Chapter 5

Modern Human Origins in Central Europe

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Introduction and a Short Historical Background

The review of Central European late Pleistocene fossil hominins included in the 1984 Smith and Spencer volume began with a 1905 quote from Marcellin Boule lamenting the limited availability of information on human remains from Central Europe to Western European (particularly French) scholars (Smith, 1984). The availability of information and the use of Central European information certainly improved between 1905 and 1984. In 1906, for example, Dragutin Gorjanović-Kramberger published his exhaustive monograph on the Neandertal remains from Krapina, the first truly comprehensive monograph on Neandertals, and Gustav Schwalbe (1906) made extensive use of Central European specimens in his treatise on the "Prehistory of Man." Similarly, Aleš Hrdlička (1915, 1930) provided significant coverage of Central European materials in his assessments of the human fossil record. Still, Boule and Vallois's 1957 version of *Fossil Men* provides a far more detailed perspective on Western than Central European hominins and includes almost no coverage of the interpretation of human evolution given by researchers like Schwalbe and Gorjanović-Kramberger, who based their interpretations more on the Central European record.

By 1984, this had certainly changed, due in no small part to a review of Central Europe by Jan Jélinek in 1969 and the impact of the Vindija Neandertal sample (Malez et al., 1980; Wolpoff, 1980; Wolpoff et al., 1981). Beginning with the mid-1980s, the Central European fossil record played a significant role in explanations of modern human origins in Europe and beyond (cf. Smith, 1982, 1984). No longer did the Western European record hold complete sway in such discussions as it had essentially since the late nineteenth century and particularly since the publication of Boule's (1911–1913) classic monograph on the La Chapelle-aux-Saints Neandertal partial skeleton. Furthermore, the Central European fossil record was crucial in dismantling the classic pre-sapiens argument, as the fossils from this region seemed to offer evidence of regional evolutionary continuity from pre-Neandertals through Neandertals to modern humans (Brace, 1964; Jelínek, 1969; Wolpoff, 1980).

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Although improved from earlier times, the chronology of the Paleolithic and hominin fossil records by the 1980s was still sufficiently loose so that gradual, in situ, continuity (Smith, 1984; Wolpoff et al., 1984) was a feasible explanation of the relationship between Neandertals and early modern humans in Central Europe. In large part this was due to the fact that a strong case could be made at this time that modern humans appeared essentially contemporaneously in the Old World, and thus that a classical multiregional pattern of modern human origins was eminently defensible (Smith, 1985). The Krapina-Vindija sequence from Croatia was central to this interpretation, but other fossils were ordered into it, as well. Like the Vindija fossils, the Šal'a frontal was interpreted as more modern-like than other Neandertals and was posited as a relatively late one (Vlček, 1969; Smith, 1984). The "well-dated" "36 ka" Hanhöfersand and "34 ka" Velika Pećina frontals were interpreted as transitional (Smith, 1984) between Neandertals and later modern Europeans, or at least as evidence of admixture between Neandertals and modern humans (Bräuer, 1984, 1989).

Since 1984, many more things have changed. Stringer and Andrews, in their 1988 *Science* paper, synthesized new genetic research[1] with the fossil record and argued that there had been no regional continuity in Eurasia across the archaic-modern boundary. Neandertals had become extinct without issue, they argued, which meant that the Central European fossil record had been misinterpreted as evidence of such continuity. The application of new chronometric techniques, particularly electron spin resonance (ESR), thermoluminescence (TL), and accelerator mass spectrometry (AMS) radiocarbon, to critical sites and specimens increasingly demonstrated that modern humans appeared early in Africa, slightly later in the Near East, and relatively late in Europe—including Central Europe (see review in Klein, 2009). This same chronology showed that Neandertals also survived at least a few millennia after moderns arrived in Central Europe (Churchill and Smith, 2000). The aforementioned genetic evidence was based on interpretations of mitochondrial DNA variation in extant peoples, but this interpretation was soon supported by other studies of both mitochondrial and somatic nuclear DNA, as well as Y chromosome analyses (cf. Underhill et al., 1997; Thomson et al., 2000). Perhaps even more influential has been the recovery of both mitochondrial and nuclear DNA from Neandertals and the former from a few European Upper Paleolithic specimens.[2] Although there were some cautionary voices (e.g., Relethford, 2001a; Templeton, 1993, 2005; Serre et al., 2004), the seemingly majority view from 1990 through 2010 was that genetic data both demonstrated a species-level difference between Neandertals and modern humans and denied any ancestral role for the former in the latter. Bolstered by the genetic studies, morphological arguments became increasingly more focused toward asserting the lack of any anatomical evidence of Neandertal–early modern human introgression. The combined effect of the genetic, chronological, and morphological studies is perhaps best exemplified by the 2009 statement that it is these "fresh data" that "have eliminated all reasonable doubt in the century-old controversy over the fate of the Neanderthals" (Klein, 2009: 751).

Specifically for Central Europe, an improved overall chronological perspective has helped to clarify many aspects of later human evolution. For example, direct dating of some specimens that were considered representatives of the earliest modern people in Central Europe (Table 5.1) has demonstrated each to be latest Pleistocene or more recent in age, and critical sites and specimens now have reliable age estimates.[3] Significant fossil samples have entered the discussion, particularly the Peştera cu Oase and Muierii material from Romania (Dobos et al., 2010; Soficaru et al., 2006; Trinkaus et al., 2003a, 2003b, 2006b) and the Mala Balanica specimen from Serbia (Roksandic et al., 2011). Also, additional discoveries have been made at Dolní Věstonice in the Czech Republic (Sládek et al., 2000), and the entire sample has undergone major reanalysis (Trinkaus and Svoboda, 2006). A complete reanalysis of the Mladeč sample, also from the Czech Republic (Teschler-Nicola, 2006), and new analyses on the Krapina Neandertals (Monge et al., 2008) have been published. While all of these studies are important

Table 5.1. Revised dating for presumed early modern human fossils from Central Europe.

	Supposed Date			Revised Date		
Specimen	^{14}C age or association	Lab No.	Reference	^{14}C age or period	Lab No.	Reference
Western						
Binshof	21,300±320	Fra-40	Henke, 1980	3,090±45	OxA-9880	Terberger & Street, 2001
Hahnöfersand	36,300±600	Fra-24	Bräuer, 1980	7,500±55	OxA-10306	Terberger et al., 2001
Kelsterbach	31,200±600	Fra-?	Protsch & Semmel, 1978	Specimen missing, cannot be redated		Street et al., 2006
Paderborn-Sande	27,400±600	Fra-15	Henke & Protsch, 1978	238±39	OxA-9879	Street & Terberger, 2002
Vogelherd	30,162±1,340	H 4054-3210	Conard & Bolus, 2003	3,980±30 to 4,995±35	KIA 19537 KIA 19540	Conard et al., 2004
Eastern						
Balla	22,300±180 20,000±190	GrN-4660 GrN-4661	Vögel & Walterbolk, 1972	6,660±50	GrA-24712	Tillier et al., 2009
Krems-Hundssteig	Gravettian?		Jungwirth & Strouhal, 1972	3,540±35 3,480±35	OxA-8291 OzA-8290	Trinkaus & Pettitt, 2000
Podbaba	Aurignacian?		Matiegka, 1924	Fossil destroyed, 1921		Churchill & Smith, 2000
Svitávka	Aurgnacian?		Klima, 1963	1,180±50	GrA-13711	Svoboda et al., 2002
Velika Pećina	> 33,850±520	GrN-4979	Vögel & Walterbolk, 1972	5,045±40	OxA-8294	Smith et al., 1999
Zlatý Kůn	Aurignacian?		Prošek et al., 1952	12,870±70	GrA-13696	Svoboda et al., 2002

in their own right, they underscore what is truly the most significant change that has impacted the study of late human evolution in Central Europe. Prior to the reunification of Germany and the subsequent collapse of the Iron Curtain, access to much of the pertinent Central European record was limited. Communication was often challenging, and permission to study many sites and samples was difficult to come by and often quite restricted. This is generally no longer the case. There has been a marked increase in cooperative studies by researchers from many countries on this material. From our perspective, the increased emphasis on the Central European role in modern human origins derives from this more extensive interaction between researchers and the more open access to some material today as compared to 1984.

The following review comments further on these issues and endeavors to bring the most recent perspectives on this critical region into a clearer focus than was possible in 1984. It is not our intention to repeat the morphological details presented in the previous review (Smith, 1984) unless there have been significant changes. As in 1984, the information presented here is divided by affinity (Neandertal or modern). Geographical coverage mirrors that in 1984, except that the division is western and eastern rather than northern and southern. The eastern region consists of the Pannonian Basin, the surrounding highlands that define the basin, and areas adjacent to the highlands but not in the basin itself (Figure 5.1). The highlands form two crescent-shaped systems, one extending from the Alps southward as the Dinaric Alps (Dinarides) along the Adriatic. Toward the south the mountains extend eastward through to the Black Sea and are essentially contiguous with the mountains of Greece to the south. The western crescent is much more rugged and imposing than the eastern crescent, which extends much more intermittently first to the east and then to the south. This eastern crescent is formed by the Transylvanian Alps, Carpathians, Tatras, Sudetes, Erz, and the Bohemian and Bavarian highlands.

Most of the eastern region sites are associated with drainage systems that extend into the highland regions surrounding the Pannonian Basin, but some are located either further into the basin itself, on the opposite side of the highlands from the basin, or in highlands technically not forming the Pannonian Basin. The best examples of the latter are the early modern human sites of Cioclovina, Muierii, and Oase in Romania. These sites are located in areas surrounding the broad Wallachian Plain that marks the Danube's flow toward the Black Sea. Sites like Mujina Pećina on the western slopes of the Dinaric Alps and others on the Adriatic Coast (Karavanić and Smith, 2011) have not yielded human fossils[4] but show that these areas were occupied during the late Pleistocene as well.

Western Central Europe is less precisely defined by geography. Here, we define it as the territory lying north of the highlands described above, extending to the North and Baltic Seas, and essentially from east to west between the Oder and the Rhine River drainages. This is essentially the German portion of the North European Plain. To some degree the separation of this plain from areas to the southwest and east is somewhat arbitrary. Also, relatively moderate highland areas separate this region from eastern Central Europe, and these are penetrated by several river systems, notably the Elbe (Labe) and Danube (Donau). Additionally, ice-free corridors likely linked them throughout the later Pleistocene (Kukla, 1978). Thus, the eastern and western regions of Central Europe were connected throughout the period of interest here, and human populations from the regions were most likely in rather close contact.

Conard and Bolus (2003; Conard, 2006) have focused on the Danube as a major artery for the spread of modern people and their cultural manifestations into Europe. While fossil evidence is non-existent currently (Conard et al., 2004), the early dates for the Aurignacian in the Swabian Jura[5] indicate that modern people may well have used the "Danube Corridor" to enter Europe. However, as discussed later in this review, more evidence is needed to assess this specific issue. Regardless, the Danube River valley was undoubtedly a major artery for movement into and through both regions of Central Europe.

Figure 5.1. Physical map of Central Europe. The dotted line demarcates the western and eastern regions of Central Europe as used in this chapter. Map made with ESRI ArcMap v.10. The basemap is the U.S. National Park Service Natural Earth physical map.

Much of this chapter comprises an overview of the Central European Late Pleistocene hominin fossil record. This overview begins with the Neandertal remains followed by the early modern human remains. Post-Gravettian human remains are, for the most part, not discussed, as our attention is on the pattern and process of Neandertal and early modern human evolution. Following the discussion of the fossil record, we endeavor to provide a critical analysis of the fossil record and the theoretical perspectives that have been applied to its interpretation. Specifically, we bring the Central European fossil record to bear on the following issues: (1) the problem of typology in understanding biology and culture across the transition, (2) the pattern of biological variation among Neandertals, (3) the appearance of modern humans and the disappearance of the last Neandertals, and (4) the degree and pattern of Neandertal and early modern human admixture. The chapter ends with what we consider to be the best interpretation of the current evidence as well as a discussion of the limitations of this evidence.

The Central European Neandertal Fossil Record

The Central European fossil record has clearly been important for our understanding of European Neandertals. In addition to the Feldhofer discovery in 1856, other nineteenth-century discoveries in Central Europe (Šipka, Krapina) were important for demonstrating the validity of Neandertals as a prehistoric hominin population (Trinkaus and Shipman, 1992). Nevertheless, by the mid-twentieth century, the more numerous and better preserved Neandertal fossils of Western Europe had helped shift focus away from Central Europe.

Today, the Central European Neandertal fossil record (see Table 5.2 and Figures 5.2 and 5.3) remains sparse relative to that of Western Europe. Furthermore, aside from the Feldhofer 1 individual, the Neandertal remains are largely fragmentary, even if such sites as Krapina and Vindija preserve many individuals. Despite the limitations of this record, it is essential for understanding the process and dynamics of the origin of modern humans.

Neandertal Fossils from Western Central Europe

Over the last few decades, the fossil record of Neandertals from western Central Europe has only grown marginally beyond the important Kleine Feldhofer Grotte (Neandertal) and Ehringsdorf (see Smith, 1984) collections. Perhaps the most significant recent discoveries have come from the former, with over sixty new skeletal fragments discovered during 1997 and 2000 excavations of discarded cave fill from the original 1856 discovery (Schmitz et al., 2002). More discoveries have come in the form of fragments and/or isolated teeth.[6]

Ehringsdorf

Although Vlček (1993) argued that the Ehringsdorf specimens were more advanced in many ways than Neandertals, the overall morphology of the cranial remains, including the H skull and the mandibles, and postcranial remains is demonstrably Neandertal-like. Henke and Rothe (1994) and Street and colleagues (2006) also suggest that the Ehringsdorf sample exhibits weak development of Neandertal features, but this argument is countered by the specific Neandertal features of the cranium (suprainiac fossa, occipital bunning), the similarity of the two mandibles to other early Neandertals (e.g., Krapina) and the form of the femur (Cartmill and Smith, 2009; Smith, 1984). An OIS stage 7 age for the Ehringsdorf sample is commensurate with all of the age indicators, including chronometric dating of the travertines to ≥ 200 ka (Street et al., 2006).

Table 5.2. Neandertal fossil remains from Central Europe.

Site	Human Remains	Cultural Association	Date(s)	Date Reference(s)
Western Central Europe[1]				
Hohlenstein-Stadel	Femur diaphysis	Mousterian	OIS 5, ≈70–120 ka	Kunter & Wahl, 1992
Hunas	Right mandibular molar	Mousterian	Würm, < 76–79 ka	Rosendahl et al., 2006, 2011
Klausenhöhle-Klausennische	di$_1$[†]	Mousterian	Ca. 50 ka	Schoch, 1973; Street et al., 2006
Klausenhöhle-Untere Klause	Scapula (acromial end)	No provenience	No provenience	Schoch, 1973; Street et al., 2006
Kleine Feldhofer Grotte (Neandertal)	Partial skeleton and fragmentary remains of multiple individuals	Mousterian (Micoquian)	38.6–41.1 ka*	Schmitz et al., 2002
Ochtendung	Frontal & anterior parietals	Mousterian	OIS 6	von Berg et al., 2000
Salzgitter-Lebenstedt	Occipital & parietal	Mousterian	Weichselian 55.6±0.9 kyr BP[2]	Hublin, 1984
Sarstedt, Heldescheim	Temporal, occipital & parietal	Mousterian?	Weichselian or Eemian	Czarnetzki et al., 2001
Sesselfelsgrotte	Two deciduous teeth, neonatal or fetal postcrania	Mousterian	M tooth: 61–91 ka (TL) G tooth & postcrania: 46–61 ka (TL & ^{14}C)	Rathgeber, 2003; Richter, 2002
Taubach	Left M$_1$, left dm$_1$	"Proto-Mousterian" (Tayacian)	OIS 5e?	Behm-Blancke, 1960
Warendorf-Neuwarendorf	Parietal fragment	Mousterian?	≈50–70 ka[2]	Czarnetski & Trelliso-Carreño, 1999; Street et al., 2006
Weimar-Ehringsdorf	Partial cranial, mandibular, and postcranial remains from at least nine individuals	Mousterian	≈230 ka	Blackwell & Schwarcz, 1986
Zeeland Ridges (North Sea)	Frontal bone fragment	None	Pleistocene	Hublin et al., 2009
Eastern Central Europe				
Crvena Stijena (Montenegro)	Canine[3]	Mousterian?[2]	> 39.3 ka[2]	Morley & Woodward, 2011
Gánovce (Czech Rep.)	Partial cranial remains, endocast & molds of radius & fibula	Mousterian	OIS 5e	Vlček et al., 1958
Krapina (Croatia)	Numerous remains of at least eighty-nine individuals	Mousterian	130±10 kyr BP (ESR)	Rink et al., 1995

(*Continued*)

Table 5.2. (*Continued*)

Site	Human Remains	Cultural Association	Date(s)	Date Reference(s)
Kůlna (Czech Rep.)	Maxilla	Mousterian (Micoquian)	45.7 + 2.9/– 2.2 kyr BP[2]	Mook, 1988
Mala Balanica, Sićevo Gorge (Serbia)	Partial mandible[3]	None	> 397–525 ka BP (US-ESR)	Rink et al., 2013
Ochoz-Švédův stůl (Czech Rep.)	Mandible, right M_3, parietal, temporal	1905: none 1964: Mousterian		
Ohaba-Ponor 1 (Romania)	Pedal phalange	Mousterian (with UP elements)	Early Würm	
Šal'a (Slovakia)	S1: frontal bone S2: parietal & partial frontal	None	OIS 5e	Sládek et al., 2002
Šipka (Czech Rep.)	Mandibular symphysis	Mousterian	OIS 3?	Kukla, 1954; Gábori, 1976; Smith, 1984
Stajnia (Poland)	Three teeth	Mousterian (Micoquian)	OIS 5c or 5a	Urbanowski et al., 2010
Suba-lyuk (Hungary)	Mandible, postcrania, partial child cranium	Mousterian (La Quina)	OIS 4[2]	Ringer, 1993
Vindija-level G_3 (Croatia)	Numerous fragmentary remains	Mousterian	≈38–45.6 ka 38.3 ± 2.1 ky BP* > 42 ky BP*	Ahern et al., 2004; Krings et al., 2000; Serre et al., 2004

† Some or all of the fossils are known to be missing or destroyed.

