



Adolescent archaics or adult moderns? Le Moustier 1 as a model for estimating the age at death of fragmentary supraorbital fossils in the modern human origins debate

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Abstract

This study documents and examines selected implications of the adolescent supraorbital anatomy of the Le Moustier 1 Neandertal. Le Moustier's supraorbital morphology conforms to that expected of an adolescent Neandertal but indicates that significant development of the adult Neandertal torus occurs late in ontogeny. As the best preserved adolescent from the Late Pleistocene, Le Moustier 1's anatomy is used to help distinguish adolescent from adult anatomy in two cases of fragmentary supraorbital fossils, the Vindija late Neandertals and KRM 16425 from Klasies River Mouth (South Africa). It has been suggested that the modern-like aspects of the Vindija and Klasies supraorbital fossils are a function of developmental age rather than evolution. Although Le Moustier 1's anatomy does indicate that two of the Vindija fossils are adolescent; these two fossils have already been excluded from studies that demonstrate transitional aspects of the Vindija adult supraorbitals. Results of an analysis of KRM 16425 in light of Le Moustier 1 are more ambiguous. KRM 16425 is clearly not a Neandertal, but its morphology suggests that it may be an adolescent form of such late archaic Africans like Florisbad or Ngalooba. Both the Vindija and Klasies River Mouth cases highlight the need to be wary of confusing adolescent anatomy with modernity.

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Introduction

In the ongoing debate regarding modern human origins, various scholars have suggested that some of the key so-called “transitional” or “early modern” fossils may represent subadults (Bräuer 1989; Smith 1992; Frayer et al 1993; Stringer & Bräuer 1994). Since it is usually straightforward to distinguish pre-adolescents from adults, the crux of the issue is the difficulty in distinguishing adolescents from adults. One anatomical region that changes considerably from adolescence to adulthood, in both Neandertals and early modern people is the supraorbital region (Smith & Ranyard 1980). Given that supraorbital fossils, such as those from Vindija Cave (Croatia) and Klasies River Mouth (South Africa), are among those that have been considered both modern-like and subadult, it is essential to establish methods for distinguishing adolescent from adult supraorbitals. This is particularly true in light of the importance of these fossils in the debate on modern human origins. Le Moustier 1 preserves the supraorbital as well as most of the rest of the skull, including a complete dentition. Given Le Moustier’s dental age of 15.5 years (Thompson 1995; Thompson & Nelson 2000) or 13 years (Wolpoff 1999), it represents perhaps the most complete Late Pleistocene adolescent hominid skull. Since Le Moustier preserves the supraorbital region, it may help in distinguishing adolescents from adults in other Late Pleistocene samples.

The supraorbital region in modern humans and Neandertals

Many morphological characteristics distinguish European Neandertals from the modern humans that succeeded them. Foremost among these characteristics is form of the supraorbital region. The supraorbital region comprises the area of the frontal bone that lies immediately above the orbits and inferior to the frontal squama. It generally includes the superior orbital rim and the brow ridges, if present. Although usually treated separately, the frontal sinus lies partially within the supraorbital region. The anatomy of the supraorbital region differs dramatically between most modern humans (Fig. 1) and archaic humans such as Neandertals (Fig. 2). Neandertals exhibit heavily developed brow ridges that form a true supraorbital torus, a continuous bar of bone across both orbits and the nasal bridge. Upper Paleolithic modern humans, by contrast, tend to have more weakly developed brow ridges that are divided into medial and lateral segments over each orbit (Cunningham 1908; Smith & Ranyard 1980).

Brow ridges (including supraorbital tori) are swellings above the orbits and nasal region that project beyond the squamal surface that lies superior to the supraorbital region. Most living and recent humans exhibit brow ridges that are divided at the midline into two halves as well as into medial and lateral segments over each orbit (Cunningham 1908). Brow ridge development in modern humans is primarily limited to the medial segment, known as the superciliary arch. Even in the medial segment, many modern children, adolescents and adult females lack any brow ridge

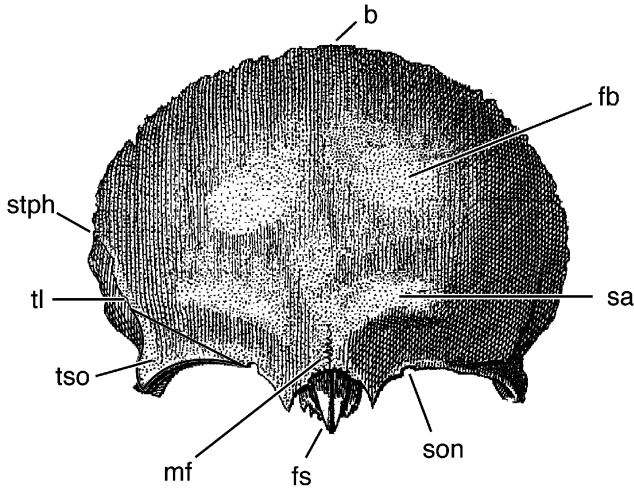


Fig. 1. Anatomy of the frontal bone in *norma frontalis*. (b) Bregma, (fb) frontal boss, (fs) frontal spine, (mf) metopic fissure, (sa) superciliary arch, (son) supraorbital notch, (stph) stephanion, (tl) temporal line, (tso) supraorbital trigon. Specimen is from a gracile recent European.

