537.

ARSUAGA, J.-L., MARTINEZ, I., GRACIA, A & LORENZO, C. (1997): The Sima de Los Huesos crania (Sierra de Atapuerca, Spain). A comparative study. *Journal of Human Evolution* 33, 219–282.

BOULE, M. & VALLOIS, H.V. (1957): *Fossil men.* New York.

HOWELLS, W.W. (1973 a): *Evolution of the genus Homo.* Reading, MA, Addison-Wesley Publishing Co.

HOWELLS, W.W. (1973 b): Neanderthal man: facts and figures. In: R.H. Tuttle (ed.), *Paleoanthropology, morphology and paleoecology,* 398–407. The Hague.

HUBLIN, J.-J. (1978): *Le Torus occipital transverse et les structures associées.* Université de Paris, Thèse 3^{me} cycle.

HUXLEY, T.H. (1863): *Man's place in nature.* New York.

KING, W. (1864): The reputed fossil man of the Neanderthal. *Quarterly Journal of Science* 1, 88–97.

MAYR, E. (1950): Taxonomic categories in fossil hominids. *Cold Spring Harbor Symposium of Quantitative Biology* 5, 109–118.

RAK, Y. (1998): Does any Mousterian cave present evidence of two hominid species? In: T. Akazawa, K. Aoki & O. Bar-Yosef (eds.), *Neanderthals and modern humans in West Asia,* 353–366. New York.

RAK, Y., KIMBEL, W.H. & HOVERS, E. (1994): A Neandertal infant from Amud Cave, Israel. *Journal of Human Evolution* 26, 313–324.

SANTA LUCA, A.P. (1978): A re-examination of presumed Neandertal-like fossils. *Journal of Human Evolution.* 7, 619–636.

SCHWARTZ, J.H. (1995): *Skeleton keys: An introduction to human skeletal morphology, development, and analysis.* New York.

SCHWARTZ, J.H. (1997): *Lufengpithecus* and hominoid phylogeny: problems in delineating and evaluating phylogenetically relevant characters. In: D. Begun, C. Ward & M. Rose (eds.), *Miocene hominoid fossils: functional and phylogenetic implications,* 363–388. New York.

SCHWARTZ, J.H. (1999): S*udden origins: Fossils, genes, and the emergence of species.* New York.

SCHWARTZ, J.H. (2001): A review of the systematics and taxonomy of Hominoidea: History, morphology, molecules, and fossils. In: C.J. Cela-Conde (ed.), *Taxonomy and systematics of the human clade. Ludus Vitalis* 15, 15–45.

SCHWARTZ, J.H. & TATTERSALL, I. (1996): Toward distinguishing *Homo neanderthalensis* from *Homo sapiens,* and vice versa. *Anthropologie* (Brno) 43, 129–138.

SCHWARTZ, J.H. & TATTERSALL, I. (1999): Toward a definition of *Homo sapiens* and *Homo neanderthalensis:* I. The nasal region. In: J. Gibert, F. Sánchez, L. Gibert & F. Ribot (eds.), *The hominids and their environments during the Lower and Middle Pleistocene of Eurasia,* 299–310. Orce.

SCHWARTZ, J.H. & TATTERSALL, I. (2000 a): The human chin: what is it and who has it. *Journal of Human Evolution* 38, 367–409.

SCHWARTZ, J.H. & TATTERSALL, I. (2000 b): Variability in hominid evolution: putting the cart before the horse? In: M. Antunes (ed.), *Last Neanderthals in Europe: Odontologic and other evidence,* 367–401. Lisbon.

SCHWARTZ, J.H. & TATTERSALL, I. (2002 c): *The human fossil record.* Volume 1: *Termiology and craniodental morphology of genus Homo (Europe).* New York.

SCHWARTZ, J.H. & TATTERSALL, I. (in press): Morphology, variability, and systematics: lessons from Krapina. In: J. Radovčić (ed.), *The Krapina Neanderthals.* Zagreb.

SCHWARTZ, J.H., TATTERSALL, I. & LAITMAN, J.L. (1999): New thoughts on Neanderthal behavior: evidence from nasal morphology. In: H. Ullrich (ed.), *Hominid evolution: Lifestyles and survival strategies,* 166–186. Gelsenkirchen, Schwelm.

STERN, D.L. (2000): Perspective: Evolutionary developmental biology and the problem of variation. *Evolution* 54, 1079–1091.

STRINGER, C.B. & ANDREWS, P. (1988): Genetic and fossil evidence for the origin of modern humans. *Science* 239, 1263–1268.

STRINGER, C.B., HUBLIN, J.-J. & VANDERMEERSCH, B. (1984): The origin of anatomically modern humans in western Europe. In: F. Spencer & F. Smith (eds.), *The origins of modern humans: A world survey from the fossil evidence,* 51–135. New York.

TRINKAUS, E. & HOWELLS, W.W. (1979): The Neanderthals. *Scientific American* 241, 118–133.

VANDERMEEERSCH, B. (1981): *Les hommes fossiles de Qafzeh (Israël).* Paris.

WOLPOFF, M.H. (1996): *Human evolution.* New York.

ZOLLIKOFER, C.P.E., PONCE DE LEON, M.S., MARTIN, R.D. & STUCKI, P. (1995): Neanderthal computer skulls. *Nature* 375, 283–285.