* Direct date(s) on human remains.

[1] All sites are in Germany unless otherwise noted.

[2] Date is very tentative or problematic and should be regarded with caution.

[3] Neandertal designation is unclear.

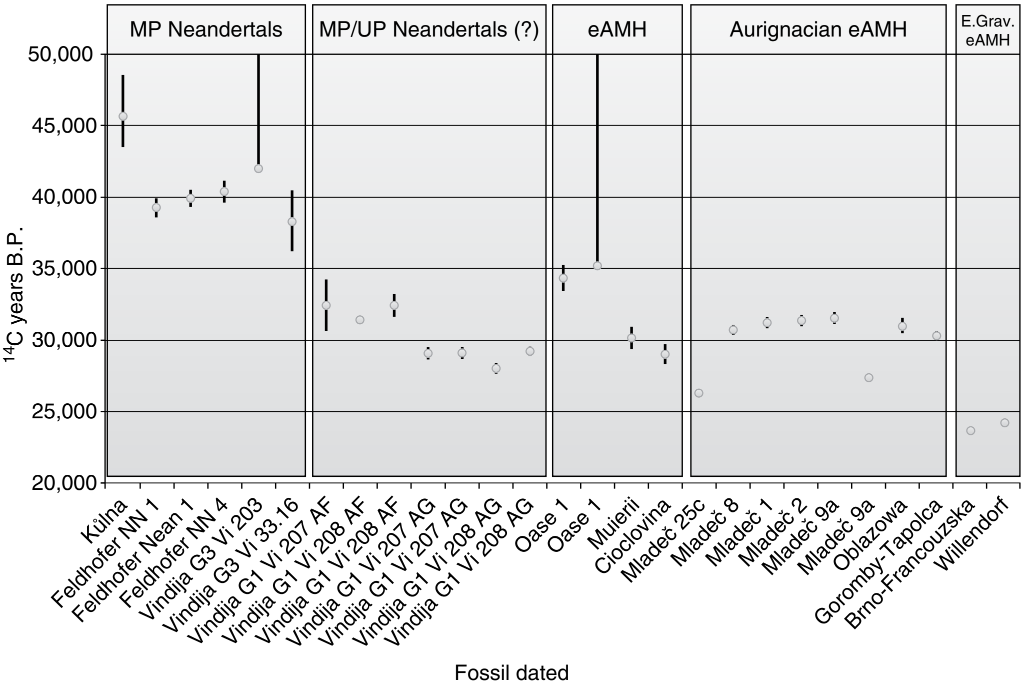

Figure 5.2. Direct radiocarbon dates of Central European Middle and early Upper Paleolithic fossils. "MP/UP Neandertals (?)" refers to fossils associated with the Szeletian *sensu lato*. The older dates for the Vindija level G_1 specimens (denoted by "AF") are ultrafiltration AMS ones. Note: This graph does not include the direct AMS date for D.V. 35 (Trinkaus et al., 1999), since its young age, relative to the archaeological deposits at D.V. I, is likely due to contamination (Pettitt & Trinkaus, 2000).

Kleine Feldhofer Grotte

The location of the discarded sediments from the Kleine Feldhofer Grotte work in 1856 was discovered in 1997 during excavations led by R. Schmitz and J. Thissen. Work in this year uncovered twenty-four fragments of human bone, including a piece that fits onto the original Feldhofer 1's left femur (Schmitz et al., 2002; Schmitz and Thissen, 2000). Artifacts were found that are attributed to both the Micoquian (late Middle Paleolithic) and the Gravettian. An additional thirty-four human specimens were found during renewed excavations in 2000. Aside from the femoral fragment, two other pieces, a left zygomatic-maxilla piece (NN 34) and piece of right temporal bone (NN 35), articulate with the original Feldhofer's remains (Figure 5.4). Additional craniodental and postcranial remains discovered may also belong to the Feldhofer 1 individual, since they do not replicate any of the 1856 specimen's preserved elements. Particularly informative are a chinless mandibular symphyseal fragment (NN 52), two large and heavily worn maxillary incisors (along with several other teeth), several hand bones—including a polical metacarpal with a characteristic flange for the *opponens* pollicis muscle, several vertebrae, and numerous other postcranial remains (Smith et al., 2006). However, some of the new fossils must have come from at least one other adult individual known on the basis of a second right humerus, a second right ulna, and other fragments, and possibly one subadult, represented only by a worn deciduous molar (Schmitz et al., 2002; Smith et al., 2006, 2008).

Although the presence of Gravettian artifacts in the cave fill elicits the possibility that some of the human remains could be modern humans, all of the diagnostic

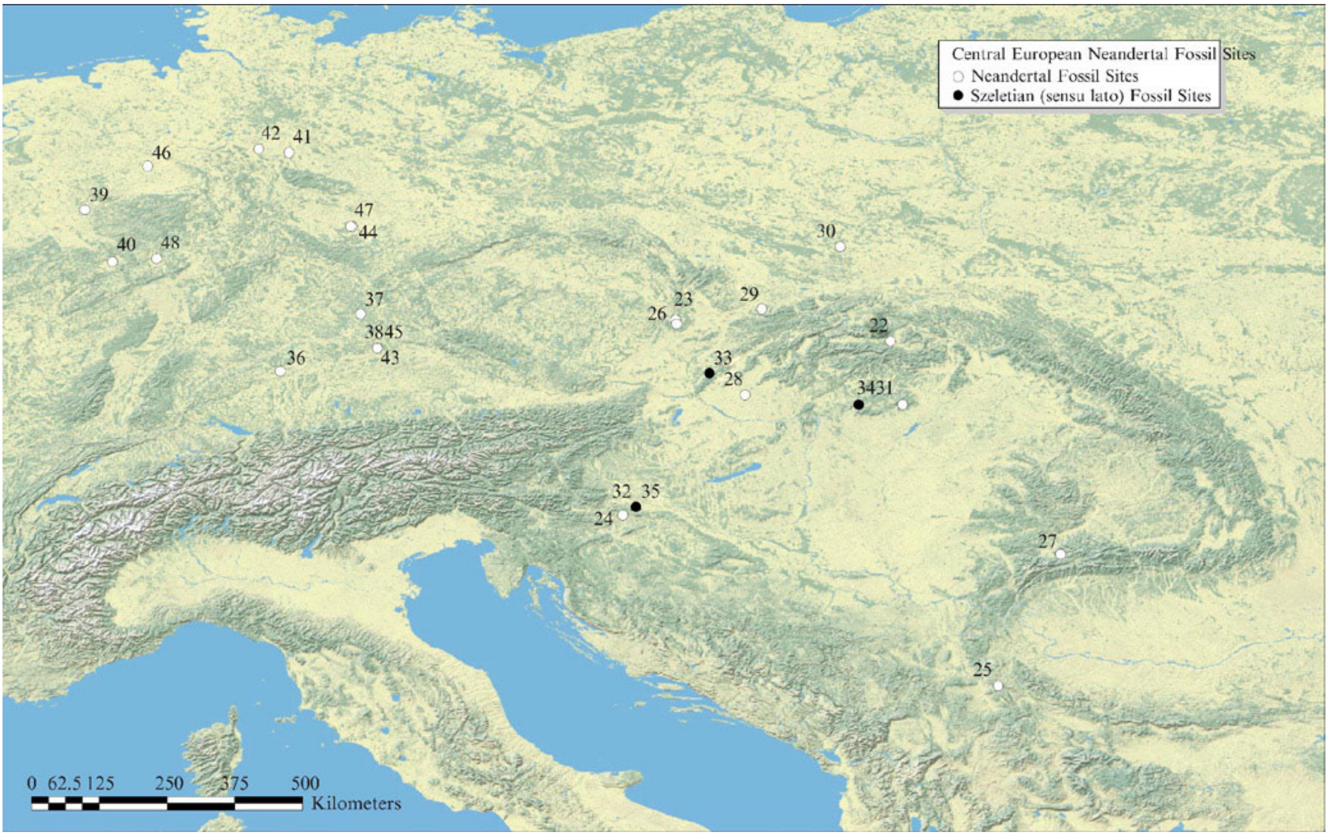

Figure 5.3. Map of Central European Neandertal fossil sites. Map made with ESRI ArcMap v.10. The basemap is the U.S. National Park Service Natural Earth physical map. Neandertal fossil sites:* 22: Gánovce; 23: Kůlna; 24: Krapina; 26: Ochoz (Švédův stůl); 27: Ohaba-Ponor; 28: Šal'a; 29: Šipka; 30: Stajnia; 31: Subalyuk; 32: Vindija G3; 36: Hohlenstein-Stadel; 37: Hunas; 38: Klausennische-Klausenhöhle; 39: Kleine Feldhofer Grotte (Neandertal); 40: Ochtendung; 41: Salzgitter-Lebenstedt; 42: Sarstedt; 43: Sesselfelsgrotte; 44: Taubach; 45: Untere Klause-Klausenhöhle; 46: Warendorf-Neuwarendorf; 47: Weimar-Ehringsdorf. Szeletian *sensu lato* (Neandertal?) fossil sites: 33: Dzeravá Skála; 34: Remete Felsö; 35: Vindija G1. **Zeeland Ridges does not appear on this map. It is located in the North Sea at 51°40′ N, 3°20′ E. Crvena Stijena also is not plotted, since questions remain about its reported Neandertal affinities and its antiquity*.

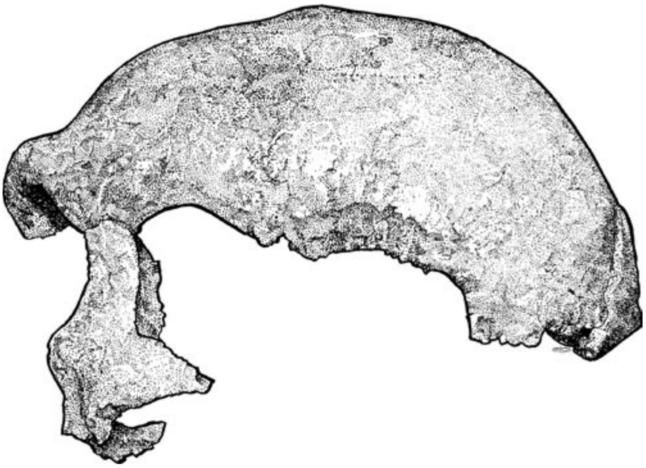

Figure 5.4. The left zygomatic-maxilla (NN 34) articulated with the Feldhofer 1 calotte. Illustration by M. Cartmill.

skeletal specimens are morphologically aligned with Neandertals. Additionally, a three-dimensional analysis indicates that the skeletal remains and Micoquian artifacts can be separated from the Upper Paleolithic tools (Feine, 2006). Stable isotopic studies of the Neandertal skeletal remains reveal a diet strongly focused on meat, but not fish (Richards and Schmitz, 2008), which is commensurate with Neandertal dietary results at other sites (Bocherens, 2011).

The NN 34 zygomatic-maxilla piece is perhaps the most informative of the new discoveries from Kl. Feldhofer Grotte. All of its anatomy is clearly Neandertal (e.g., multiple zygomaticofacial foramina, a columnar lateral orbital pillar, an oblique inferior zygomaxillary margin, and an enlarged maxillary sinus), and this further highlights the "classic" Neandertal appearance of the Feldhofer individual. Under previous interpretations (e.g., Smith, 1984) of the Feldhofer individual, the "classic" Neandertal gestalt was argued to be consistent with it not being a late Neandertal such as those found at Kůlna and Vindija. However, recent AMS ^{14}C dating of both the original Feldhofer 1 as well as two of the recently discovered specimens place the Feldhofer sample as very late. The dates range from 39.24±0.67 ka ^{14}C BP for NN1 to 40.36±0.76 ka ^{14}C BP for NN4, with Feldhofer 1 falling in between (Schmitz et al., 2002). The only Central European Neandertals that are directly dated and more recent are the potentially Upper Paleolithic–associated ones from Vindija G_1, while the Vindija G_3 Mousterian-associated fossils are approximately contemporary to the Feldhofer ones. This new chronological information demonstrates late survival for "classic" Neandertal morphology in Central Europe and contrasts with the "progressive" appearance of the Vindija remains.

In addition to the new fossil discoveries from Feldhofer, work in the 1990s also resulted in the first sequencing of Neandertal DNA extracted from the Feldhofer 1 humerus (Krings et al., 1997). For the 357 bp of mtDNA that was sequenced, the Feldhofer 1 individual fell outside the observed range for paired differences among living humans (although still within the range of probability) and suggested a Middle Pleistocene date of divergence between Neandertal and modern human mtDNA (Krings et al., 1997, 1999). Although much about Neandertal genetics has been learned since (Green et al., 2006, 2010; Hawks, this volume; Krause et al., 2010; Noonan et al., 2006; Schmitz et al., 2002; Serre et al., 2004), the original Feldhofer 1 sequencing was a breakthrough.

Zeeland Ridges

In 2001, the first Neandertal from the Netherlands was recovered off the Zeeland coast in the North Sea (Hublin et al., 2009). This area, known as the Zeeland Ridges, is a part of a large area called "Doggerland." Though now submerged, this relatively shallow region was a part of the European mainland during much of the Pleistocene and earlier, and it has yielded extensive Pleistocene mammal collections over the years. Because of the circumstances, there are some questions regarding the exact age and context of the specimen (Hublin et al., 2009). Morphologically, however, it is a Neandertal frontal bone fragment from the left side that preserves a segment of the supraorbital torus and the squama above it. The torus is projecting, with a slight midorbital reduction, and the squama indicates a relatively flat frontal. The frontal sinus seems restricted to the torus, and all these features indicate the specimen was a Neandertal. There is no direct dating on the specimen, and the oft-cited 50–60 ka date derives from the specimen's similarity to specimens like La Chapelle-aux-Saints.

Regardless of the specimen's date, this specimen shows that Neandertals extended farther north in Central-Western Europe than was previously demonstrated by paleontological evidence. If the 50–60 ka time range proves reliable, it would mean that Neandertals were able to adapt to harsher conditions than previously demonstrated. Although the Zeeland Ridges dating is uncertain, the fact they were inhabiting territory usually submerged in more temperate periods suggests they may have been here during colder times. Tools, potentially made by Neandertals, are found off the coast of East Anglia in Britain (Keys, 2008), suggesting Neandertals ranged even farther north; but these finds are undated and do not help indicate exactly when Neandertals were there. Isotopic analysis of the Zeeland Ridges specimen indicates a diet similar to that indicated for Neandertals in Germany and Belgium (Hublin et al., 2009).

Sarstedt

In 1986, three hominin cranial fragments along with artifacts were discovered during suction dredging of gravel deposits in the Leine River valley south of Hannover, Germany, at the site of Sarstedt (Czarnetzki et al., 2001, 2002). Although their exact age is far from clear, they most likely derive from a warm period during the Weichsel or Eemian glaciations. Although not clearly associated with the human remains, the artifacts indicate either Lower or Middle Paleolithic.

The three fossils comprise a juvenile temporal (Sst I), an occipital fragment (Sst II) with clearly Neandertal anatomy, and a piece of left parietal (Sst III) (Czarnetzki et al., 2001). Czarnetski and colleagues (2001) contend that the temporal, despite an estimated 2–4 years of age at time of death, is likely female based on petrous anatomy. The small mastoid and proportions of the surrounding anatomy clearly align it with Neandertal juveniles such as Krapina 1. Furthermore, Czarnetski and colleagues note two pathological conditions, hydrocephalus internus as well as non-specific meningitis. The Sarstedt II occipital piece exhibits lambdoidal flattening and commensurate occipital bunning, a suprainiac fossa, and an occipital torus, all of which align it with Neandertals. Finally, the Sarstedt III parietal fragment also aligns with Neandertals in its meningeal arterial pattern as well as its curvature (Czarnetzki et al., 2001). Thus, the Sarstedt remains are clearly Neandertal although, without better chronological context, little more can be said.

Hohlenstein-Stadel

Other fragments of Neandertals have been found in western Central Europe during the years since 1984 (Street et al., 2006). A right femoral diaphysis was recovered from

Hohlenstein-Stadel (Swabian Jura) in 1937 but was first analyzed by Kunter and Wahl in 1992. This specimen lacks both epiphyseal ends, but the shaft is well preserved. It lacks a pilaster, giving the specimen a characteristically Neandertal cross-section. The specimen also exhibits a distinct proximal-lateral femoral flange, a characteristic feature for European Neandertals (Cartmill and Smith, 2009). The Hohlenstein-Stadel femur was found in a dark layer in association with fauna correlated to the Eemian (OIS 5), suggesting an age of ~70–120 ka (Kunter and Wahl, 1992).

Hunas

In southeastern Bavaria, the site of Hunas has produced an isolated lower right molar, possibly an M_3, from layer F2 and in direct association with Pleistocene fauna and Middle Paleolithic artifacts (Alt et al., 2006).[7] A speleotherm at the base of the deposits is dated to 76–79 ka by TIMS-U/Th (Alt et al., 2006; Rosendahl et al., 2011). The tooth is younger than this date range, but it is not possible to specify how much younger. First described 20 years earlier (Groiß, 1986), the molar is moderately worn and essentially complete. Alt and colleagues note correctly that the absence of taurodontism in Hunas does not preclude a Neandertal classification (Smith et al., 2006) and consider that the dimensions, enamel thickness, presence of a C-6 cusp, and other features are commensurate with assignment of the specimen to a Neandertal. Kupczik and Hublin's (2010) analysis of the molar root morphologies of Neandertals and modern humans places the Hunas tooth with the latter, yet this may just further demonstrate overlap of the two populations.