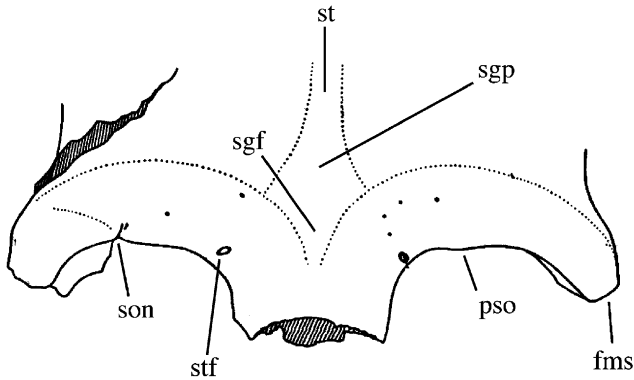


Fig. 2. Illustration of the Feldhofer Neandertal's supraorbital region. This specimen exhibits a true supraorbital torus. (fms) frontomalar suture, (pso) supraorbital process, (sgf) supraglabellar fossa, (sgp) supraglabellar prominence, (son) supraorbital notch, (st) sagittal torus, (stf) supratrochlear foramen. From [Cunningham \(1908\)](#).

development ([Cunningham 1908](#); [Russell 1983](#)). The lateral segment is also variable among living humans, ranging from no development to full development that combines with the medial segment to form a true supraorbital torus ([Russell 1985](#); [Vinyard & Smith 2001](#)). If the supraorbital torus is particularly projecting and if the frontal squama is particularly rounded, a supratrochlear sulcus is present between the torus and the squama. On individuals lacking significant supraorbital development,

the lateral brow ridge segment is a flattened surface, the supraorbital trigon. This trigon is demarcated by the temporal line laterally, the base of the frontal squama superomedially and the orbital margin anteriorly (Fig. 1). In most living human populations, the supraorbital sulcus separates the medial and lateral segments (Cunningham 1908; Weidenreich 1943). This sulcus runs superolaterally from a point that usually corresponds to the place of the supraorbital foramen or notch. When the supraorbital sulcus is present, a true supraorbital torus is not (Cunningham 1908).

Among adult Neandertals and other archaic humans, supraorbital tori are ubiquitous (Cunningham 1908; Smith 1980; Wolpoff 1999). Early and Middle Pleistocene hominid fossils generally exhibit supraorbital tori that are continuously thick and projecting across the orbits and the nasal bridge. Among Neandertals the torus is less projecting and sometimes is at least partially divided above the nose. Fossils of early anatomically modern humans tend to lack true supraorbital tori and possess brow ridges that are divided into medial and lateral segments, as described above. However, among a small portion of modern humans, the brow ridge is continuous across the orbit and across the midline, forming a true supraorbital torus. Larnach and Macintosh (1970) report that 6.1% of Australian Aborigines exhibit such a condition. Tierra del Fueguians and Melanesians also often exhibit true supraorbital tori (Gusinde 1939; Vinyard & Smith 2001). Even when present, the shape of the torus in modern humans tends to differ from that of Neandertals. While Neandertal tori tend to curve over the tops of the orbits, modern human brow ridges tend to be more angular and bent sharply at the junction between the medial and lateral segments. Late Neandertals such as St. Cesaire and the Vindija hominids exhibit more angular, although still continuous, tori.

Where the frontal squama meets the supraorbital region, the internal and external tables of bone diverge. The endocranial surface continues to form around the curving frontal cerebral lobe, while the external surface of the frontal bulges out to varying degrees to form the brow ridges. In the glabellar region and often extending into the medial segments of the supraorbital region, cavities fill up the space left between the diverging external and internal tables of bone. These cavities are the frontal sinuses. The frontal sinuses typically consist of an asymmetrical pair, one on either side of the midline. Each sinus may have multiple lobes and may extend superiorly well into the frontal squama and laterally as far as the lateral most point of the medial segment in modern humans. Each frontal sinus is continuous with the nasal cavity by way of the nasofrontal duct. The sinuses may also be continuous with each other and with intrusive digitations of the ethmoid or maxillary sinuses.

Sinus morphology varies considerably among both fossil and extant humans. According to Szilvássy and colleagues (1987), fossil and living Europeans (including Neandertals) tend to have maxillary and frontal sinus cavities of similar sizes, while Africans tend to have proportionally larger frontal sinuses and Asians have proportionally larger maxillary sinuses. According to Vlček (1967), the frontal sinuses of Neandertals are laterally extensive but superiorly restricted to the inside of the supraorbital torus. Frontal sinuses of modern humans, on the other hand, are limited to the medial supraorbital but extend into the frontal squama. A

pre-Neandertal, the Petralona cranium (Greece), which exhibits a mosaic of Neandertal and erectine features, has extensive frontal sinuses throughout the frontal squama (Seidler et al 1998).

Two other aspects of anatomy that tend to distinguish Neandertals and modern humans lie along the superior orbital rim. The supraorbital process (Weidenreich 1943) appears frequently among Neandertals and other archaic humans and occasionally among modern humans with particularly robust brow ridges. The supraorbital process is an inferior and often anterior bulging of the brow ridges approximately half way across each orbit. The indentations formed on either side of this structure are not strictly homologous to the supraorbital notch, although the supraorbital nerve and vessels may pass through them. In most modern humans the supraorbital nerve and vessels pass through either a supraorbital foramen (or foramina) or a supraorbital notch. Such perforations that run through the orbital plate and pierce through the superior orbital rim are rare among Neandertals. Among early Neandertals from the Krapina Rockshelter no true supraorbital foramina or notches are present. However, among the late Neandertals from Vindija Cave, five of six specimens that preserve the region exhibit supraorbital notches or foramina. Late archaic African crania (e.g., Florisbad) also often preserve this feature.