Sesselfelsgrotte, Klausennische, and Untere Klause

Also in Bavaria, three caves in the Altmühl Valley (Sesselfelsgrotte, Klausennische, and Untere Klause) have yielded fragmentary Neandertal remains (Rathgeber, 2003; Street et al., 2006). In Sesselfels, two deciduous teeth (both lost at about 12 years of age) and a partial postcranial skeleton of a probable fetal skeleton come from three different levels (Orschiedt, 2000). Unfortunately these have not been described in detail. The skeleton and one tooth derive from the G complex at the site and are associated with TL dates of 51–61 ka and radiocarbon dates that span a larger range but cluster at 46–48 ka (Richter, 2002). The second tooth comes from the earlier level M, with TL dates from 61 to 91 ka (Richter, 2002). Street and colleagues (2006) describe the Untere Klause specimen as the acromial end of a Neandertal clavicle and the Klausennische specimen as a deciduous lower central incisor associated with tools typical of the Middle Paleolithic in much of Germany.

Warendorf-Neuwarendorf

Further northwest, at Warendorf-Neuwarendorf, near Münster and just east of the Rhine, an anterior right parietal was discovered in so-called bone gravels (Czarnetzki and Trelliso-Carreño, 1999). The specimen is purportedly associated with Pleistocene fauna and Middle Paleolithic artifacts, but there is some uncertainty as to the parietal's stratum of origin (Street et al., 2006). The specimen is assigned to an interstadial in OIS 4 at ~50–70 ka, although this must be viewed as an estimation. The Warendorf parietal is described as being practically identical to the specimens from La Chapelle-aux-Saints and Feldhofer in terms of relative curvature and has an archaic pattern of the middle meningeal artery impressions on the bone's internal table, leading Czarnetzki and Trellisó-Carreño (1999) to designate the specimen as a Neandertal. In addition, Scholtz and colleagues (2000) identified a Neandertal genetic signal from this specimen using the southern blot hybridization technique.

Ochtendung

Positioned slightly west of the Rhine but still lying in the greater Rhineland Basin is a partial Neandertal cranium from Ochtendung (von Berg, 1997a, 1997b; von Berg et al., 2000). Ochtendung was recovered close to deposits of Middle Paleolithic tools and Pleistocene fauna (von Berg, 1997b). Von Berg and colleagues (2000) also reported the specimen was found in association with three purportedly Middle Paleolithic tools, and it is considered likely that the Ochtendung skull derives from deposits of the Saal glacial period—OIS 6. The specimen is a frontal and anterior parietals of an adult (probably male) individual, but the supraorbital region is unfortunately missing. The sagittal curvature is described as slight, with a low position and weak development of the parietal tuber (indicating a characteristically Neandertal oval coronal profile). Furthermore, the marked thickness of the specimen, and its large overall size (Condemi, 1997; von Berg et al., 2000) are commensurate with a Neandertal designation.

Neandertal Fossils from Eastern Central Europe

Unlike the case for western Central Europe, hardly any new sites have yielded Neandertal fossils in eastern Central Europe since Smith's 1984 review. A partial mandible from Mala Balanica (Serbia), originally thought to be Neandertal-aged (Roksandic et al., 2011), is now much too early (Rink et al., 2013), while the age and affinities of a single canine from Crvena Stijena (Montenegro) are uncertain (Roksandic, personal communication; R. Whallon, personal communication).[8] Although new, important specimens have been described from the previously known sites of Krapina and Vindija and a new locality at the site of Šal'a, the major contributions have come in the form of new analyses of previously known fossils.

Neandertal Fossils from Moravia

Smith's (1984) descriptions of the Ochoz and Šipka fossils from Moravia remain valid today, and little further analysis has been conducted on these fragmentary remains. The Ochoz fossils[9] comprise a mandible, two cranial fragments, and a molar (Smith, 1984; Vlček, 1969), while the Šipka fossil is a mandibular symphysis piece. Anatomically, both fall with Neandertals.

Šal'a

The frontal bone from the Slovakian site of Šal'a was discovered in 1961 (Smith, 1984; Vlček, 1969). In the mid-1990s, a left parietal and portion of a frontal bone (Šal'a 2) were found in secondary deposits along the Váh River near the find spot of the 1961 specimen (Jakab, 1996; Sládek et al., 2002). Jakab (1996) identifies these new remains as Neandertal. Reinvestigation of the Šal'a site's biostratigraphy indicates that the fossils date to OIS 5e, making them similar in age to the Neandertals from Krapina and Ganovcé (Sládek et al., 2002).

Early interpretations of Šal'a 1 (Jelínek, 1969; Smith, 1982, 1984; Vlček, 1969) saw it as representing a transitional population between more robust Neandertals and Upper Paleolithic modern humans. Key to this interpretation was the overall thinness of Šal'a's supraorbital torus with its midorbit pinching (Smith and Ranyard, 1980). Furthermore, Wolpoff (1999) contended that the Šal'a 1 frontal was just as similar to the Skhūl-Qafzeh hominins as it was to Neandertals. However, a recent morphometric analysis (Sládek et al., 2002) demonstrates that the Šal'a specimen is most like Neandertals. In some respects, it is similar to the Skhūl-Qafzeh fossils, but its sagittal curvature and supraorbital morphology are more like Neandertals.

Suba-lyuk

Adult and juvenile fossils associated with La Quina type Mousterian artifacts were discovered in 1932 at the cave site of Suba-lyuk (Hungary) (Bartucz et al., 1940; Mester, 2004; Tillier et al., 2006). Based upon faunal evidence, the remains may date to OIS 4 (Ringer, 1993), although, as Tillier and colleagues (2006) point out, this needs to be confirmed by absolute dating. The adult fossils (Suba-lyuk 1) comprise a partial mandible as well as teeth and some postcrania (Smith, 1984). It is unclear whether or not these adult remains belong to the same individual (Tillier et al., 2006). Suba-lyuk 2 is the partial cranium and isolated teeth of an approximately 3-year-old child (Tillier et al., 2006). Anatomically, the Suba-lyuk specimens align with Neandertals, although Pap, Tillier, and colleagues (Pap et al., 1996; Tillier et al., 2006) emphasize their mosaic appearance and stress that the Suba-lyuk fossils demonstrate the variability of Middle Paleolithic Europeans.

Krapina

The largest sample of Neandertal skeletal remains from Central Europe comes from deposits removed from a rock shelter on Hušnjakovo Brdo (Hušnjak Hill) on the outskirts of the town of Krapina in northern Croatia. The site was excavated between 1899 and 1905 by the eminent Croatian paleontologist Dragutin Gorjanović-Kramberger. Gorjanović published just under one hundred papers on Krapina from 1899 until 1929, but his best-known work is a detailed monograph published in 1906. Gorjanović's work at Krapina has been assessed by Radovčić (1988), who situates this work in a historical and current context.

The impressive Krapina sample continues to be a wealth of information about Neandertals (Frayer, 2006; Frayer et al., 2007). The papers, books, theses, and dissertations focusing on this collection since Smith's (1976b) pioneering work are far too many to list and cover fully here. Since Smith's 1984 overview of the site, the skeletal sample has grown from just under nine hundred to over a thousand elements, mainly through careful searching of the faunal sample from the site. These additional fossil identifications and associations (Ahern, 2006b; Caspari and Radovčić, 2006; Minugh-Purvis et al., 2000; Radovčić et al., 1988) have added to the already unparalleled perspective on populational variation within Neandertals. Unfortunately, most specimens are isolated teeth, complete smaller bones (especially hand and foot bones), and fragments of other bones. Krapina has five informative partial crania and some eleven maxillae and twelve mandibles (excluding sixteen rami) in various states of completion. There are, however, relatively large samples of specific bones or parts of bones that have allowed a fuller understanding of various aspects of Neandertal anatomical variability. A systematic catalog of the Krapina hominin remains was published in 1988 (Radovčić et al., 1988), and an updated edition is currently in press.

Several other informative publications by the Croatian Natural History Museum followed the 1988 skeletal catalog. A radiographic atlas of the collection was published 11 years later (Kricun et al., 1999). A systematic bibliography for the years 1899 through 2004 was assembled for the centennial of the publication of Gorjanović's 1906 monograph (Frayer, 2006). A series of thirty-two papers on various aspects of the Krapina sample were published by the Croatian journal *Periodicum Biologorum*, also in 2006; and 2 years later these were reprinted in a volume published by the Croatian Natural History Museum (Monge et al., 2008).

Finally, a thorough analysis of the fauna from Krapina and what these remains can tell us about certain aspects of Neandertal behavior is provided by Miracle (2007).[10] These and other publications since 1984 reflect the openness of the Krapina collection for research by qualified scientists regardless of their theoretical orientation. This continued open access policy has resulted in a great deal of important research and has enhanced the importance of the Krapina collection for the understanding of Neandertal paleobiology.

One of the most significant changes in our knowledge about Krapina involves the age of the deposits. Gorjanović recognized thirteen stratigraphic levels at the site, with eight containing Mousterian artifacts and human skeletal elements (Gorjanović-Kramberger, 1906; Simek and Smith, 1997; Smith, 1976b). Based on his observation that the rock shelter matrix at Krapina disintegrated rapidly, Gorjanović (1913) estimated that the culture-bearing deposits accumulated over about an 8,000-year period. Based on the fauna, he (1906) assigned the deposits to a warm, interglacial period. More recent analysis by Malez (1978) concluded that the deposits represented a much longer period, stretching from the last interglacial until well into the last glaciation, perhaps into mid-OIS 3. Malez's perspective had important implications for the fossil human remains. While the majority of the remains derive from levels 3 and 4, Gorjanović's "Homo Zone" correlated to the last interglacial (OIS 5e); isolated finds were also found in levels 5–7, with a second mini-concentration of hominin fossils in level 8 (Radovčić et al., 1988; Smith, 1976b). Except for the level 8 remains, all of the other specimens were definitively Neandertal in morphology, and no evidence for change over time could be identified (Smith, 1976b). However, if level 8 was really "late," the suggestion of "transitional" anatomy in the remains from this level would take on added significance (Minugh-Purvis et al., 2000).

In 1995, Rink and colleagues presented a series of ESR dates for the Krapina site. The dates from levels 1, 5–6, and 7–8 are indistinguishable from each other and clustered about a mean of 130 + 10 kya, which indicates the entire sequence was deposited within OIS 5e, the last interglacial. Miracle's faunal analysis indicates that habitation at Krapina extended beyond the last interglacial (OIS 5e) into the subsequent colder stage of 5d (Miracle, 2007). He notes no support for Malez's extended habitation through the later Würm but suggests that the extent of occupation may have been around 20,000 years, from 130 to 110 kya (Miracle, 2007). Analysis of the Krapina lithics reveals a behavioral shift from levels 3/4 and level 8 in material procurement and in site use but nothing that falls out of the realm of Neandertal behavior (Simek and Smith, 1997). In total, this new evidence supports Gorjanović's perspective on the age and length of occupation of the site.

The dating firmly establishes Krapina as an "early" Neandertal sample. It also specifically impacts the interpretation of the level 8 remains. Most prominent is the Krapina (Kr 1) cranium, also known as the A skull. It is a partial calvarium of a juvenile, aged 6–8 years (Minugh-Purvis et al., 2000; Smith, 1976b). The specimen has been suggested to show progressive features compared to other Neandertals (cf. Škerlj, 1958), particularly in frontal curvature, frontal boss development, glenoid fossa morphology, and browridge shape and development. Detailed analysis of these and other features, however, demonstrates that all can be matched in other Neandertals (Minugh-Purvis et al., 2000). Thus, the total morphological pattern, viewed in a comparative context, "strongly supports the contention that Krapina 1 derives from a European Neandertal population" (Minugh-Purvis et al., 2000: 422). Therefore, the evidence indicates that all of the Krapina hominin skeletal remains are Neandertals, commensurate in morphology with their relatively early age. Again, this result supports Gorjanović's interpretation that more modern humans were not present at Krapina (Gorjanović-Kramberger, 1913).

Debate still surrounds the predepositional treatment of the Krapina human bones. Some have argued that the bones show evidence of human processing, perhaps related to dietary

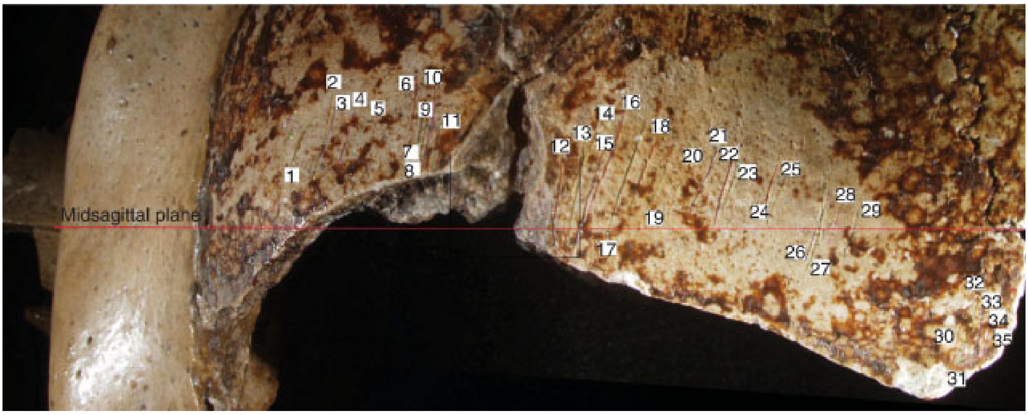

Figure 5.5. Krapina 3 frontal bone exhibiting a series of cutmarks that Frayer and colleagues (2008) have interpreted as a funereal behavior not related to cannibalism or defleshing. Each number labels one of the thirty-five identified cutmarks. Image from Frayer et al. (2008) and courtesy of D. W. Frayer.

cannibalism (White, 2001), while others have interpreted the level of preservation of the remains as requiring some form of burial (Russell, 1987a,b; Trinkaus, 1985). To some extent, both may be true. Most investigators have recognized some post-mortem manipulation of the Krapina human remains (see discussion in Smith, 1976b), including the recent suggestion of ritual treatment of the Krapina C (Kr 3) skull (Figure 5.5; Frayer et al., 2008). Gorjanović (1904) noted that the manner of breakage and burning of the human bones reflects an "Akt des Kannibalismus." In his description of the Krapina deposits in the same publication, Gorjanović notes that animal bones were discarded toward the walls of the rock shelter rather than the center. He then states that the human bones were treated in the same manner and that these bones were preserved in concentrated bone middens ("Knochenhaufen") near the walls of the rock shelter (Gorjanović-Kramberger, 1904). This circumstance contributed to the state of preservation of the fragmentary remains, both animal and human, at the site. Thus the "burial" of the Krapina human bones may not relate to any form of intentional interment.

The description of the Krapina people provided earlier (Smith, 1984) is fundamentally accurate today, although it has certainly been enhanced by many subsequent studies (Monge et al., 2008). That description noted that despite the variation present in the Krapina sample, no feature or specimen in that sample falls outside the Neandertal morphological realm, a conclusion also emphasized in recent discussions (Cartmill and Smith, 2009; Schwartz and Tattersall, 2008). Some studies have enhanced the Neandertal signature of the Krapina remains particularly in the clavicle (Voisin, 2008), posterior dentition (Bailey, 2008) and occipital bones (Caspari, 2008). In the latter context, reconstruction of the rear vault of Krapina 5 (Figure 5.6) demonstrates the presence of occipital bunning in adult specimens at the site, a condition already documented for the subadult Krapina 2. Pearson and Busby (2008) find that many postcranial aspects of the Krapina sample do not exhibit the extent of development of later "classic" Neandertals. However, there is a strong possibility of an overabundance of females in the sample (Ahern, 2008). Thus the perceived differences noted by Pearson and Busby (2008) are likely due to a sex bias in the sample. Overall then, there is nothing at Krapina that questions their recognition as "typical" Neandertals in terms of morphology or behavior.

Figure 5.6. The Krapina 5 reconstruction by Caspari and Radovčić (2006) showing the three newly associated temporal pieces. Image courtesy of R. Caspari.

Vindija

Excavations at Vindija Cave (Croatia) during the 1970s and 1980s yielded late Mousterian and early Upper Paleolithic human remains representing the best evidence about late Neandertals in Central Europe (Janković et al., 2006; Malez and Ullrich, 1982; Wolpoff et al., 1981). While the majority of the Vindija collection was described in 1981 (Wolpoff et al., 1981), additional specimens were published in later years (Ahern et al., 2004; Smith and Ahern, 1994; Smith et al., 1985). Although fragmentary, multiple individuals are preserved for many anatomical elements, especially in the case of mandibles and frontal bones. This has made Vindija the focus of numerous analyses from the 1980s onward.

All of the Pleistocene Vindija hominin fossils with known provenience derive from stratigraphic complexes G and F.[11] Most of these specimens come from level G_3 within the G complex, while the remainder derive from G_1, F_d or $F_{d/d}$. Archaeologically, the G and F deposits span the Middle to Upper Paleolithic transition, with level G_3 containing a late Mousterian assemblage, G_1 an initial Upper Paleolithic assemblage,[12] and F_d and $F_{d/d}$ an Aurignacian-like assemblage. Over time within the Mousterian sequence of the site there is an increase in the frequency of the Upper Paleolithic elements and higher quality raw materials (Ahern et al., 2004; Janković et al., 2006, 2011). Parallels for this can be seen within the Late Mousterian of neighboring Italy (Peresani, 2011).