The supraorbital region of Le Moustier 1

The Le Moustier site is a complexly stratified rockshelter from the Dordogne region of southwestern France. Le Moustier 1 was a complete skeleton when discovered by Hauser in 1908 (Klaatsch & Hauser 1909). The skeleton was lost, apparently in the aftermath of World War II, but the skull was subsequently found in 1965 (Hesse & Ullrich 1966). Le Moustier 1 was probably recovered from bed J at the site, which contains a typical Mousterian lithic assemblage (Perony 1930). Electron spin resonance and thermoluminescence dating (Mellars & Grün 1991) establish that Le Moustier 1 is a relatively late Neandertal with a maximum age of 40–42 ka.

The frontal bone of Le Moustier 1 is well-preserved (Fig. 3). It originally comprised at least 12 individual pieces, the largest of which was the right third of the frontal including the lateral segment of the right supraorbital. The right posterior external squama is missing along 68 mm of the coronal suture. The missing table extends as far anterior as 23 mm from the coronal suture, whose articulation is not preserved inferior to the right stephanion, but is present for all of the rest of its course except inferior to left stephanion and for a 19 mm segment posterior left where a large fragment (19 × 13 mm) is missing. A square-shaped piece, measuring approximately 15 mm wide by 17 mm high, is missing from the medial segment of the left supraorbital torus exposing the left frontal sinus. A past attempt to reconstruct the skull left plaster (painted to match the bone, unfortunately) that currently still obscures parts of the frontal bone (Thompson & Illerhaus 1998). Fortunately, recent computer-assisted reconstructions (Ponce de León & Zollikofer 1999; Thompson &

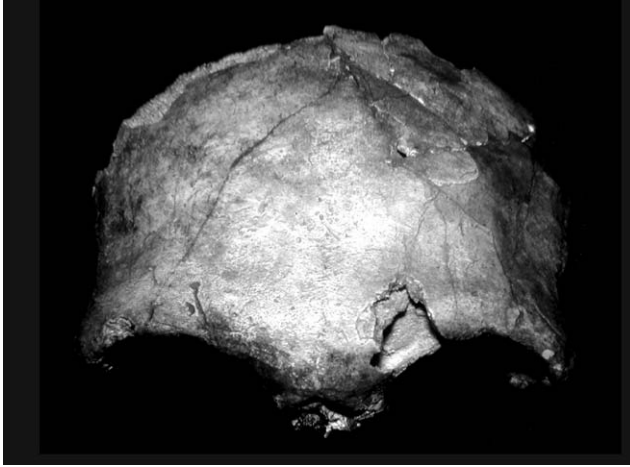


Fig. 3. The frontal of Le Moustier.

Illerhaus 1998) have helped to elucidate which portions of the Le Moustier 1 frontal are real bone and which portions are plaster. Although part of the left frontal squama comprises false material, only a small portion of left brow ridge at midorbit is obscured by plaster reconstruction.

Le Moustier 1 exhibits a true supraorbital torus. Like adult Neandertals such as La Chapelle, the torus is double-arched and is not sharply bent at the junction between the medial and lateral segments as on modern humans. Unlike most adult Neandertals, the torus is thin laterally compared to the toral thickness medially (Table 1). Torus thickness at medial and midorbit fall within one standard deviation of the adult Neandertal mean, while lateral thickness is just smaller than one standard deviation below the adult Neandertal mean (Table 1). While Le Moustier 1's lateral and midorbit thicknesses fall below the adult mean, medial thickness is nearly a full standard deviation greater than the adult average. Due to damage, medial thickness can only be measured on the right torus of Le Moustier 1. Nevertheless, it appears that the right medial torus is dramatically thicker than the left. The frontal sinuses are limited to the medial segments of the torus and do not extend into the frontal squama (Thompson & Illerhaus 1998).

Le Moustier 1 exhibits supraorbital processes, which are distinct anteroinferior bulges along the superior orbital rims, on both sides of the supraorbital torus. The right supraorbital process appears to be slightly larger than that of the left. A distinct supraorbital notch is preserved on the right side. It is not distinct in terms of depth or breadth and is actually barely visible in *norma frontalis*, but when viewed on the orbital plate it is discernible as a vascular groove running anteriorly from the posterior orbital plate. Approximately 4 mm posterior to the orbital rim the groove curves strongly toward glabella and runs in this direction crossing over the orbital rim 16.89 mm lateral to glabella where it again becomes slightly more vertically oriented before disappearing 6 mm superiomedial from the point at which it crossed the orbital rim.

Table 1. Measurements of the supraorbital region

	Projection ^a			Thickness		
	Lateral	midorbit	Medial	Lateral	midorbit	Medial
Le Moustier 1	21.0	15.0	13.0	10.7	9.9	21.9
Vindija 224	19.5	17.5	17.0	9.1	9.7	15.1
Vindija 279	16.0	13.0	11.0	7.6	7.0	15.1
KRM 16425	—	—	13.0	—	—	18.0
<i>Adult Neandertals^b</i>						
Mean	24.8	23.7	21.7	12.5	11.0	18.9
95% bootstrap C.I. ^c	23.9–25.7	22.9–24.5	20.5–22.9	11.9–13.2	10.4–11.6	17.1–20.5
SD	2.0	1.9	2.2	1.5	1.6	3.2
N	17	20	12	21	23	12
<i>Krapina (adults)^d</i>						
Mean	24.3	23.9	19.4	12.5	10.7	14.8
95% bootstrap C.I. ^c	23.5–25.2	23.3–24.6	17.5–20.8	11.6–13.4	9.7–11.6	11.9–16.6
SD	1.4	1.2	1.7	1.6	1.8	2.6
N	8	11	3	11	13	3
<i>Vindija (adults)^e</i>						
Mean	22.1	18.9	—	10.6	8.6	—
95% bootstrap C.I. ^c	20.6–23.5	16.9–21.1	—	10.3–11.0	8.2–9.1	—
SD	1.8	2.9	—	0.5	0.6	—
N	5	6	—	5	5	—
<i>Adult UP Moderns^f</i>						
Mean	19.5	16.0	13.0	8.8	6.2	18.5
95% bootstrap C.I. ^c	17.7–21.4	14.0–17.9	10.8–5.6	8.1–9.5	5.6–6.9	17.0–20.0
SD	3.6	3.7	4.1	1.6	1.6	3.3
N	14	14	10	20	20	18

^aMedial, midorbit, and lateral were originally defined by Smith and Ranyard (1980). Rather than being actual points, the landmarks refer to definable parasagittal planes along the supraorbital region. Medial lies on the orbital segment of the supraorbital torus (or superciliary arch) just lateral to the medial orbital margin. This landmark invariably corresponds to the thickest and highest points on the torus. Lateral corresponds to the thickest point on the lateral segment of the torus that is lateral to a parasagittal plane that passes through frontotemporale. Midorbit corresponds to the thinnest point on the torus between medial and lateral.

^bThe Adult Neandertal sample comprises: La Chapelle, La Ferrassie I, Guattari 1, La Quina V, Forbes Quarry, Spy I and II, St. Césaire, Feldhofer, La Chapelle, Sacopastore 2, Krapina (Kr) 3, Kr 4, Kr 6, Kr 28, Kr 37.1, Kr 37.3, Kr 37.4, Kr 37.5, Kr 37.6, Kr 37.7, Kr 37.8, Kr 37.10, and Kr 37.11.

^cStandard bootstrap confidence interval estimate for the mean (cf., Manly 1997) with 10,000 bootstrap samples. “C.I.” = confidence interval.

^dSample consists of: Krapina (Kr) 3, Kr 4, Kr 6, Kr 28, Kr 37.1, Kr 37.3, Kr 37.4, Kr 37.5, Kr 37.6, Kr 37.7, Kr 37.8, Kr 37.10, and Kr 37.11.

^eExcludes Vi 224, 279, and clear infant, Vi 227. Sample consists of Vindija (Vi) 202, Vi 260, Vi 261, Vi 262, Vi 284, Vi 305.

^fThe adult Upper Paleolithic modern sample comprises: Cromagnon 1–4, La Madeleine 1, Abri Pataud 1, Engis (1) 2, Oberkassel F, Oberkassel M, Podbaba, Kelsterbach, Paderborn, Stetten 1 and 2, Mladeč 1, 2, and 5, Brno 2, Dolni Vestonice 3, and Pavlov.

Anterior projection of Le Moustier 1's supraorbital torus is dramatically less than seen in adult Neandertals and is very similar to that seen in adult Upper Paleolithic modern humans. At midorbit and medial, toral projection is more than one standard deviation below the adult Neandertal mean, while lateral projection falls slightly less than one standard deviation below the adult Neandertal mean. When viewed from above, glabella is particularly projecting and the general shape of the torus when viewed from above is a shallow "v" with glabella at its apex. The general lack of supraorbital torus projection combined with a flattened frontal squama along the midline means that Le Moustier 1 exhibits a very shallow supratotal sulcus separating the torus from the frontal squama. The supratotal sulcus is slightly more developed above the orbits where right and left frontal eminences help set off the torus from the squama.

Due to the shallowness of the supratotal sulcus and the lack of toral projection, Le Moustier 1's torus appears more as a bulge than a distinct bar of bone. Such a pattern is typical of subadult Neandertals (Smith & Ranyard 1980). Vermiculate patterned bone is present on both medial and lateral toral segments as in many adult Neandertals, which may signal the beginning of adult torus formation in Le Moustier. The supraorbital torus only has a real anterior face along the medial segment. Laterally, the torus's surface faces anterosuperiorly and not anteriorly. This and other aspects of the Le Moustier supraorbital region make it somewhat like modern supraorbitals. However, Le Moustier's brow ridge is continuous rather than being divided by a supraorbital sulcus as in most modern humans. Although continuous, the torus thins laterally with thickness at lateral and midorbit being approximately the same. This is unlike early modern Europeans, whose tori tend to be thinner at midorbit relative to lateral. Given that Le Moustier 1 died at a dental age of 13 (Wolpoff 1999) or 15.5 years (Thompson 1995), most if not all of the modern-like aspects of its supraorbital region are likely related to the fact that significant supraorbital growth occurs between late adolescence and early adulthood (Smith & Ranyard 1980; Russell 1983; Ahern 1998) and perhaps even throughout adulthood (Ahern 1998). Table 2 lists the aspects of Le Moustier 1's supraorbital region that differ from adult Neandertals and perhaps reflect its adolescent age.