Chronologically, level G_3 likely represents the Lower Würm stadial (~38–45.6 ka) based upon the composition of the fauna as well as direct AMS radiocarbon dating of two hominin specimens (> 42 ka ^{14}C BP, Krings et al., 2000; 38.31 ± 2.31 ka ^{14}C BP, Serre et al., 2004) as well as a U-Th (41.0 + 1.0/–0.9 ka BP, Wild et al., 2001) dating of cave bear bone. The chronology for level G_1 appears to be somewhat more complex. Sedimentologically, G_1 is a reddish-brown clay that is distinct in the Vindija sequence. This clay represents a warmer

Figure 5.7. A split-based bone point (Vi 3437) and a diagnostically Neandertal mandibular ramus (Vi 207) excavated from level G_1 at Vindija Cave. Direct ultrafiltration AMS ^{14}C dating of the ramus provided a date that is consistent with the early Upper Paleolithic. Attempts at direct dating the point have, thus far, not been successful. The scale is 1 centimeter.

period and has been suggested to be from the Podhradem interstadial (Musil and Valoch, 1966) in age (Ahern et al., 2004; Wolpoff et al., 1981). The radiometric dates for G_1, including direct AMS and ultrafiltration AMS dates on two of the Neandertal specimens as well as AMS radiocarbon and U-Th dates on cave bear bones, indicate that the deposits date to sometime between 29 and 34 ka. Two radiocarbon dates, both from cave bear bone, have yielded spuriously young (18.28±0.44 ka ^{14}C BP, Z-2432, Obelić et al., 1994) and old (46.8 + 2.3/–1.8 ka ^{14}C BP, VERA-1428, Wild et al., 2001) dates. Although the younger non-AMS date is likely due to contamination by young carbon, the older date highlights the possibility that the G_1 collection includes items mixed in from under- and/or overlying levels via cryo- and/or bioturbation (Zilhão, 2009). Such possible mixture has been used to explain away the apparent Neandertal–Upper Paleolithic association in level G_1 (Kozlowski, 1996; Montet-White, 1996; Stringer, 1982; Zilhão, 2009; Zilhão and d'Errico, 1999). None of the artifacts recovered from G_1 exhibit characteristics consistent with such movement (Karavanić and Smith, 1998) and the Upper Paleolithic split-base bone point (Figure 5.7) and most of the Neandertal fossils came from areas in the cave lacking any observable cryoturbation (Wolpoff et al., 1981). Furthermore, the direct AMS radiocarbon dates of two of the G_1 hominin fossils are consistent with an early Upper Paleolithic age (Higham et al., 2006). However, recent lithic refitting analysis by Bruner (2009, 2011) clearly indicates more level mixing than had previously been realized. Furthermore, attempts to directly date the typologically Aurignacian split-base bone point (Figure 5.7) from G_1 have thus far proven futile. Nevertheless, it is important to keep in mind that, for those hominin remains that have been directly dated, these dates have been consistent with the fossils' level designations (i.e., G_3 fossils date older than G_1 ones; but see Zilhão, 2009). Finally, a cave bear bone from level $F_{d/d}$ has been radiocarbon dated to 26.6±0.93 ka ^{14}C BP (Z-2433, Obelić et al., 1994), while three other dates on charcoal from complex F range from 24±3.3 ka 14C BP to 29.7±0.6 ka ^{14}C BP. Although these dates are fairly consistent, the presence of Neandertal-like hominin remains from $F_{d/d}$ and F_d combined with Bruner's (2009, 2011) work suggests that some mixing may have affected the F complex. Unfortunately, we may never have a precise understanding of the chronology of all of the fossils, artifacts, and fauna from Vindija. Further direct dating of the hominin remains and, perhaps, bone artifacts may improve our understanding, but questions will likely always remain.

Early interpretations of the biology of the Vindija late Neandertals, such as those by Smith (1982, 1984), posited that the Vindija sample represented a population transitional between earlier Neandertals, such as those represented at Krapina, and Upper Paleolithic modern humans. Aspects of the Vindija remains that appear intermediate include reduced midfacial prognathism, reduced nasal breadth, thinner cranial vaults, reduced postorbital constriction, development of incipient chins, reduction and shape changes in the supraorbital region, a broad braincase relative to upper facial breadth, a higher vault with a more vertical forehead, and a modern-like scapular glenoid breadth (Ahern, 1998; Ahern et al., 2002, 2004; Smith, 1982, 1984; Smith and Ranyard, 1980; Smith and Trinkaus, 1991; Wolpoff et al., 1981).

Although Vindija's morphological intermediacy was interpreted by many as evidence of an evolutionary transition from Neandertals to modern humans, others offered alternative explanations. Howell (1984) and others (Bräuer, 1989, 1992; Klein, 1999; Stringer et al., 1984) suggested that the morphological intermediacy of the Vindija hominins stemmed from an overabundance of females and/or juveniles in the sample or that the Vindija population had small body size compared to other Neandertals and thus were more gracile than the earlier Neandertals from Krapina. However, simulation analyses as well as comparisons with extant referent populations demonstrate that neither sex- nor age-related sample bias is a likely explanation of the Vindija sample's intermediacy (Ahern, 2006b; Ahern et al., 2002; Ahern, 1998; Ahern and Smith, 2004; Kesterke and Ahern, 2007). Furthermore, the body sizes of the Vindija hominins were not significantly smaller than other Neandertals (Trinkaus and Smith, 1995). Although the morphological intermediacy of the Vindija late Neandertals may have not been evolutionary but caused by independent factors (Klein, 2009), we contend that gene flow with modern populations is the most parsimonious explanation.

As chronological revisions and new genetic and fossil data during the late 1980s and 1990s called into question equipolycentric explanations of modern human origins such as classic Multiregional Evolution, newly identified fossils from Vindija combined with new analyses, including the direct AMS ^{14}C dating of some of the remains discussed above, have required a rejection of the idea that the Vindija population was an intermediate step in a gradual evolution of Neandertals into modern humans. What has resulted is a more nuanced interpretation of the Vindija sample (Ahern et al., 2004; Janković et al., 2006, 2011). Some of the Vindija fossils published since the 1980s, such as the gracile Vi 308 medial supraorbital (Smith and Ahern, 1994) and the Vi 284-255-256 partial calotte (Figure 5.8; Ahern et al., 2004) confirm the sample's morphological intermediacy, while other specimens, such as the robust Vi 307 zygomatic (Smith and Ahern, 1994) and the Vi 13.8 radius (Ahern et al., 2004) fall well within the Neandertal range of variation. While the more modern-like aspects of the late Mousterian-associated Neandertals from Vindija likely reflect gene flow from outside of the region prior to any significant modern colonization of Europe, the persistence of level G_1 specimens with Neandertal gestalt at approximately 29–34 ka (Higham et al., 2006) possibly associated with an initial Upper Paleolithic industry indicates a complex biocultural scenario (Ahern et al., 2004; Janković et al., 2011). Ahern and colleagues (2004) suggest that the Vindija evidence is consistent with a scenario whereby Neandertals, as illustrated by the Krapina – Vindija sequence, changed over time through gene flow and common selection with contemporary peoples, but that some European populations, including those represented by the G_1 (and possibly F) hominins, remained identifiably Neandertal upon the arrival of intrusive modern humans.

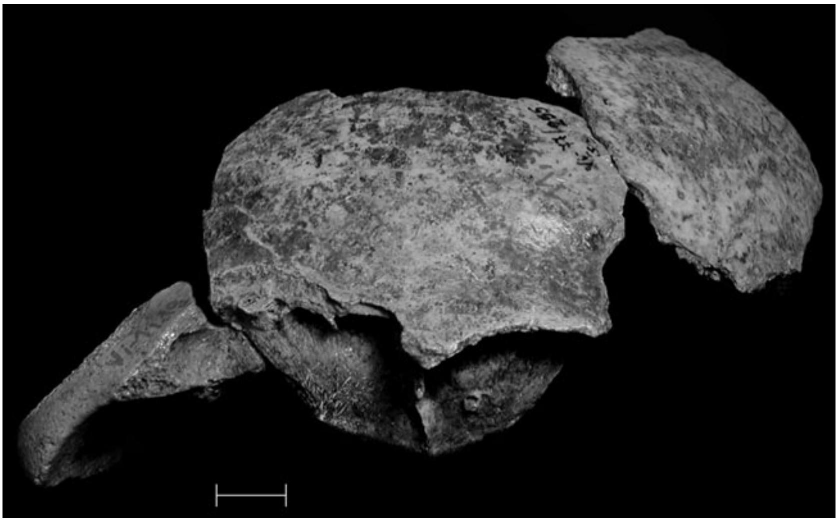

Figure 5.8. Vindija 284-255-256. This is the most complete cranial specimen from Vindija Cave. A fourth piece, the Vi 230 parietal, that was associated with Vi 256 by Wolpoff et al. (1981) and Ahern et al. (2004) is likely from a younger individual. The scale is 1 centimeter.

Mala Balanica

A recently discovered partial mandible from Mala Balanica, Serbia (Roksandic et al., 2011), raised questions about the pattern of Middle to Late Pleistocene evolution in southeastern Central Europe. The mandible, comprising a piece of left corpus preserved from the canine alveolus to the anterior margin of the ramus, exhibits a suite of characteristics that align it more with Early and Middle Pleistocene *Homo* than with Neandertals (Roksandic et al., 2011). Most surprisingly, the original interpretation of the archaeological, geological, and radiometric evidence suggested possible contemporaneity with the OIS 5e Krapina Neandertals (Roksandic et al., 2011). However, recent ESR dating of associated animal teeth provided an estimated age of at least 397–582 ka BP (Rink et al., 2013). Thus, Mala Balanica's primitive anatomy must be considered within the context of Middle Pleistocene human evolution and is not directly relevant to modern human origins in Central Europe.

Stajnia

Stajnia Cave (Poland) is located in the highlands about 100 km north of the Carpathian Mountains. At this site, three human teeth were excavated from deposits yielding Middle Paleolithic (Micoquian) artifacts and Pleistocene fauna. A cave bear bone from these deposits yielded an AMS radiocarbon age of > 49 ka; and the overall archaeological and faunal context suggests an age of either late OIS 6 or 5d (Urbanowski et al., 2010), which could mean an age in excess of 100 ka. One tooth, a right M^2, has been described to date, with the others still in analysis. The molar is heavily worn, thus precluding the identification of specifically Neandertal crown morphology, but crown dimensions, hypocone size, and pattern of relative cusp sizes are commensurate with Neandertal affiliations (Urbanowski et al., 2010). Urbanowski and colleagues also report that DNA was extracted from the specimen. This yielded a male genotype not typical of recent humans or chimpanzees, but the sample was too degraded to allow conclusive determination of Neandertal affinities.

Neandertals of the Initial Upper Paleolithic?

Artifact assemblages, exhibiting a mixture of Middle and Upper Paleolithic elements and dating to the Hengelo interstadial and the beginning of the following stadial, have been described from a variety of sites across Eastern and Central Europe. These assemblages are characterized by the presence of leaf-shaped points and can be classified as Szeletian *sensu lato* (cf. Allsworth-Jones, 1986; Churchill and Smith, 2000). Only three sites have any hominin remains found in association with these "transitional" assemblages: Vindija, Dzeravá Skála, and Remete-Felső (Figure 5.3 and Table 5.3). Vindija has only one Szeletian tool.

At Vindija, diagnostically Neandertal remains; Mousterian, Szeletian, and Aurignacian lithics; and bone points (including a split-base one, Figure 5.7) were recovered from level G$_1$ (Ahern et al., 2004; Smith and Ahern, 1994; Wolpoff et al., 1981). These co-occurrences may have been the result of mechanical mixing of sediments (Allsworth-Jones, 1986; Bruner, 2009, 2011; Zilhão, 2009; Zilhão and d'Errico, 1999). However, as discussed above, there are compelling reasons to accept a co-occurrence of Neandertal remains and initial Upper Paleolithic artifacts at Vindija. One reason, not discussed above, is that the Vindija situation is not unique (Svoboda, 2005). Aurignacian-like bone and antler points have been found in association with Szeletian points at Mamutowa, Istálloskö, Szeleta, and Dzeravá Skála in addition to Vindija level G$_1$ (Svoboda, 2005). As Svoboda (2005) notes, such archaeological associations are not easy to explain away as the result of mechanical mixing when they are found at so many sites.

The unerupted hominin mandibular molar from Dzeravá Skála, Slovakia, was discovered during the sorting of faunal remains after excavation (Allsworth-Jones, 1986; Hillebrand, 1914). Although likely an M$_2$, Bailey and colleagues (2009) suggest that an M$_1$ designation cannot be ruled out. According to Hillebrand (1914), the tooth exhibits a well-developed anterior fovea, like Neandertals. While Tillier and colleagues (2005) see the taxonomic attribution of this tooth as ambiguous, Bailey and colleagues' (2009) analysis on non-metric aspects places the Dzeravá Skála tooth with Upper Paleolithic modern humans. As is the case with Vindija level G$_1$, the associated artifact assemblage is a mixture of Szeletian lithics and Aurignacian-like bone points (Hillebrand, 1914; Prošek, 1953). Also, like Vindija G$_1$, cryoturbation may have caused some level mixing at Dzeravá Skála (Prošek, 1953). Excavations at

Table 5.3. Central European human remains[1] associated with transitional assemblages (Szeletian *sensu lato*)

Site	Human Remains	Cultural Association	Date(s)	Date Reference(s)
Dzeravá Skála (Slovakia)	M$_1$ or M$_2$ germ[1]	Szeletian *sensu lato*[2]	> 44.6 ky BP	Davies et al., 2005
Remete Felsö (Hungary)	Two incisors and a canine[1]	Szeletian *sensu lato*[2]	OIS 3	Gábori-Csák, 1983; Vörös, 2000; Tillier, 2006
Vindija—level G$_1$ (Croatia)	Fragmentary cranial, dental, and postcranial remains	Szeletian *sensu lato*[2]	OIS 3 30.6–34.2 ka[*,3]	Higham et al., 2006

*Direct date(s) on human remains.

[1] The taxonomic affinities of these remains is contentious. See text.

[2] Questions remain about the co-association of all of the artifacts and the human remains. See text.

[3] Time span based on direct ultrafiltration AMS dates only (Higham et al., 2006). Earlier direct AMS (non-ultrafiltration) provided a time span of ≈ 28.7–29.6 ky BP (Smith et al., 1999).

Dzeravá Skála during 2002–2003 (Kaminska et al., 2005) focused on establishing a better chronology for the cave sediments, especially in regard to the Middle–Upper Paleolithic transition. Unfortunately only a single date was obtained for layer 11 (the Szeletian *sensu lato* level from which the tooth reportedly derives). This AMS radiocarbon date of > 44.6 ka ^{14}C BP (OxA-13973, Davies and Hedges, 2005) is considerably older than the dates for other "transitional" industries in Central Europe. Davies and Hedges (2005) suggest that the layer 11 artifacts may actually be Middle Paleolithic rather than Szeletian, based upon this single date. The single, minimal date, combined with the taxonomic ambiguity of the hominin tooth and the potential that cryoturbation caused level mixing at the site, all undermine the importance of the Dzeravá Skála tooth for understanding modern human origins in Central Europe.

As was the case with the Dzeravá Skála tooth, the two right lower incisors and a canine from Remete Felsö, Hungary, are reported to have been found among faunal remains that were found in association with twelve lithics (Gábori-Csánk, 1983; Tillier et al., 2006). The lithic assemblage appears to be a Szeletian variant (Gábori-Csánk, 1983). According to Tillier and colleagues (2006), the heavily worn Remete Felső teeth are morphologically undiagnostic in terms of whether they are Neandertal or modern human.

In sum, the Szeletian *sensu lato*–associated hominin remains are scarce. The Dzeravá Skála tooth may be modern-like but is not clearly so. Furthermore, its current dating seems to indicate that it may be Middle Paleolithic and not Szeletian at all. Although the Vindija G_1 fossils are the most numerous and the most diagnostic of the hominin remains associated with a "transitional" industry, questions remain about their co-occurrence with the Szeletian (*sensu lato*) artifacts. Finally, the population affinity of the Remete Felsö teeth is ambiguous. Thus, it is possible that only Neandertals are associated with the Szeletian in Central Europe, but it seems to be equally possible that only modern humans are. If such an association is confirmed, it would appear to be similar to the situation on the Italian peninsula, where recent analysis of hominin deciduous molars associated with another "transitional" industry, the Uluzzian, indicates that they were from anatomically modern humans (Benazzi et al., 2011). Yet, as Riel-Salavatore and colleagues (2012) point out, it may be more productive to interpret the biology and culture associated with "transitional" industries in less typological terms than the Neandertal-modern and Middle–Upper Paleolithic dichotomies. Thus, it is possible that the ambiguous anatomy of the Szeletian *sensu lato* remains reflects varying degrees of traits that characterize earlier archaic and later modern populations.

The Central European Fossil Record of the Earliest Modern Humans

Since Smith (1984) reviewed the Central European early modern human fossil record, it has changed much more dramatically than has the Neandertal record. This has been in large part due to the application of AMS ^{14}C direct dating and redating of many fossils. Many fossils once thought to be Aurignacian or Gravettian have been demonstrated to be much more recent. In addition to chronological and sample changes, significant research has gone into better understanding previously known fossils, such as those from Dolní Věstonice, Pavlov (Sládek et al., 2000; Trinkaus and Svoboda, 2006), and Mladeč (Teschler-Nicola, 2006). Finally, and perhaps most importantly, the fossils discovered from Peştera cu Oase are currently the oldest known modern human fossils from Europe and exhibit a mosaic of modern and archaic anatomy (Rougier et al., 2007; Trinkaus et al., 2003b). The Oase discoveries have thrown fresh light upon the Romanian early modern human record, resulting in the recent direct dating of and reanalysis of the remains from Cioclovina (Harvati et al., 2007) and Muierii (Soficaru et al., 2006). Table 5.4 lists early modern human fossils from Central Europe, while Figure 5.9 maps their locations.

Table 5.4. Early modern human remains from Central Europe.