Table 2. Aspects of Le Moustier 1's supraorbital region that differ from most adult neandertals and may reflect its adolescent age

Le Moustier features that differ from most adult neandertals:

Supraorbital torus

- Less projecting/shallow supratotal sulcus
- Lateral torus much thinner than medial torus
- Lateral torus lacks anterior face, torus surface faces

Frontal sinus is limited to the medial torus

Le Moustier 1 as a model for Neandertal adolescent supraorbital morphology

The Le Moustier 1 hominid is the best preserved adolescent Neandertal and perhaps the best preserved adolescent of the Late Pleistocene. No other adolescent Neandertal fossils have a dentition associated with a supraorbital region. Therefore, Le Moustier 1 provides a unique perspective regarding the ontogeny of the Neandertal supraorbital region. As such it can be used to help separate adolescent Neandertal individuals from adults.

Limits of a Le Moustier model for Late Pleistocene adolescent morphology

As described above, the supraorbital region of Le Moustier 1 differs in many respects from the supraorbitals of most adult Neandertals. It is possible that all of these differences reflect Le Moustier's adolescence. However, how "typical" is Le Moustier likely to be for a Neandertal adolescent? Two factors indicate that a Le Moustier model for Neandertal supraorbital adolescence should be used with caution. These factors are: (1) geographic and temporal variation and (2) the robusticity of the Le Moustier supraorbital.

Le Moustier 1 is a single fossil from a single locality and from a single point in time. As such, some of the ways it differs from other Late Pleistocene hominids likely reflects individual, geographical and temporal variation. Temporal variation may be especially important in the case of Le Moustier. According to Mellars and Grün (1991), the remains cannot be older than 40–42 kyr B.P. If this dating is correct, Le Moustier 1 is a fairly late Neandertal. Another late Neandertal from France, St. Césaire, exhibits a supraorbital torus that is relatively thin laterally (Wolpoff 1999) like Le Moustier, but it is an adult. Thus, it is possible that some differences between Le Moustier and adult Neandertals may be temporal rather than ontogenetic. However, the supraorbital torus in St. Césaire projects anteriorly in a manner commensurate with adult status (Smith et al 1989a), whereas Le Moustier 1's torus does not. Another indication that Le Moustier 1's supraorbital may not be typical for a Neandertal adolescent is that medial thickness of the supraorbital torus is almost a full standard deviation above the adult Neandertal average. Fundamentally, what Le Moustier can tell us is to be aware that the supraorbital region differs significantly between adolescent and adult Neandertals.

Fragmentary fossils in the modern human origins debate: transitional or adolescent?

Because anatomy can vary with age, only fossil samples of similar age composition should be compared when testing evolutionary hypotheses (Clark 1964). Since

subadults tend not to exhibit robust superstructures such as large brow ridges, it is possible to mistake adolescent anatomy for more modern-like anatomy. In the controversy surrounding modern human origins, proponents of replacement models have implied that supporters of continuity have made this very mistake (Bräuer 1984, 1992; Stringer & Bräuer 1994) and vice versa (Smith 1992; Frayer et al 1993, 1994). Debate has focused upon two samples of Late Pleistocene hominids, those from Vindija Cave (Croatia) and Klasies River Mouth (South Africa) and have been especially heated in the exchange between Frayer and colleagues (Frayer et al 1993, 1994) and Stringer & Bräuer (1994). Since Le Moustier 1 is one of the few Late Pleistocene adolescents that can actually be given a dental age, it may shed some light upon the debate surrounding these two samples of fragmentary fossils.

The Vindija late Neandertals: transitional or adolescent?

Since the original description of the late Neandertal fossils from Vindija Cave (Croatia), the specimens have often been touted as transitional between earlier Neandertals (e.g., Krapina) and the first anatomically modern Central Europeans (Malez et al 1980; Wolpoff et al 1981; Smith 1982, 1984, 1985, 1994; Smith et al 1985; Smith & Trinkaus 1991; Wolpoff 1999). Detailed analyses of many modern-like aspects of the Vindija hominids support this conclusion (Smith & Ranyard 1980; Smith 1984; Ahern & Smith 1993; Wolpoff 1999). Perhaps the strongest evidence for genetic continuity from Neandertals to early modern Europeans is the pattern of supraorbital reduction exhibited in the Vindija late Neandertals (Smith & Ranyard 1980; Wolpoff et al 1981). The Vindija supraorbital sample comprises ten fossils, nine of which derive from level G₃, dating to ≥ 40 k.a. (Krings et al 2000). The 10th specimen, Vi 308, does not preserve any metric points and comes from level G₁, which dates to approximately 28–29 k.a. (Smith et al 1999). Most of the Vindija supraorbitals preserve a partial supraorbital torus and a limited portion of frontal squama. In terms of both projection and lateral and midorbit thickness chords, the Vindija supraorbitals lie intermediate between earlier Neandertals from Krapina (Croatia) and modern Europeans (Table 1, Fig. 4). In terms of an index that measures projection shape (midorbit/lateral projection), the Vindija sample falls intermediate between earlier Neandertals from Krapina (Croatia) and modern Europeans (Fig. 5). While the differences for the chord measurements (Fig. 4) could possibly be explained allometrically, the observed shape change (Fig. 5) is less likely related to allometry. Interestingly, the mean midorbit/lateral thickness index for the Neolithic Altendorf sample is more similar to the Neandertal samples than it is to the Upper Paleolithic sample. Thus, although the Vindija sample falls intermediate between the Krapina and Upper Paleolithic for this index, it should not be regarded as evidence of Vindija's anatomical intermediacy between earlier Neandertals and modern humans.