Site	Human Remains	Cultural Association	Date(s)	Date Reference(s)
Western Central Europe				
Pre-Gravettian (all from Germany)				
Hohlenstein-Stadel	Premolar	Aurignacian?		Orschiedt, 2000; Street et al., 2006
Geißenklösterle	Deciduous tooth	Aurignacian?		Orschiedt, 2000; Street et al., 2006
Honerthöhle	Fragmentary cranial, mandibular, and dental[†]	Aurignacian?		Gielser, 1971; Street et al., 2006
Kleine Ofnet	Tooth	Aurignacian?		Orschiedt, 2000; Street et al., 2006
Schafstall	Molar	Aurignacian?		Orschiedt, 2000; Street et al., 2006
Schelklingen, Ulm	Left mandibular molar & canine	Aurginacian?		Street et al., 2006
Sirgenstein	Right C^1	Aurignacian?		Street et al., 2006
Gravettian				
Geißenklösterle	Two deciduous teeth	Gravettian		Pasda & Hahn, 1991; Street et al., 2006
Hohle Fels	Deciduous molar & cranial fragment	Gravettian		Haas, 1991; Street et al., 2006
Eastern Central Europe				
Pre-Gravettian				
Bacho Kiro (Bulgaria)	Cranial and mandibular fragments, isolated teeth	Lv 11: “Proto-Aurignacian” Lv 6–7: Aurignacian	Lv 11: ≈32.9–40.2 ka Lv 6–7: ≈28.2–33.0 ka	Hedges et al., 1994
Bordu Mare (Romania)	Three phalanges[3]	Aurignacian?[1]		Alexandrescu et al., 2010
Cioclovina (Romania)	Calvarium	Unclear	28.5 ± 0.2 ky BP*	Soficaru et al., 2007
Görömböly-Tapolca (Hungary)	Occipital	?	30.3 ± 0.3 ky BP*	Tillier, 2006; Davies & Hedges, 2008–2009
Istállós-kő (Hungary)	M_1 or M_2 germ[3]	Aurignacian[1]	≈39.7 ka[1]	Allsworth-Jones, 1990; Tillier, 2006
La Adam (Romania)	Molar germ	Aurignacian?[1]		Alexandrescu et al., 2010
Miesslingtal (Austria)	Juvenile mandibular symphysis	Aurignacian (Late?)[1]		Felgenhauer, 1950; Churchill & Smith, 2000
Mladeč (Czech Rep.)	Cranial and postcranial remains from multiple individuals[†]	Aurignacian (Middle to Late)	30.7–31.5 ky BP*	Wild et al., 2005, 2006

Malu Roșu (Romania)	Frontal fragment	Aurignacian?[1]		Alexandrescu et al., 2010
Oblazowa (Poland)	Distal thumb phalanx	?	31.0 ± 0.55 ky BP*	Hedges et al., 1996
Peștera Mică (Romania)	Femoral fragment	Aurignacian?[1]		Alexandrescu et al., 2010
Peștera cu Oase (Romania)	Mandible (Oase 1) and cranium (Oase 2)	None	1: 34.3 + 1.0/–0.9 ky BP* 2: 28.9 + ∞/–170 ky BP*	Trinkaus et al., 2003; Rougier et al., 2007
Peștera Muierii (Romania)	Skull, temporal and postcranial remains	Mousterian?[2]	M1: 30.2 ± 0.8 ky BP* M1: 29.9 ± 0.2 ky BP* M2: 29.1 ± 0.2 ky BP*	Soficaru et al., 2006; Dobos et al., 2010
Vindija—F complex (Croatia)	Three anterior teeth, two articulating parietals[3]	Aurignacian?	≈20.7–31.7 ka[1]	Srdoc et al., 1984
Gravettian				
Brno-Franzcouská (Czech Rep.)	Calvarium and postcrania	Gravettian (Willendorf-Kostienkian)	22.8 ± 0.2 ky BP*	Pettitt & Trinkaus, 1999
Dolní Věstonice (Czech Rep.)	Five associated skeletons plus numerous other cranial, dental, and postcrania remains[†]	Gravettian (Pavlovian)	≈23.1–27.2 ka[4]	Svoboda, 2006
Grub/Kranawetberg (Austria)	Two deciduous tooth fragments	Gravettian (Willendorf-Kostienkian)	24.4–25.5 ka	Antl-Weiser, 1999; Antl-Weiser & Teschler-Nikola, 2000/2001
Krems-Wachtberg (Austria)	Three infant skeletons	Gravettian (Willendorf-Kostienkian)	26.6 ± 0.2 ky BP	Einwögerer et al., 2005, 2006
Pavlov (Czech Rep.)	Associated skeleton (Pavlov 1), maxilla, mandible, mandibular fragment, and twenty-six isolated teeth	Gravettian (Pavlovian)	26.2 ± 0.5 ky BP	Svoboda, 2006
Předmostí (Czech Rep.)	Remains of approximately thirty individuals, at least two associated skeletons[†]	Gravettian (Pavlovian)	≈25–27 ka	Svoboda, 2001
Willendorf I & II (Austria)	I: Femoral diaphysis, II: mandibular symphysis	Mousterian	I: 24.3 ± 0.2 ky BP*	Teschler-Nikola & Trinkaus, 2001

[†] Some or all of the fossils are known to be missing or destroyed.

* Direct date(s) on human remains.

[1] Date is tentative and should be regarded with caution.

[2] The association of the Muierii skull with Mousterian artifacts is regarded as being due to level mixture (Dobos et al, 2010).

[3] The taxonomic affinities of these remains is contentious. See text.

[4] Range (including single errors) of radiocarbon dates from the Dolní Věstonice II site (Svoboda, 2006). Generally, the Dolní Věstonice remains are regarded as being ≈ 25–27 ka.

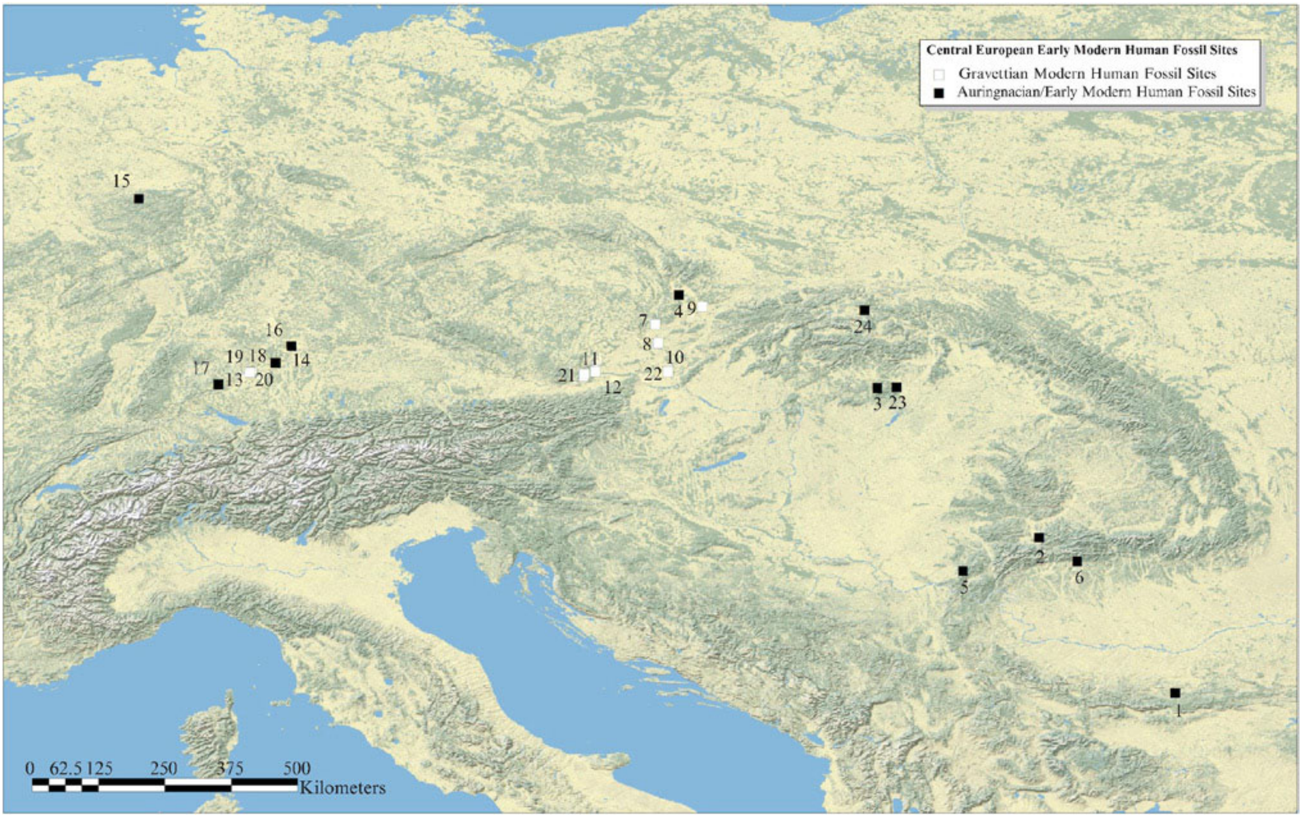

Figure 5.9. Aurignacian/early modern human fossil sites:* 1: Bacho Kiro; 2: Cioclovina; 3: Istállóskö; 4: Mladeč; 5: Peştera cu Oase; 6: Peştera Muierii; 14: Hohlenstein-Stadel; 15: Honerthöle; 16: Kleine Ofnet; 17: Schafstall; 18: Sirgenstein; 19: Geißenkösterle; 21: Miesslingtal; 23: Görömby-Tapolca; 24: Oblazowa. Gravettian modern human fossil sites: 7: Brno-Fracouzská; 8: Dolní Véstonice; 9: Předmostí; 10: Pavlov; 11: Willendorf; 12: Krems-Wachtberg; 13: Geißenkösterle; 20: Hohle Fels; 22: Grub/Kranawetberg. **Four Romanian sites (La Adam, Bordu Mare, Malu Roşu, Peştera Mică) with fragmentary remains are not mapped.*

Pre-Gravettian Modern Human Fossils from Western Central Europe

We have come to expect the fossil record of any region to constantly grow, but, in the case of early modern humans from western Central Europe, the opposite has happened. Presumed early specimens, such as those from Binshof-Speyer, Hahnöfersand, Vogelherd (Stetten), and Paderborn-Sande, have all been redated to the Holocene (with the last being less than 300 years old!) (Conard et al., 2004; Street and Terberger, 2002; Street et al., 2006; Terberger et al., 2001). Radiocarbon dates (Müller-Beck, 1983), as well as the numerous Aurignacian artifacts from the two strata from which the Vogelherd human remains were collected (Riek, 1934), had indicated that the remains dated to > 30 ka. However, recent direct AMS ^{14}C analyses yielded dates for the human remains that span from 3,560 ± 30 years ^{14}C BP for Stetten 2 to 5,175 ± 30 years ^{14}C BP for Stetten 3 (Conard et al., 2004). Thus, all of the Vogelherd human remains were from intrusive Neolithic burials that were not detected during excavation.

Although the incorrect and, until recently, accepted dates for the Vogelherd remains can be understood as the result of early and imprecise excavation, the incorrect dates for Binshof-Speyer, Hahnöfersand, and Paderborn-Sande (Table 5.1) have their origin in outright forgery (Harding, 2005; Pincock, 2005; Street et al., 2006). "Direct dates" for all three of these specimens were provided by the now-defunct Frankfurt University radiocarbon lab. As AMS dating was later applied to these specimens, it became apparent that the Frankfurt dates were consistently incorrect and gross overestimations (Street and Terberger, 2002, 2004; Street et al., 2006; Terberger et al., 2001). Kelsterbach, another specimen that was also given an early date by the Frankfurt laboratory, was used by Protsch as evidence for an early presence of modern humans in Central Europe (Protsch and Semmel, 1978). This specimen has gone missing and its date cannot be verified or, more likely, falsified by new dating (Street et al., 2006). We concur with Street and colleagues' (2006) suggestion that Kelsterbach's Aurignacian-age date be rejected as well.

So, what is left of the early modern human fossil record in western Central Europe? Unfortunately, none of the remaining candidates have been directly dated, and, even if we accept that these remains are Aurignacian, they are few and largely not diagnostic anatomically. Street and colleagues (2006) provide the following as "possibly Aurignacian Age" (p. 563; see also Table 3): a single premolar from Hohlenstein-Stadel, three teeth from Sirgenstein, two teeth from Schelklingen, a tooth from Kleine Ofnet, another tooth from Schafstall, and yet another single tooth from Geißenklösterle. They, furthermore, mention fragmentary remains from Honerthöhle as having a possible but uncertain association with Aurignacian artifacts. Thus, it is currently unclear what biological population was associated with the Aurignacian of western Central Europe.

The relative lack of early modern human remains from this region is ironic given the wealth of Aurignacian archaeological discoveries that have been made in the last couple of decades, especially in the Swabian Jura (Conard, 2009; Conard et al., 2009). The basal Aurignacian in this area may be as old as 40,000 years BP and has yielded the oldest undisputed bone and ivory flutes and a venus figurine from Hohle Fels (Conard, 2009; Conard et al., 2009). Additional, albeit more recent, Aurignacian flutes are known from Geißenklösterle (Hahn and Münzel, 1995) and Vogelherd (Conard and Malina, 2006). Recent work at Hohle Fels documents a significant technological shift across the Middle to Upper Paleolithic boundary, indicating, perhaps, a shift in human population as well (Conard and Bolus, 2008). Although Conard and colleagues (Conard, 2009; Conard et al., 2004) and others (Street et al., 2006) contend that the Aurignacian was likely brought into the Swabian Jura by invading modern humans, perhaps as the initial colonization of Central Europe by this population, the available evidence is insufficient to test such a hypothesis at this time.

Gravettian Modern Human Fossils from Western Central Europe

It is only in comparison with the Gravettian fossil record of western Central Europe that the region's Aurignacian fossil record looks rich. With the redating of the Binshof specimen to the Bronze Age (Terberger and Street, 2001), the Gravettian human fossil record of western Central Europe now comprises only two teeth from Geißenklösterle and a single tooth and cranial fragment from Hohle Fels. The Geißenklösterle teeth comprise a right upper deciduous molar and another deciduous molar (Haas, 1991; Hahn et al., 1990). The Hohle Fels Gravettian tooth is a right lower deciduous molar, while the cranial fragment may be from a young adult (Haas, 1991). As Street and colleagues (2006) point out, the paucity of Gravettian fossils in Germany contrasts with the number of documented Gravettian sites in the country as well as with the large Gravettian skeletal samples from Moravia. As is the case for the Aurignacian-associated remains from western Central Europe, the Gravettian remains are largely uninformative about the biology of the Gravettian peoples in this region.

Pre-Gravettian Modern Human Fossils from Eastern Central Europe

Although the eastern part of Central Europe has now traded places with the western part as the area with the most information about the biology of the first modern humans in the region, the record is far from perfect. The Mladeč fossils have played a role in understanding modern human origins in this region for some time, but the claim of unclear association with the Aurignacian, at least for some of the human fossils, and the lack of direct dates (but see Wild et al., 2005) have made their role, at times, tenuous. Questions still remain about the chronology and context of the Mladeč remains as well as how to interpret their mosaic anatomy. As in the case of the German Upper Paleolithic fossil record, direct AMS ^{14}C dating (Smith et al., 1999; Svoboda et al., 2002) has assailed the "early" status of three modern fossils that had featured prominently in earlier discussions (cf. Churchill and Smith, 2000; Smith, 1976a, 1982, 1984; Smith and Ranyard, 1980). The fragmentary remains from Svatý Prokop (Bohemia), the Velika Pećina frontal (Hrvatsko Zagorje), and the partial skeleton from Zlatý Kůn (Bohemia) all succumbed to such redating (Table 5.1). While Zlatý Kůn remains (barely) Pleistocene in age following direct dating (Svoboda et al., 2002), the Svatý Prokop and Velika Pećina remains are now dated to the Holocene (Smith et al., 1999; Svoboda, 2005). Other remains[13] that have been suggested as potentially early (cf. Churchill and Smith, 2000) have not been directly dated and have unclear or no associations with artifact industries. In the case of the Podbaba calvarium, direct dating will never be possible since the specimen was destroyed in 1921 (Churchill and Smith, 2000). Given the lessons of Velika Pećina, Zlatý Kůn, and the numerous German fossils discussed earlier, the Podbaba and Silická Brezova remains should not be included in discussions of early modern humans in Central Europe. The molar germ of Istállós-kő lacks a direct date, but its association with the Aurignacian may be more acceptable (Tillier et al., 2006) than the speculative dates for Podbaba and Silická Brezova. Yet its age should also be treated with caution.[14]

Despite more than 25 years, little still can be reported on some early modern human fossils that Smith (1984) was only able to describe briefly. For example, the Miesslingtal juvenile mandibular corpus remains undated but is reported to come from an Aurignacian context (Felgenhauer, 1950; Sombathy, 1950). Anatomically, Sombathy reports that it is modern human, and its dental metrics fall with the early Upper Paleolithic (Smith, 1984). The reportedly Aurignacian germ M_1 (Bailey et al., 2009) or M_2 (Malán, 1955; Tillier et al., 2006) from Istállós-kő lacks an anterior fovea and exhibits a buccolingual dimension closer to

Upper Paleolithic modern humans than to Neandertals. Nevertheless, Tillier and colleagues (2006) contend that no features of the tooth can distinguish it from Neandertals or modern humans. More recently, Bailey and colleagues (2009) note that the tooth lacks both a hypoconulid and a midtrigonid crest, aligning it with Upper Paleolithic modern humans. The three anterior teeth from the Aurignacian F_d stratum at Vindija Cave, as noted by Smith (1984), are large and anatomically fall with both Neandertals and early modern humans. An additional Aurignacian fossil, the Vi 302 left parietal fragment, was published by Smith and colleagues (1985). This specimen articulates with the previously unprovenienced Vi 204 right parietal. These conjoined pieces exhibit moderate lambdoidal flattening combined with greater biparietal expansion than that usually seen in Neandertals. Overall, the Vindija Aurignacian-associated remains are not diagnostic. Furthermore, given chronological uncertainties and lessons learned from directly dating other supposed early modern human fossils, the Miesslingtal, Istállós-kő, and Vindija F fossils should be only tentatively placed in the pre-Gravettian modern human sample until direct dates and/or additional chronological information become available.