As the role of the Vindija hominids in the support of regional continuity became prominent, opponents of continuity turned a critical eye toward the sample. Two

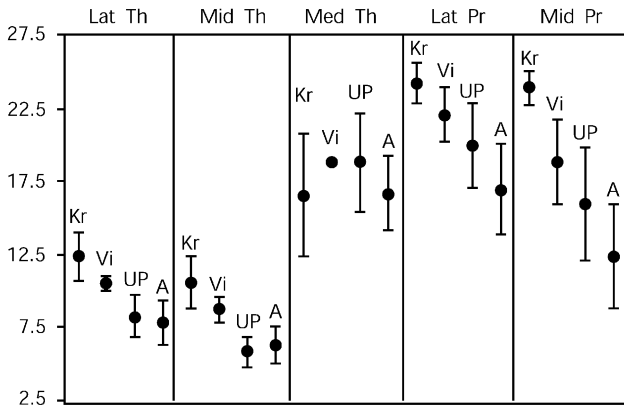


Fig. 4. Plot of means and single standard deviations for supraorbital thickness and projection measurements. Medical thickness and projection measurements are not included, since no Vindija adults preserve these. See Table 1 and Smith and Ranyard (1980) for definitions of measurements. “Kr”: Krapina, “Vi”: Vindija, “UP”: Central European Upper Paleolithic, “A”: German Neolithic sample from Altendorf. Note that the Vindija sample is intermediate between the earlier Krapina Neandertals and the Upper Paleolithic post-Neandertals.

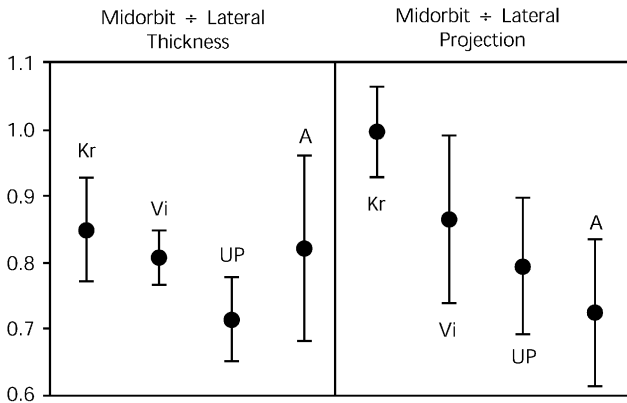


Fig. 5. Plot of means and single standard deviations for indices of supraorbital shape. See Table 1 and Smith and Ranyard (1980) for definitions of the measurements and indices. “Kr”: Krapina, “Vi”: Vindija, “UP”: Central European Upper Paleolithic, “A”: German Neolithic sample from Altendorf. Note that the Vindija sample is intermediate between the earlier Krapina Neandertals and the Upper Paleolithic Central Europeans.

primary critiques emerged to explain the “transitional” features of the Vindija remains: (1) small body size and (2) an over representation of females and/or young individuals (Howell 1984; Stringer et al 1984; Bräuer 1989, 1992; Stringer & Bräuer 1994; Klein 1999). The fragmentary nature of the Vindija remains has made them

difficult to diagnose in terms of overall body size, sex composition and age distribution. Klein (1999), Howell (1984) and others (e.g. Bräuer 1989) claim that the transitional aspects of the Vindija hominids are all related to a reduction in robusticity and overall size. However, as Trinkaus and Smith (1995) have demonstrated, the Vindija hominids were not significantly smaller in overall body size than other Neandertals. Furthermore, mean robusticity measures of the Vindija mandibles are significantly greater than those of early Neandertal mandibles (Ahern & Smith 1993). These results indicate that the Vindija hominids were not less robust versions of earlier hominids.

Stringer and Bräuer (1994) argue that the age and sex distributions of the Vindija hominid sample are unknown and females and/or young could be over represented. More firmly, Bräuer (1989: p. 137) states, "... it is possible that the observed trends from the older Krapina to the Vindija hominids, such as reduction in mid-facial prognathism and thinner and less projecting supraorbital tori, are at least partly due to larger frequencies of female and juvenile individuals in the Vindija sample." If the Vindija supraorbital sample appears more modern-like than earlier Neandertals because of its age composition, the argument for continuity between Neandertals and early modern Europeans is less certain. Thus the issue of whether or not adolescents have been mistaken for adults in the Vindija sample is directly relevant to the question of the fate of the Neandertals.

When we use the anatomy of Le Moustier 1's supraorbital region to assess the individual ages of the Vindija supraorbitals, it is clear that at least two of the Vindija fossils (Vi 224, Vi 279) are probably adolescents. However, both of these specimens and a third, clearly infant fossil (Vi 227/254) are excluded in both the original analysis of supraorbital evolution (Smith & Ranyard 1980) and subsequent studies (Smith et al 1989b; Ahern 1998; Ahern et al 2002) because they appear to be subadults. The other Vindija supraorbitals, however, exhibit morphology consistent with adulthood. Thus, the use of Le Moustier 1 for comparison and age assessment only confirms previous age designations for the Vindija supraorbital sample. Therefore, the transitional appearance of the Vindija supraorbitals is not due to the inclusion of adolescents in the sample. Recent analyses by one of us indicate that other types of sample composition bias, such as a skewed sex distribution, are also not valid explanations for the more modern-like aspects of the Vindija supraorbital sample (Ahern 1998, 1999; Ahern et al 2002).

The Vi 224 and Vi 279 supraorbital tori are similar in many respects to the torus of Le Moustier 1 (Figs. 6 and 7). Although some of these similarities are common to all Neandertals (e.g., a continuous supraorbital torus), many of these similarities concern anatomy that distinguishes Le Moustier from adult Neandertals. Le Moustier, Vi 224 and Vi 279 all exhibit markedly less supraorbital projection than adult Neandertals (see Table 1). This is especially the case for projection of the medial torus, where all three exhibit toral projection that is more than two standard deviations below the adult Neandertal average. Vi 224, Vi 279 and Le Moustier 1 all have tori that are slightly thinner at lateral and midorbit than the Neandertal average. Vi 224 and Vi 279 also have medial tori that are thinner than average, but Le Moustier's medial torus is considerably thicker than average for adult

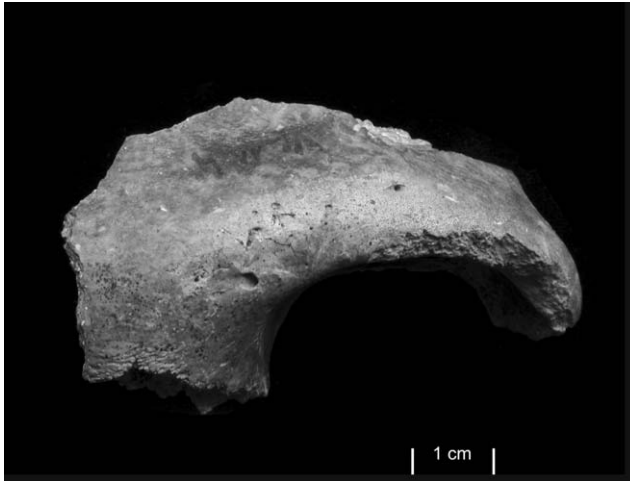


Fig. 6. The Vindija 224 adolescent supraorbital fossil.

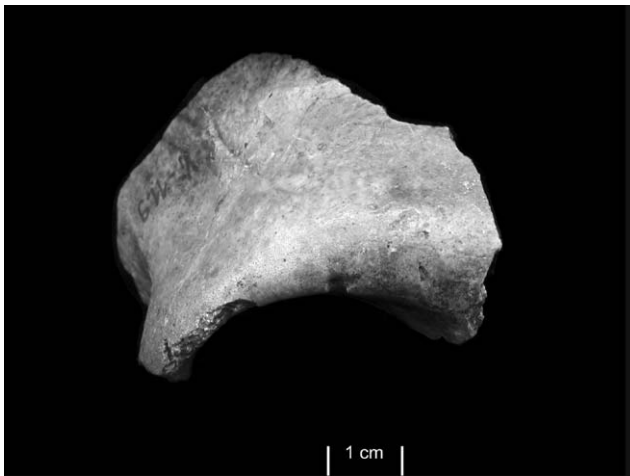


Fig. 7. The Vindija 279 adolescent supraorbital fossil.

Neandertals. In terms of thickness of the torus, all three specimens are considerably thinner at lateral than at medial. Like Le Moustier 1, Vi 224 and Vi 279 have lateral torus segments that face anterosuperiorly and thus lack an anterior face. Vi 224 and Vi 279 have frontal sinuses that are limited to the medial segment of the torus. Vi 224's frontal sinus (left) fills the medial 44% of the supraorbital torus, while Le Moustier 1's (left) frontal sinus fills the medial 43% of the supraorbital torus. A small sample of adult Neandertals ($N = 4$) yields an average lateral frontal sinus extent of 59.3% ($s = 10.4$). The percentage extent of Vi 279's sinus cannot be

measured, but it appears to be confined to the medial segment of the torus. The lack of torus projection, a dramatically thinner lateral torus, a lateral torus segment that faces more superiorly and a medially restricted frontal sinus are all features shared by Le Moustier, Vi 224 and Vi 279. All of the other Vindija supraorbital specimens (except the obviously infant Vi 227) differ from Le Moustier, Vi 224 and Vi 279 in terms of these aspects of anatomy and conform to the adult Neandertal pattern.

Klasies River Mouth 16425: modern or adolescent?

Unlike the Vindija late Neandertals which have been cited as merely transitional between archaic and modern humans, the early Late Pleistocene hominids from Klasies River Mouth Cave (South Africa) have been posited by some as some of the earliest representatives of anatomically modern humans (Bräuer 1984, 1989, 1992; Rightmire & Deacon 1991; Stringer & Gamble 1993; Stringer & Bräuer 1994). Most of the Klasies fossils date to between 80 and 100 kyr BP (Deacon & Geleijnse 1988; Grün & Stringer 1991) and are associated with a Middle Stone Age technocomplex (Singer & Wymer 1982). The sample comprises mostly fragmentary remains and exhibits a high degree of variation. Some modern features are present among the fossils and include a true chin (KRM 41815) and a gracile supraorbital region that lacks a supraorbital torus (KRM 16425) (Rightmire & Deacon 1991).

Although some individual Klasies fossils exhibit modern anatomy, the sample shows a mosaic of archaic and modern features (Smith 1992, 1994). Furthermore all of the specimens are very fragmentary. Smith (1992), Frayer et al (1993, 1994) and Wolpoff (1999) suggest that at least one of the fossils, the supraorbital/nasal specimen KRM 16425, may appear modern-like because it is subadult. According to Frayer et al (1993:p. 95), "... the reduced brows in this specimen may be more a function of age than an indication of taxonomic modernity." If KRM 16425's gracile anatomy is a function of age, then the position of the Klasies hominids as one of the earliest modern human samples is weakened. Only KRM 41815 would remain as an especially modern-looking fossil if KRM 16425 is dismissed.