Mladeč

The oldest directly dated, Aurignacian-associated modern human remains from Europe come from the Moravian site of Mladeč, a cave system located inside of Třesin Hill in the Czech Republic. The remains from this site, as well as possibly associated Upper Paleolithic artifacts, were not the result of habitation but rather were likely dropped through a vertical chimney (Svoboda, 2000, 2006). Excavations led by Szombathy in 1881–1882 uncovered numerous elements from the "Dome of the Dead" area of Chamber D in the Main Cave. These remains include the two, possibly female, crania Mladeč 1 and 2 as well as the Mladeč 8 maxilla, Mladeč 3 child, and several postcranial pieces. In 1904, the so-called "Quarry Cave" was accidentally discovered some 43 meters west of the Main Cave. Although many artifacts and bones were lost during and initially after the original discovery of this chamber, the possibly male crania, Mladeč 5 and 6 and other elements, as well as many artifacts, were recovered and curated (Frayer et al., 2006; Svoboda, 2006c). Additional human remains were found as late as 1922. Unfortunately, most of the at least 137 skeletal elements were lost in 1945 during the burning of Mikulov Castle, where the specimens discovered after Szombathy's original excavations were stored. Only the Szombathy collections (at the Natural History Museum in Vienna), four hand bones and four cranial fragments from the private collection of Jan Knies, and Mladeč 5 remain, the last having survived the Mikulov fire.

The Mladeč remains, recognized as potentially early and associated with the Aurignacian, gained attention by the late 1970s. While Stringer (1974, 1978) viewed them as fully modern and lacking any Neandertal aspects, others (Frayer, 1986; Smith, 1984; Wolpoff, 1999) saw otherwise, especially in specific details of anatomy. This gulf in interpretation of the evolutionary significance of the Mladeč fossils persists with Bräuer (Bräuer and Broeg, 1998; Bräuer et al., 2006) reiterating Stringer's interpretation while Frayer and colleagues (Frayer et al., 2006; Wolpoff et al., 2006), Churchill and Smith (2000), Cartmill and Smith (2009), and Trinkaus (2005, 2007) continue to argue in favor of the presence of Neandertal features among the Mladeč remains.

Confounding interpretations of the Mladeč fossils has been the difficulties in understanding their provenience, chronology, and archaeological associations (Frayer et al., 2006; Svoboda, 2006c). The fact that the more gracile, and presumably female, crania (1 and 2) and a large, likely male maxilla (Mladeč 8) came from Szombathy's excavations of the Dome of the Dead in Chamber D, while the robust, presumably male, crania (5 and 6) came from the adjacent Quarry Cave, questions whether or not all of the Mladeč fossils represent the same population and/or time period. Direct dating of Mladeč 1, 2, 8, 9 and 25c (proximal ulna), all from Chamber D, has helped tighten up the chronology for the Main Cave specimens, but the lack of direct dates for the only surviving Quarry specimen, Mladeč 5,[15] does not help clarify the question of contemporaneity between the two samples. AMS ^{14}C dating of Mladeč 1, 2, 8, and 9 (canine—white colored collagen) provide age estimates ranging from 30,680 to 31,500 radiocarbon years ago (Wild et al., 2005; Wild et al., 2006).[16] Wild and colleagues (2006: 155–156) also note that these are uncalibrated ages and that "a shift of the 'true ages' by several thousand years towards higher ages might be possible."

Lithic artifacts from Mladeč are rare and largely non-diagnostic, with only one distinctively Aurignacian carinated end scraper found (Oliva, 2006). There is, however, an extensive bone tool sample made up of numerous bone points (especially massive based/Mladeč points), awls, worked animal metacarpals (some with drilled holes), carnivore and beaver teeth with bored holes in the roots, and other items (Oliva, 2006). As noted by Oliva (2006), most of these bone artifacts derive from the Main Cave, but some were recovered in the Quarry Cave. This indicates the Quarry and Main Caves are roughly contemporaneous (see also Frayer et al., 2006). Oliva (2006) assigns the artifacts to middle to late Aurignacian.

The postcranial remains from Mladeč are basically modern (Trinkaus et al., 2006a). These remains are somewhat fragmentary and some are quite robust. Several features (e.g., cervical vertebral height, radial tuberosity position, shape of the proximal femora, talar trochlear size) overlap with the same features in Neandertals but also fall into the Skhūl-Qafzeh early modern range from the Near East. Thus they are not conclusive evidence of a Neandertal contribution to the Mladeč people. Both femora exhibit the proximal-lateral femoral flange that tends to be found in European Neandertals and early moderns but not in the Near Eastern Neandertals and early moderns (Cartmill and Smith, 2009). This might be evidence of European continuity, but the polarity of this trait is not clear. One of the lost specimens, a proximal femur (Mladeč 78), shows strong anterior-posterior curvature, a trait common in Neandertals but not uncommon in early moderns.

The craniodental remains have traditionally been considered as showing the best evidence of continuity (Churchill and Smith, 2000; Frayer, 1986; Jelínek, 1969; Smith, 1982). The robust male crania (Mladeč 5 and 6) have been emphasized in this respect. In their recent analysis of the Mladeč males, Frayer and colleagues (2006) note that these are not Neandertals but that a hypothesis of equal ancestry from Neandertals on one hand and the Skhūl-Qafzeh group on the other cannot be rejected (see also Wolpoff et al., 2001). Frayer and colleagues (2006) focus on overall shape of the vault (particularly the low vault height), parietal bone shape, the presence of occipital bunning and lambdoidal flattening, pronounced browridges, a projecting upper face (but with a pattern of flatness different from Neandertals), and an inferior bulging of the occipitomastoid region, resulting in relatively non-projecting mastoid processes, as particularly demonstrating continuity with European Neandertals. They also note the large tooth size, especially the canines of Mladeč 8 and 9, and the shoveling of the latter as further indicators. The possible female crania (Mladeč 1 and 2) are described as showing less evidence of continuity but still exhibiting occipital bunning and lambdoidal flattening (only present in Mladeč 1), and the same mastoid-occipitomastoid area morphology as the males (Wolpoff et al., 2006). The morphology of the Mladeč 3 child's skull (aged to > 2 years) is described as being intermediate between Neandertal and modern human juvenile neurocrania (Minugh-Purvis et al., 2006). Medial browridge development, the prominent occipitomastoid area, lambdoidal flattening, and occipital bunning are all indicators of the specimen's intermediate status, while several other features are more clearly alligned to the modern human pattern. In summing up their views on Mladeč, Frayer and colleagues (2006: 266) note that "the exact details of the ancestry of

Mladeč may never be worked out", but they interpret the data as supporting a minimum of 25–50% of Neandertal ancestry for the Mladeč people.

Not everyone accepts the Mladeč morphology as indicative of a Neandertal contribution to early modern Europeans. In a recent investigation of overall cranial form, Weber and colleagues (2006) compare the Mladeč 1, 5, and 6 neurocrania to a sample of anatomically modern humans and archaic humans, the latter consisting of Neandertals and earlier members of the genus *Homo*. The results of this analysis led them to conclude that the Mladeč crania "are clearly anatomically modern except the shapes of Mladeč 5 and 6 in the parieto-occipital region" (Weber et al., 2006: 465). They note more overlap in the morphology of this latter region in their analyses and conclude that overall posterior cranial form does not distinctly separate Neandertals and anatomically modern humans. Earlier Bräuer and Broeg (1998) argued that analysis of discrete cranial features does not show evidence of continuity, nor did a metric analysis of the fronto-facial region (Bräuer et al., 2006). Frayer and colleagues (2006) dispute the discrete trait study, but the other two studies underscore what earlier multivariate metric studies have generally found: the Mladeč crania have a basically modern form. This mirrors the conclusions based on the postcranial remains.

One feature that figures prominently in discussions of Mladeč and the issue of continuity is occipital bunning. Often it is suggested that the bunning in Neandertals and that in early modern Europeans was not homologous. It has long been recognized that the buns in early moderns were generally not as laterally extended as in Neandertals and were located relatively more inferiorly in the former (Smith, 1982; Cartmill and Smith, 2009). However two recent studies of bunning in Neandertals and early modern Europeans conclude that the structures are homologous (Gunz and Harvati, 2007, 2011; contra Nowaczewska and Kuzminski, 2009). The Harvati and Gunz studies conclude that the bunning morphology is a part of the integrated form of the cranium and should not be used as an independent trait to argue for European continuity. Of course, most everything in the cranium is integrated to some extent at least, but the fact is that European Neandertals and early moderns commonly exhibit a character state where the structure of a bun is specifically definable morphologically (Cartmill and Smith, 2009). Given this, it seems unreasonable to discount the definability of the feature. Interestingly, the external geometrical results presented by Weber and colleagues (2006: 465) found that this region of the Mladeč 5 and 6 crania was the only area in which they are not "clearly anatomically modern."

Another occipital feature that figures prominently in the debate on Mladeč and the question of Neandertal–early modern European continuity is the suprainiac fossa (Figure 5.10). In Neandertals, this is a horizontally elongated, elliptical depression just above the superior nuchal line, normally identified by a grainy appearance of the external table in the depression. Frayer and colleagues (2006) maintain that Mladeč 6 is the only early modern European that has a Neandertal-like fossa, albeit weakly developed. Mladeč 5 has a small, circular depression with similar surface characteristics located at the midline just above the superior nuchal line. There has been considerable controversy concerning the relationship of the Neandertal suprainiac fossa to a variety of similar manifestations in early modern Europeans, including the two Mladeč variants (Ahern, 2006a; Balzeau and Rougier, 2010; Cartmill and Smith, 2009; Nowaczewska, 2011). It seems clear that some of the variants recognized as possible suprainiac fossae in the past represent something not homologous to the Neandertal feature, a fact first noted by Caspari (1991). The most convincing study is by Balzeau and Rougier (2010), who demonstrate a structural difference in the fossa of Neandertals and those of modern humans. Neandertal depressions are the result of diploic thinning, while the moderns' result from external bone table thinning. If confirmed this would essentially remove the suprainiac fossa from the debate on continuity as the depression would be clearly non-homologous. One issue that needs to be addressed is that

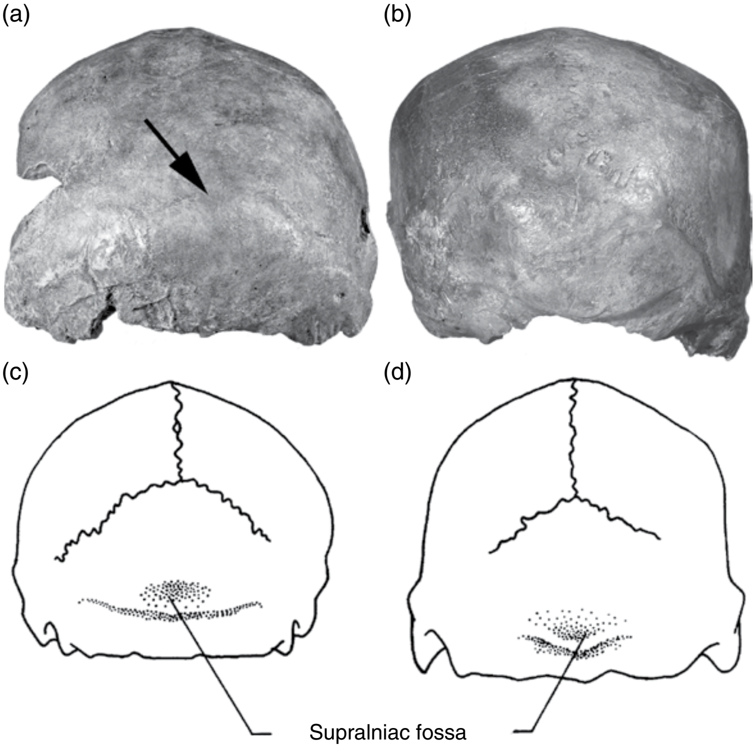

Figure 5.10. Mladeč 6 (a) and Mladeč 5 (b) in posterior view with a diagram, below, showing the (c) Neandertal-pattern and the (d) Upper Paleolithic modern-pattern suprainiac fossae. The arrow points to Mladeč 6's Neandertal-pattern suprainaic fossa. Mladeč 5 lacks a suprainiac fossa. Figure from Frayer et al. (2006). Photographs by Wolfgang Reichmann. Illustration by D. W. Frayer. Figure used courtesy of D. W. Frayer.

Balzeau and Rougier do not include any early Upper Paleolithic Europeans in their study. The fact that the structure might represent a functional adaptation (Caspari, 1991; Nowaczewska, 2011) would not necessarily remove the possibility of homology.

Peştera cu Oase

The site of Peştera cu Oase, located in southwestern Romania, was discovered during speleological exploration in 2002. A human mandible, Oase 1, was discovered at that time lying on the surface (Trinkaus et al., 2003b). Further exploration between 2003 and 2005 yielded most of a human cranium, Oase 2. Direct AMS ^{14}C dating of the Oase 1 mandible yielded dates of 35.2 ka ^{14}C BP (OxA–11711) and 34.29 + 0.97/–0.87 ka ^{14}C BP (GrA–22810) (Trinkaus et al., 2003b). Attempts at dating the Oase 2 cranium yielded a minimum date of 28.89 + ∞/–0.17 ka ^{14}C BP (Rougier et al., 2007), although Rougier and colleagues contend that Oase 2 may be contemporary with Oase 1. Unfortunately, there are no artifacts associated with the Oase remains.

The anatomy of the Oase 1 mandible (Figure 5.11) affiliates it with both later Upper Paleolithic humans as well as contemporary modern humans from elsewhere such as Nazlet Khater (Trinkaus et al., 2003b). Metrically, Trinkaus and colleagues' (2003b) discriminant function analysis (Neandertals vs. early Upper Paleolithic) places Oase 1 clearly among the early Upper Paleolithic specimens (posterior probability = 0.994). In details of anatomy,

Figure 5.11. The Oase 1 mandible. Right lateral (a) and medial views of the (b) left and (c) right rami. Scale is in centimeters. Images courtesy of E. Trinkaus.

Oase 1 presents a chin but with only slight development of the mental tubercles and a fairly vertical symphyseal angle (Trinkaus et al., 2003b). It lacks a retromolar space and presents a mental foramen in line with the second premolar and a symmetrical mandibular incisure, all of which align it more with modern humans than Neandertals. Like the roughly contemporary North African specimen Nazlet Khater 2 as well as many Middle Pleistocene mandibles, but unlike those from the European Upper Paleolithic, Oase 1's ramus is especially broad. Given Oase 1's date and its anatomy, it is the oldest known anatomically modern human in Europe.

Nevertheless, two features of the Oase 1 mandible are specifically Neandertal-like. First, it exhibits a slight medial pterygoid tubercle as well as a horizontal-oval mandibular foramen pattern[17] (Trinkaus et al., 2003b). The former is nearly ubiquitous among Neandertals and present among only 10% of early Upper Paleolithic specimens. The latter feature is found among 52.6% of Neandertals and 18% of early Upper Paleolithic (Cartmill and Smith, 2009; Frayer, 1992; but cf. Trinkaus et al., 2003b, for different but very similar frequencies). These are not features found among African or west Asian early modern humans, and their presence in Oase 1 suggests some Neandertal genetic contribution (Cartmill and Smith, 2009; Trinkaus et al., 2003b).

The Oase 2 cranium (Figure 5.12) exhibits a more intriguing morphological mosaic. It is unclear if this specimen is as old as the Oase 1 mandible, but the direct minimum radiocarbon

Figure 5.12. The Oase 2 cranium in anterior (a) and left (b) lateral views. Scale is 10 centimeters. Images courtesy of E. Trinkaus.

date (see above) certainly places it in the larger group of the oldest known European modern humans that includes those from Mladeč, Cioclovina, and Muierri (Dobos et al., 2010; Rougier et al., 2007). The gestalt of the cranium places it clearly as a modern human. The vault is high, especially posteriorly. The zygomatics are large and the lateral cheeks are fairly anteriorly placed, unlike Neandertals. Oase 2 also exhibits well-excavated canine fossae, a fairly narrow nasal aperture, and a short face in comparison to Neandertals. In posterior view, Oase 2 exhibits the *en maison* form with vertical sides, contrasting with the *en bombe* form of most Neandertals. Metrically, Oase 2's vault is similar to that of Nazlet Khater 2 as well as other early modern humans (Rougier et al., 2007). The supraorbital region shows the modern pattern of separate medial and lateral segments divided by a supraorbital sulcus (Smith and Ranyard, 1980). Based upon wear on the first two molars combined with the presence of the third molars in their crypts (Rougier et al., 2007), Oase 2 was likely a late adolescent. Given that browridge morphology does not usually develop fully until the third decade of life in males (and, perhaps, even later in females) (Ahern, 1998), not too much should be made of Oase 2's relatively gracile supraorbital morphology.

Other aspects seem to align Oase 2 with Neandertals. Its flat frontal is similar in form to Neandertals (specifically Shanidar 1) and is similar to Cioclovina in this respect, according to Rougier and colleagues (2007). Oase 2 also exhibits a "hemibun" type of occipital bunning. Although debate still exists as to whether or not this morphology is homologous to Neandertal occipital bunning (see above), its presence in Oase 2 and as many as 60% of Upper Paleolithic specimens may align them with Neandertals. Perhaps more intriguingly, Oase 2 exhibits a prominent juxtamastoid eminence. Although this feature is not as large as in the majority of Neandertals, it is similar in size to a minority as well as Mladeč 2 and Qafzeh 3. Mladeč 1 and 5 exhibit large juxtamastoids similar to the usual Neandertal condition. Dentally, Oase 2 exhibits unusually large molars that are significantly larger than Neandertals and other early modern humans. Rougier and colleagues (2007) make special note of the order of size progression, in that Oase 2's first molar is smaller than its second and its second is smaller than its third. Such a pattern is not present among other early modern humans but is present in a minority of Neandertals (Rougier et al., 2007).