KRM 16425 comprises a small portion of glabellar and right medial supraorbital that articulates with superior portions of both nasal bones and the perpendicular plate of the ethmoid (Fig. 8). The preserved mediolateral breadth is 61 mm and the preserved height from nasion is 23.5 mm. Most of the right medial supraorbital segment is preserved along with a small portion of inferomedial lateral segment. The browridge may thin laterally and exhibits a distinct supraorbital notch. Both of these features are characteristic of modern human browridges but are also found in adolescent Neandertals, as our observations on Vindija 224 and 279 show. They are also present on late archaic African specimens such as Florsibad. KRM 16425's glabella is bulging, but not nearly as much as on the Florisbad or Ngaloba adults, MSA-associated frontals. Thus, while KRM 16425 is clearly not Neandertal-like in morphology, it may be a subadult version of late archaic Africans. Adult



Fig. 8. Klasies River Mouth 16425. Photo courtesy of M.H.Wolpoff.

representatives of this group include Florisbad, Ngaloba and Jebel Irhoud (Bräuer 1984; Smith 1994) and may include Herto (White et al 2003).

Although Le Moustier 1 adolescent represents a population far-removed from the population represented by the Klasies fossils, it may shed some light regarding whether or not KRM 16425 is adolescent or adult. Unfortunately, the fragmentary nature of the Klasies supraorbital specimen makes a comparison with Le Moustier difficult. For example, damage to the Klasies fossil precludes all browridge measurements except at the medial point. Nevertheless, some things are clear. KRM 16425's and Le Moustier's brow ridges project equally at this points (Table 1). Thickness at the medial point is different between the two fossils with Le Moustier's brow ridge being nearly 4 mm thicker. The very little frontal squama preserved on KRM 16425 indicates that there was virtually no sulcus overlying the brow ridge. Unfortunately, the small portion of lateral supraorbital that is preserved indicates little regarding whether or not KRM 16425's lateral brow had an anterior face and whether or not the lateral brow was considerably thinner than the medial brow. The small preserved portion seems to indicate that very little actual brow was probably present laterally. KRM 16425's frontal sinus is respectable, but so are the sinuses of the adolescents from Vindija (see above) and Le Moustier 1. Examination of CT images of KRM 16425 indicates a large, single-lobed sinus chamber on the preserved right side of the specimen. The sinus extends slightly above the level of the superior orbital rim. Utilizing the Bolton Standards of frontal sinus development (Broadbend et al 1975) this suggests an age of at least 10 years at death by recent human standards. However, the sinus does not appear to extend superiorly into the frontal squama or laterally along the brow ridge. This pattern is commensurate with an adolescent age estimate for this specimen.

Although KRM 16425 is similar to Le Moustier in some respects, this does not necessarily indicate that the Klasies specimen is adolescent. The similarities between KRM 16425 and Le Moustier are shared with modern humans. Both Le Moustier and KRM 16425 have medial projections of 13 mm. This figure is well within one standard deviation of the Upper Paleolithic modern human mean. Furthermore the shallow sulcus above the medial brow in both Le Moustier and KRM 16425 is also found in modern humans. KRM 16425's supraorbital sulcus is unlike Le Moustier, but like modern humans. However, the Klasies fossil's interorbital breadth can only be matched by archaic African fossils such as Florisbad and Kabwe (Fruyer et al 1993). Given the differences between Le Moustier's and adult Neandertal's medial supraorbitals and given the similarities between Le Moustier and KRM 16425, we should be cautious about assuming that the Klasies fossil exhibits adult morphology. This is especially the case given that KRM 16425 is the only frontal specimen from the Klasies Middle Stone Age deposits and is the only potential adolescent from this period in Africa. KRM 16425 is certainly not a Neandertal, but it may represent a sub-adult of an archaic hominid form akin to Florisbad rather than a fully anatomically modern human. If an actual sample of supraorbital fossils was preserved, even if it comprised fragmentary specimens, or if we had a series of contemporary subadult supraorbitals from Africa (The obviously non-adult Herto 5 is much younger, developmentally (White et al 2003)), we would be in a better position to assess the age of KRM 16425.

Conclusions

The importance of fragmentary fossils in the discussion concerning modern human origins demands that we attempt to distinguish subadults from adults. This is especially the case regarding fossils preserving the supraorbital region, since dramatic growth and remodeling of this region occurs fairly late in ontogeny. Since Le Moustier 1's dental age is known, it can provide some indication regarding adolescent supraorbital anatomy in the Late Pleistocene. Fundamentally, Le Moustier 1's supraorbital anatomy demonstrates that we should be wary of confusing adolescence with modernity. Although it is not difficult to distinguish pre-adolescent and adult supraorbital specimens, separating adolescents from adults can pose a conundrum. This is especially the case when dealing with samples like the late Vindija Neandertals or with individual fossils like KRM 16425. Since the Vindija Neandertals are late, proponents of Assimilation or Multiregional Evolution might expect to them to be more modern-like than earlier Neandertals. The supraorbital fossils Vi 224 and Vi 279 fit this expectation. However, when compared with Le Moustier, these two fossils are clearly adolescent and the transitional aspects of the Vindija supraorbital sample must rely upon other specimens. KRM 16425 is gracile and modern-like in some features. In these features, it may support the expectation of Recent African Evolution that modern human morphology was present at 100 ka in Africa (e.g., Stringer & Gamble 1993). However, our comparison with Le

Moustier indicates that KRM 16425 is just as likely to be an adolescent as it is an adult. Given this, it is unclear whether KRM 16425's gracile anatomy reflects adolescence or modernity. Thus like the Vindija example, claims of full anatomical modernity for the Klasies River Mouth fossils must be based on specimens that are definitely adult.

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