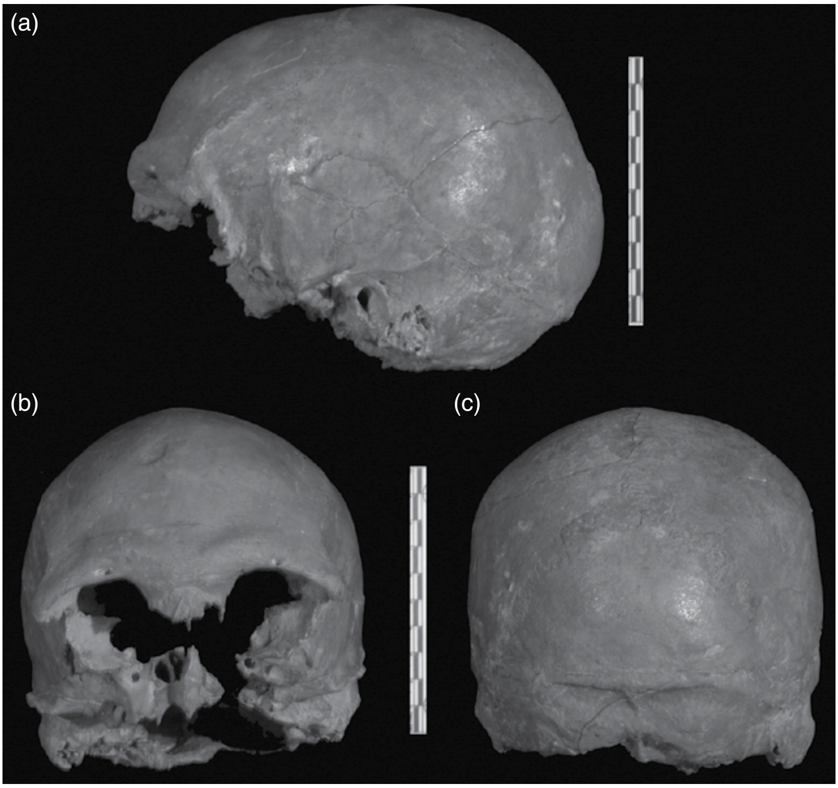

Figure 5.13. The Cioclovina cranium in left (a), anterior (b), and posterior (c) views. Images courtesy of E. Trinkaus.

Cioclovina and Peştera Muierii

In part because of the Oase discoveries, other early Romanian modern fossils have received renewed attention. Both the Cioclovina and Muierii fossil human remains have been known for more than a half-century, and specimens from both sites have recently been directly ^{14}C dated to 28.5–29.0 and 29.0–30.0 ka ^{14}C years BP (Dobos et al., 2010), respectively. This places both specimens among the earliest, securely dated modern human remains in Europe. Like Oase, however, neither specimen has firm archaeological associations. The Cioclovina 1 specimen is a probable male calvarium of uncertain associations and context found accidentally in 1940 or 1941 (Soficaru et al., 2006). Peştera Muierii has been known archaeologically since the late nineteenth century, and excavations in the early 1950s yielded a series of human remains associated with Middle Paleolithic tools in the back of one of the cave galleries (Galeria Musteriană) at the site (Dobos et al., 2010). Dobos and colleagues report that these remains were recognized as modern human, and thus their association with Middle Paleolithic artifacts was considered to result from artificial mixture in the cave. While there is also Upper Paleolithic at Muierii, it is not possible to establish the archaeological association of the human remains.

The Cioclovina 1 calvarium (Figure 5.13) is similar to the Mladeč (especially 1 and 2) and Oase crania in combining a basically modern form with some features potentially reflecting Neandertal influence. Soficaru and colleagues (2007) note the presence of a small hemibun,

Figure 5.14. The Muierii cranium in lateral view. Image courtesy of E. Trinkaus. Scale is 5 centimeters.

a suprainiac fossa, and other details of the occipital bone as examples of the latter group of features (see also Churchill and Smith, 2000; Smith, 1984). On the other hand, the form of the moderately robust browridge, the form of the mastoid process and occipitomastoid eminence, and other occipital features align the specimen with modern humans. This is also reflected in the form of the endocranial cast (Kranioti et al., 2011). Harvati and colleagues (2007) reaffirm the fundamental modern affinities of Cioclovina 1 and question the presence of possible Neandertal reminiscent features. However, they treat this specimen as a possible hybrid in their analysis, which would infer a greater amount of Neandertal influence than the previous studies would assert. Furthermore, most of their analysis compared overall cranial form using geometric morphometrics. All studies cited above agree that the overall cranial form is modern. The controversy over occipital bunning and suprainiac fossae discussed above is applicable also to the interpretation of Cioclovina 1.

The Pleistocene-aged human remains from Muierii comprise three individuals (Dobos et al., 2010): Muierii 1 (Figure 5.14)—a relatively gracile (likely female) cranium with the major portions of the neurocranial vault, a zygomatic bone and the maxillae, a right partial mandible, ten teeth (both maxillary and mandibular), a scapula and tibia; Muierii 2—a robust (likely male) left temporal bone; Muierii 3—a fibular fragment. Dobos and colleagues' (2010) description of Muierii 1 emphasizes the presence of several features that are derived for recent humans. Along with a high, rounded vault, these characteristics include a modern supraorbital region, infraorbital regions with distinct canine fossae, a high frontal profile, a small face with anteriorly positioned zygomatic roots, a narrow nasal aperture, and a modern dentition with extensive attrition. They also point out that Muierii 1 has a prominent occipital bun, an incipient development of a suprainiac fossa, and complete absence of an external occipital protuberance. These features are similar to those of

Cioclovina 1 and indicate possible evidence of a small Neandertal contribution to the population of which Muierii 1, Oase, and Cioclovina 1 are a part.

The same appears true for the Muierii 1 mandible, which preserves the lateral corpus from the P_3 alveolus to the ramus and most of the ramus. In keeping with the facial morphology of Muierii 1, the mandible is a small, gracile bone and indicates modern human levels of orthognathism. According to Dobos and colleagues (2010), the Muierii 1 mandible contrasts with those of most early modern humans in exhibiting features that suggest some affiliation with Neandertals. It has a high coronoid process with an asymmetrical mandibular notch. The anterior ramus lacks a distinct concavity. The mandibular notch crest does not meet the condyle clearly laterally. Dobos and colleagues do not see these as secondary reflections of spatial and/or biomechanical relationships within the face, particularly given the modern form of the Muierii 1 upper facial skeleton.

In the postcranium, Muierii 1 preserves a scapula with a bisulcate axillary border pattern (though trending toward a dominant dorsal sulcus) and a relatively narrow glenoid fossa, patterns that are found in other Upper Paleolithic specimens but also overlapping Neandertals and other archaic forms (Dobos et al., 2010). The Muierii 1 tibia and the Muierii 2 temporal are solidly modern human in form, but the Muierii 3 partial fibula is more archaic. Unfortunately, its context is uncertain, and it might derive from the Middle Paleolithic levels at the site.

As was the case for the Mladeč remains, the Romanian sample of Cioclovina, Muierii, and Oase represent a human sample that is immediately identifiable as modern. However, they also show individual features that likely reflect a small contribution of Neandertals. Interestingly, these tend to be found in the same anatomical regions in both samples, particularly the occipital (including the occipitomastoid eminence). The Romanian mandibular sample also exhibits some possibility of Neandertal contribution, but this is difficult to evaluate for Mladeč because the mandibles there were not carefully studied before their destruction.

La Adam, Bordu Mare, Peştera Mică, and Malu Roşu

Fragmentary fossils from four additional Romanian sites have been reported as deriving from Aurignacian contexts (see Table 5.4) (Alexandrescu et al., 2010). None of these fossils have published dates, much less direct ones.

Bacho Kiro

Eight human fossils were recovered from Aurignacian and "proto-Aurignacian" stratigraphic units at the cave site of Bacho Kiro, Bulgaria (Kozłowski, 1982). The oldest specimen, a left mandibular corpus preserving dm_1 (Backo Kiro 1124), derives from stratigraphic level 11. Although originally dated to > 43,000 ^{14}C years BP (Mook, 1982), four AMS radiocarbon dates from level 11 (Hedges et al., 1994) are all younger than the original date; they range from 33.8 ± 0.9 ka BP to 38.5 ± 1.7 ka BP This time span for a single level may indicate a long period of accumulation, although contamination and/or level mixing may also apply (Hedges et al., 1994). The other Bacho Kiro specimens are associated with Aurignacian assemblages and derive from younger strata (6 and 7). They comprise five isolated teeth, a right parietal fragment, and a right mandibular corpus preserving dm_2 and M_1 (Churchill and Smith, 2000; Kozłowski, 1982). The dates for the level 6–7 material range from 32.7 ± 0.3 ka ^{14}C BP (Level 7/6b) to 29.15 ± 0.95 ka ^{14}C BP (level 6a/7) (Kozłowski, 1982). While Glen and Kaczanowski (1982) and Churchill and Smith (2000) found that the Bacho Kiro specimens fall, anatomically, in the area of overlap between Neandertals and Upper Paleolithic moderns, the latter concluded that the sample tended toward the Upper

Paleolithic modern human side of variation. Recently, Bailey and colleagues (2009), in their examination of a cast of one of the chronologically youngest Bacho Kiro Aurignacian specimens (#599 from Level 6a/7), tentatively concluded that it was most like Upper Paleolithic modern humans and not like Neandertals.

Görömby-Tapolca and Oblazowa

A robust but "fully modern" (Tillier et al., 2006: 99) occipital from Görömböly-Tapolca, Bükk Mountains, Hungary, was originally thought to be of Gravettian age (Tillier et al., 2006), but recent direct dating (30.3 ± 0.30 ka ^{14}C BP) places it earlier (Davies and Hedges, 2008–2009). A single distal thumb phalanx from the southern Polish site of Oblazowa has been directly dated to 31.0 ± 0.55 ka ^{14}C BP (Hedges et al., 1996).

Gravettian Modern Human Fossils from Eastern Central Europe

Postdating the earliest modern fossils and earliest Upper Paleolithic in eastern Central Europe are numerous human remains from the Eastern Gravettian. Chronologically, these remains fall into two time periods. First, as represented by the majority of the human remains, is the Pavlovian (~25–30 ka), followed by the Willendorf-Kostienkian (~20–25 ka). The remains from Dolní Věstonice, Krems-Wachtberg, Pavlov, and Předmostí are all probably Pavlovian, while Brno-Franzcouska, Grub/Kranawetberg, and Willendorf (I and II) derive from the later period. Most of the remains are from Moravia, while the others are from Austria. The sites form three spatial clusters (Figure 5.9): (1) Krems-Wachtberg and the Willendorf sites come from the Danube valley west of Vienna; (2) Brno-Franzcouska, Dolní Věstonice, Pavlov, and Grub/Kranawetberg lie in southern Moravia/northeatern Austria; and (3) Předmostí lies the farthest to the northeast. Although robust and, in a few cases, exhibiting some Neandertal-esque features (Trinkaus, 2007), the Gravettian remains are decidedly anatomically modern.

As with the other samples and regions discussed in this chapter, direct dating of human remains has helped exclude some that were once thought to be Gravettian in age (Table 5.1). Most notably, Svitávka (Vlček, 1971) has been dated to 1,180 ± 50 ^{14}C BP (Svoboda et al., 2002). This specimen's morphological similarities to Brno 3 were used to support an Upper Paleolithic age. However, Brno 3, now lost, is itself of questionable age (Svoboda et al., 2002), and for that reason we do not include it in our discussion of the early modern material from Central Europe. The Balla subadult remains from Hungary were once thought to be Gravettian in age (Vögel and Waterbolk, 1972), but recent direct dating places them in the early Neolithic (Tillier et al., 2009). Other direct dates on presumed Gravettian fossils have yielded results consistent with this designation. A rib from Dolní Věstonice 35 yielded a date of 22.84 ± 0.2 ka ^{14}C BP (Svoboda et al., 2002; Trinkaus et al., 1999), while dating of Brno-Franzcouska resulted in a date of 22.68 ± 0.21 ka ^{14}C BP (Pettitt and Trinkaus, 2000). The Willendorf-Kostienkian date for the former is probably due to contamination, since other dates and the archaeology from Dolní Věstonice I all indicate an earlier, Pavlovian, age (Svoboda et al., 2002; Trinkaus et al., 1999). Dates on associated charcoal for the Dolní Věstonice II and Pavlov remains date them to ~25–27 ka (Trinkaus and Svoboda, 2006).

Pavlovian Remains from Eastern Central Europe

Pavlovian human remains are known from Předmostí, Dolní Věstonice, and Pavlov in Moravia. Additionally, the three infant skeletons from Krems-Wachtberg in the Danube valley west of Vienna also date to this earlier period of the Eastern Gravettian. Much of the Moravian material has been known since before the 1980s and, thus, has figured prominently in discussions of modern human origins (Smith, 1984; Trinkaus and Svoboda, 2006; Veleminská and Brůžek, 2008). The Předmostí remains were excavated periodically between 1884 and 1928. The fossils from the Dolní Věstonice I site were uncovered between 1925 and 1974, and the Pavlov remains in 1954 and 1957 (Holliday et al., 2006; Svoboda, 2006a). Continuing excavations at Dolní Věstonice (DV II locality) during the 1980s as well as the identification of numerous human teeth and bone fragments from the faunal remains during 1997–1998 (Holliday et al., 2006) yielded considerably more Pavlovian remains. Additionally, major analyses of the Dolní Věstonice and Pavlov fossils and reanalyses of the Předmostí remains in light of recently discovered documentation have been published during the past decade (Trinkaus and Svoboda, 2006; Veleminská and Brůžek, 2008). The single and double infant burials discovered during 2005–2006 at Krems-Wachtberg have been briefly described and are dated (26.58 ± 0.16 ka ^{14}C BP) to the Pavlovian period (Einwögerer, 2005; Einwogerer et al., 2006).

The remains of approximately thirty individuals were excavated at the site of Předmostí (Matiegka, 1934–1938; Veleminská and Brůžek, 2008). Although most of the remains were once thought to have come from a mass or communal grave (cf. Smith, 1984), recent work has shown that the Předmostí "cemetery" resulted from consecutive interments of remains over a long period of time (Brůžek and Veleminská, 2008; Svoboda, 2008). The time span was long enough that it is possible that a small minority of the Předmostí remains may date from the later Willendorf-Kostienkian phase of the Gravettian (Svoboda, 2008). As in the case of Mladeč, most of the Předmostí remains were destroyed in the Mikulov fire at the end of World War II. However, two mandibular fragments, Předmostí 21 and 26, survived and have been described and analyzed in recent years (Drozdová, 2001; Vlček, 2008). Předmostí 21 preserves the premolars and molars from the right side and exhibits the sort of artificial buccal wear (Drozdová, 2001) seen in many other Gravettian teeth (Hillson, 2006; Teschler-Nicola et al., 2004; Trefný, 2008). Vlček's (2008) brief description of Předmostí 26 does not report any similar artificial wear.

Veleminská and colleagues (see works in Veleminská and Brůžek, 2008) undertook a reappraisal of the Předmostí evidence based largely on Matiegka's glass negatives and notes, as well as excavation notes left by K. J. Maška. The results of the works in the Velminská and Brůžek volume (2008) largely confirm Matiegka's (1934–1938) results and conclusions. Yet the reviews of the Matiegka and Maška documents fail to clarify the exact number of individuals as well as many of the bone associations. Seemingly, the only postcranial-cranial associations that are assured are for Předmostí 3 and Předmostí 4 (Frayer and Wolpoff, 2008).

To the southwest of Předmostí lie the adjacent sites of Dolní Věstonice and Pavlov (Figure 5.9). Although most of the remains from these sites were known prior to Smith's (1984) review, the significant DV 13–15 triple and DV 16 single burials were discovered during the late 1980s (Holliday et al., 2006). DV 13 and 15 were in their early 20s at death, while DV 14 was slightly younger (Hillson et al., 2006). All three appear to be males, although some congenital abnormalities resulted in DV 15 appearing more female than normal (Brůžek et al., 2006). The male skeleton DV 16 was at least 45 years old at death, making it the oldest of all known Pavlovian individuals (Hillson et al., 2006). Evolutionarily, the anatomy of the DV 13–16 individuals largely confirms what was seen in the previously known Dolní Věstonice sample, although DV 16 is somewhat notable for its robusticity and archaic appearance (Franciscus and Vlček, 2006). At least one Neandertal-like characteristic of DV 16, its inflated infraorbital region, Franciscus and Vlček (2006) contend is due to postmortem change and/or congenital deformation. Furthermore, some degree of DV 16's robusticity may be due to its more advanced age at death compared to other Pavlovian remains, as some aspects of cranial robusticity development continue during adulthood (Ahern, 1998; Behrents, 1985; Enlow and Hans, 1996; Israel, 1968, 1971, 1973, 1977).

Cranially, the Pavlovian peoples are clearly modern, with tall, gabled vaults, browridges divided into medial and lateral segments, narrow nasal apertures (except DV 13 and Pavlov 1), and excavated infraorbital regions. Metrically, they cluster with later Europeans (Franciscus and Vlček, 2006; Jantz and Owsley, 2003; Veleminská et al., 2008). Yet some details of anatomy of the Pavlovian remains are not especially similar to recent Europeans. Most of the male crania exhibit fairly large browridges, albeit of modern form with distinct medial and lateral segments. Although their vaults are taller than Neandertals and, at least some pre-Gravettian modern humans, they are shorter than most recent Europeans. Furthermore, the Gravettian crania exhibit greater prognathism than recent Europeans, reflecting larger average teeth. Many of the Pavlovian crania exhibit hemibuns (or even true occipital buns, according to Trinkaus, 2007) and suprainiac fossae, although the latter are medially restricted (not horizontally oval) and not particularly similar to Neandertals (Franciscus and Vlček, 2006). Mastoid processes are large, protrude well below the juxtamastoids, and lack anterior tubercles.

Postcranially, the Pavlovian remains are modern. The upper limbs are less robust than Neandertals but also less robust than many recent modern humans (Trinkaus, 2006). Trinkaus (2006) attributes this to having a more efficient tool kit than Neandertals as well as lacking the rigors of agricultural life.[18] Limb proportions and stature of the Pavlovian humans, as well as those of many other Upper Paleolithic moderns, are different from the earlier Neandertals and are more similar to those of the Skhūl-Qafzeh peoples as well as recent sub-Saharan Africans (see Table 5.5). Holliday (2006) and others contend that the Gravettian limb proportions reflect a tropical climatic adaptation retained in recent migrants to glacial Europe. Countering this explanation, others have argued that the differences between Neandertals and the Gravettian limb proportions are mechanical ones (Caspari, 1992; Formicola, 1986; Frayer et al., 1993; Higgins and Ruff, 2011); that is, Neandertals were adapted for stronger quadriceps femoris reaction (Pearson, 1997), perhaps related to moving over rough, uneven terrain. While Holliday and Falsetti (1995) found no relationship between mobility and lower limb length among recent foraging populations (see also Weaver and Steudel-Numbers, 2005), Higgins and Ruff's (2011) analysis supports the contention that Neandertal lower limb anatomy was advantageous on sloped terrain.

Willendorf-Kostienkian Remains from Eastern Central Europe

Some of the Předmostí remains may have been Willendorf-Kostienkian in age, although we will likely never know if this was the case, much less which specimens were of this time period. The Willendorf-Kostienkian-age direct date from Dolní Věstonice 35 is probably due to contamination by younger carbon (Svoboda et al., 2002; Trinkaus et al., 1999). Of almost certain Willendorf-Kostienkian age are the human remains from Brno-Franzcouska, Willendorf (I and II), and Grub/Kranawetberg. The Brno-Franzcouska burial (Brno 2) was excavated in 1891. Its mode of burial, with numerous grave goods and covered by mammoth tusks, is consistent with a Gravettian classification. Furthermore, direct dating of the specimen confirms this (Pettitt and Trinkaus, 2000).

In Austria just up the Danube from Krems-Wachtberg, the Willendorf I and II sites have yielded two fragmentary fossils dating to the Willendorf-Kostienkian phase of the Gravettian. Willendorf 1 (from Willendorf I) comprises a femoral diaphysis that exhibits a pronounced pilaster and *linea aspera* as well as robustness that falls in the middle of the Upper Paleolithic range (Teschler-Nicola and Trinkaus, 2001). It has been directly AMS

Table 5.5. Limb proportions in the eastern Central European Gravettian and comparative samples.[1]

	Brachial Index	Crural Index
Eastern Central European Gravettian		
Dolní Vestonice 3	76.7	86.0
Dolní Vestonice 13	77.1	86.6
Dolní Vestonice 14	76.2	82.5
Dolní Vestonice 15	77.3	89.6
Dolní Vestonice 16	79.2	83.5
Pavlov I	75.7	
Předmostí 3	77.2	86.5
Předmostí 4	78.1	87.1
Předmostí 9[2]	78.7	79.4
Předmostí 10[2]	78.5	85.1
Předmostí 14[2]	79.1	87.0
Average	77.6	85.3
(s, n)	(1.2, 11)	(2.9, 10)
W. Asian Neandertal	78	77
(s, n)	(2.4, 5)	(2, 5)
Qafzeh-Skhūl	76.5	83.7
(s, n)	(5.5, 3)	(5.9, 2)
Recent Europeans	75.0	82.7
(s, n)	(2,5, 391)	(2.4, 436)
Recent sub-Saharan Africans	78.6	85.3
(s, n)	(2.8, 152)	(2.4, 158)
European Neandertals	73.2	78.7
(s, n)	(2.5, 5)	(1.6, 4)
All European Gravettian	77.7	85.1
(s, n)	(2.0, 20)	(1.8, 18)

[1] Data from Holliday (1995, 2006) and courtesy of M.H. Wolpoff.

[2] The postcranial associations for these specimens are not certain (Frayer & Wolpoff, 2008).

radiocarbon dated to 24.25 ± 0.18 ka ^{14}C BP (Teschler-Nicola and Trinkaus, 2001). Willendorf 2 (from Willendorf II) is a mandibular symphysis whose anatomy is similar to other early Upper Paleolithic mandibles. Although a *planum alveolare*, inferior lingual torus, and "indistinct" lateral mental tubercles are somewhat archaic features, the specimen exhibits a clear mental trigone, *fossa mentalis*, and other aspects of modern chin development (Teschler-Nicola and Trinkaus, 2001). Willendorf 2 derives from layer 9, which is approximately 23.9–24 ka BP.

At the site of Grub/Kranawetberg, two deciduous tooth fragments were discovered in 1996 and 1998 from Gravettian deposits dated to 24,400–25,500 BP (Antl-Weiser, 1999; Antl-Weiser and Teschler-Nicola, 2000/2001). One is a right first dm_1 (Grub/Kranawetberg 1: GK 96/634) and the other a left di^2 (Grub/Kranawetberg 2: GK 98/4028)

(Teschler-Nicola et al., 2004). According to Teschler-Nicola and colleagues (2004), both could have belonged to the same individual. The molar shows artificial buccal wear like other Gravettian teeth (see above; Hillson, 2006; Trefný, 2008). Metrically, the incisor is small compared to the few other Gravettian di^{2}s. Although the small mesiodistal measure (5.1 mm) could be explained as due to interproximal and occlusal wear, the especially small buccolingual dimension (4.5) cannot. Nevertheless, comparative sample sizes preclude any significance to Grub/Kranawetberg 2's small dimensions (Teschler-Nicola et al., 2004).

Discussion

Our understanding of the evolutionary origins of modern humans in Central Europe and elsewhere has significantly matured since the middle of the nineteenth century. In the last twenty-nine years since Smith's 1984 review of the Central European evidence, there have been considerable advances, both in terms of evidence and theory. At the evidentiary level, new fossil discoveries (in particular the Oase and post-1984 Vindija specimens) have been important. However, the most dramatically new evidence has come from the application of new techniques to old fossils. In particular new dating methods and genomic analyses have transformed our available dataset. At the theoretical level, the debate has shifted from a relatively polarized one positing complete replacement of archaic Eurasians versus overall regional continuity to a discussion of how much admixture and its temporospatial pattern.

Evidentiary Level

Improved dating, especially the widespread application of direct AMS (including ultrafiltration) radiocarbon dating (cf. Higham et al., 2006; Jöris, 2011; Soficaru et al., 2007; Street et al., 2006; Wild et al., 2005, 2006), has provided a tighter chronology of the transition. For example, the direct dates for two of the Vindija G_1 specimens (Higham et al., 2006; Smith et al., 1999) as well as of the Oase (Trinkaus et al., 2003b) and Mladeč (Wild et al., 2005) remains have established that Neandertals and modern humans in eastern Central Europe were penecontemporaries. The incredible trimming of the early Upper Paleolithic human fossil record by the application of direct dating techniques, especially in the case of western Central Europe, has highlighted how little we know about the first modern humans in this area. The gracile, recent-European anatomy of Binshof-Speyer, Vogelherd (Stetten), and Paderborn-Sande remains all seemed to support a complete replacement of Neandertals, while the more robust Hahnöfersand frontal was used by Bräuer (1980) and others (e.g., Smith, 1984) as evidence of Neandertal-modern admixture. Direct AMS dating of these to the Holocene now makes them irrelevant for understanding modern human origins (Table 5.1). In addition to direct dating of fossils, further explorations of many sites have led to improved understandings of fossils' ages. For example, the new OIS 5e age for the Ša'la fossils makes them too early to be "transitional," as had once been argued (Smith, 1982).

Over the last 30 years, the genetics and genomics revolution has helped shape our understanding about modern human origins. For many years, starting with the mtDNA analysis by Cann et al. (1987), an exclusively African origin for all modern humans seemed likely (Stringer and Andrews, 1988). However, some (cf. Harpending and Eswaran, 2005; Harpending and Rogers, 2000; Relethford, 2001a,b,c and references therein) suggested different explanations were possible, and several studies have shown a considerable depth for some non-African genetic polymorphisms (Eswaran et al., 2005; Harding, 1997, 2000; Harding et al., 1997; Templeton, 2002, 2005; Yu et al., 2001), as well as some archaic non-African contributions to the modern human gene pool (Evans et al., 2006).

Likewise, analyses of mtDNA isolated directly from Neandertal specimens have added another dimension to the debate (Caramelli et al., 2006; Krings et al., 1997, 2000; Lalueza Fox et al., 2005, 2006; Orlando et al., 2006; Ovchinnikov et al., 2000; Schmitz et al., 2002; Serre et al., 2004). Although many interpreted the genetic evidence as supporting completely separate Neandertal and modern lineages (cf. Schwartz and Tattersall, 2010), developments in the field of ancient genomics illustrated that various processes (e.g., population expansions, migrations, bottlenecks, etc.) could cloud our insight into how past events affect modern human gene pools, and many haplotypes of mtDNA could have been lost over time (Adcock et al., 2001; Relethford, 2001a,b,c). What seems to emerge from all the ancient DNA studies is a low diversity of Neandertal mtDNA compared to living humans, suggesting a drastic bottleneck event. This must be taken into account in all explanatory models that use differences in genetic sequences as their datasets.

A new age for paleogenomics started with the successful extraction of nuclear DNA from one of the Vindija specimens (Vi 33.16) that previously yielded an mtDNA sequence similar to other Neandertal specimens (Serre et al., 2004). Interestingly, Green and colleagues (2006) show that the Vi 33.16 genome shares approximately 30% of SNP[19] derived alleles with modern humans. This is best explained by gene flow between some Neandertal and early modern populations. More recently, Green and colleagues' (2010) analysis showing a 1–4% Neandertal contribution to living Eurasians provides further support of significant Neandertal-modern gene flow. Due to the aforementioned processes and the action of evolutionary mechanisms, this estimation must be seen as a minimum assessment. More recently, Sankararaman and colleagues (2012) report that the last gene flow from Neandertals into subsequent modern Europeans occurred 37,000–86,000 years ago. In short, current data do not support the distinction of Neandertals at a species level (Janković et al., 2011; Smith et al., 2005; Weiss and Smith, 2007).

Both mtDNA and the nuclear parts of the genome from recently found specimens from Denisova Cave in Siberia suggest more complex patterns of contact in various geographical areas (Krause, 2010; Reich et al., 2010, 2011). While Neandertal contribution, as noted above, is seen in contemporary Eurasians, the Denisovan contribution can be detected in present-day peoples of Melanesia. Although based on the DNA sequences it can be argued that the Denisovans are a sister group to Neandertals, caution is needed, as the reported bottleneck in Neandertals likely happened after the separation of their lineages (Reich et al., 2010) and thus limits our knowledge of Neandertal genetic variation.

Theoretical Level

Two models dominated the discussion of modern human origins from the late 1980s through the 1990s: (1) Out-of-Africa (Stringer, 1989), and (2) Multiregional Evolution (Wolpoff et al., 1984). Trinkaus (2007) contends that both of these models, at least in their strict senses, are now untenable, given the wealth of fossil, genetic, and archaeological data. A complete replacement of Eurasian archaics is just as unlikely as a pattern of overall in situ regional continuity. The middle ground, where there was both an origin for modern humans in Africa as well as subsequent admixture with archaic populations, remains the only viable explanation, according to Trinkaus (2007). Various models occupy this middle ground with the most prominent one being the Assimilation Model (Smith et al., 1989; Smith et al., 2005). However, it should be noted that various proponents of the two older and polarized models (Out-of-Africa and Multiregional Evolution) also have claimed this middle ground (cf. Cann, 1992; Caspari and Wolpoff, this volume; Hawks and Wolpoff, 2001a,b; Stringer, 1992; but see Smith et al., 2005). Hawks and Wolpoff (2001) argue that Multiregional Evolution has never required a worldwide pattern of overall regional continuity and that it even allows for some local extinction of archaic populations. Stringer (1992), Cann (1992), and other out-of-Africa proponents (e.g., Bräuer, 1989) have stated that limited gene flow between modern humans and Eurasian archaics may have occurred but that this would not be inconsistent with the out-of-Africa model.

Models that encompass a wide range of possible admixture scenarios, such as Multiregional Evolution and Out-of-Africa, are useful for explaining the overall pattern of evolution of our species. However, such models, because of their breadth, may not be the most useful of explanations to test when it comes to understanding the temporospatial details of the origin of modern humans. These broad models may encompass the middle ground, but we must focus on testing more focused hypotheses in order to better understand these details.

The Evolution of Modern Humans and the Evidence from Central Europe

Few other regions have as much potential for understanding the details of modern human origins as Central Europe. We would like to bring the Central European record to bear on the examination of the following issues: (1) the problem of typology in understanding biology and culture across the transition, (2) the pattern of biological variation among Neandertals, (3) the appearance of modern humans and the disappearance of the last Neandertals, and (4) the degree and pattern of Neandertal and early modern human admixture.

Typology of Biology and Culture

A common thread to research on Neandertals since their first discovery has been an emphasis on demonstrating the distinctiveness of Neandertals from modern humans. Early on this was often used to demonstrate that Neandertals were not just another extinct race of humanity or pathologically deviant modern humans, but were, in fact, human ancestors (King, 1864; Schaaffhausen, 1857). By the early twentieth century, the motivation for making Neandertals distinct had shifted from seeing them as primitive ancestors of humans to being a fundamentally distinct and extinct branch on the family tree (Boule, 1921). Despite Brace's (1964) attack on this "pre-sapiens" perspective as typological and non-evolutionary, followed by the dismissal of the supposed fossil record of "pre-sapiens" (Trinkaus and Shipman, 1992), accepting Neandertals as an extinct side branch of our evolution continues to promote seeing them as different *in type* from ourselves. Numerous recent studies appear to begin with the assumption of distinctiveness and then demonstrate it (cf. Benazzi et al., 2011; Harvati et al., 2004; Ponce de Léon and Zollikofer, 2006; Tattersall and Schwartz, 2006). The revolution of geometric morphometrics, although an important methodological step forward, has been repeatedly used within a typological framework that emphasizes Neandertal-modern separation. Such a typology, as with all typologies, works well when our focus is away from the area of transition between two categories. Thus, as long as we continue to compare samples of mostly pre-OIS 3 Neandertals with mostly post-Aurignacian modern humans (cf. Benazzi et al., 2011; Harvati et al., 2004; but see Ahern et al., 2005), "Neandertal" and "modern" will appear to be distinct types. Furthermore, most of the well-preserved fossils of Neandertals come from the end of their range, Western Europe, which was farthest from their contemporaries. Thus, focusing on these well-preserved specimens to the exclusion of the fragmentary but numerous fossils from other regions, such as Central Europe, has helped further the Neandertal versus modern human typology. Yet, when it comes to understanding the process of the origin of modern humans in Western Eurasia, we must focus, at least in part, on the period of the transition. Variation has the potential to be continuous across transitions. Thus, a typological perspective can potentially make us miss, or at least misunderstand, the very evolutionary process that interests us.

Categories like Middle or Upper Paleolithic are no less problematic and should be considered just general terms of convenience, not necessarily reflecting the reality of processes at various regions and at different times (indeed, not even in the same time). Growing archaeological data over the last hundred or more years have shown that the elegant schemes in which there is a clean break between these two periods of early prehistory do not really reflect reality (see Clark, 2009). Thus numerous scholars talk about so-called "transitional industries" that can be recognized within Europe (and elsewhere) between roughly 30 and 50 ka. As Straus (2009) rightfully notes, the problem lies in the emphasis on "transition" between two distinct entities, the Middle and the Upper Paleolithic, as this taxonomy implies there is a real and sharp break and change. However, it also implies that it stands between two other entities (in this case the Middle and the Upper Paleolithic) that are static in nature. This cannot be further from the truth. Many of the aspects and traits commonly associated with the Upper Paleolithic, like the use of blade technology, even prismatic blade technology, bone tools, non-utilitarian objects, and so forth, are found in various earlier contexts (i.e., Middle Paleolithic) (Straus, 2009). They may not be as common as in the Upper Paleolithic, but are there, and therefore one cannot easily define the abrupt change and breakup with earlier traditions. If one wants to find a sharper break, it is seen during the last glacial maximum and within the later phases of the Upper Paleolithic, not at the "Middle" to "Upper" Paleolithic transition. One additional problem with the term "transitional industries" is that most scholars try to ascribe it to biological groups (i.e., Neandertals or anatomically modern humans). It is accepted that Neandertals in Europe were responsible for the Middle Paleolithic, while the classical industries of the Upper Paleolithic were produced by anatomically modern newcomers (albeit in Western Asia this is not so and both groups are associated with Middle Paleolithic, Mousterian tools). Thus the same approach is applied to these "transitional" industries that are either attributed to late Neandertal groups or to the first anatomically modern humans in the region (see Adams, 2009; Chabai, 2003; Hoffecker, 2011 and references therein). Furthermore, the explanations for their appearance range from independent inventions (see Zilhão and d'Errico, 2003; Zilhão et al., 2006) by local Neandertals, to "acculturation" that came from the "moderns" (Harrold, 1989; Mellars, 1996; Mellars, 2006). This may have been a useful model, or models, to think about and test, but too much time and energy has gone into trying to fit the data into the preferred explanation. Harrold (2009) puts the "transition debate" in a historical context, outlining some of the major problems (see also Riel-Salvatore, 2009).

Realizing the conceptual problem, in recent years numerous authors have been trying to find novel and more productive ways of thinking about this "transition" (Brantingham et al., 2004; Clark, 2009; Peresani, 2011; Soffer, 2009; Straus, 2009 and references therein). Neandertals were very variable in time and space and in behavior as well as in biology. They sucessfully adapted to local needs and environments and used the available resources. The almost lack of specialization compared to later humans of the (later) Upper Paleolithic more likely was due to lower population density and different ways of life and resource use. Smaller groups did not need to waste their time and energy in massive game hunting. As Brantingham and colleagues (2004) note, the presence of a specific behavior or behavioral system is not necessarily an accurate predictor of biological phylogeny. We need to turn to site-by-site analysis. As Straus (2009) points out, there were many "transitions" at different times and places, at different rates and for different reasons. When approaching a specific assemblage, we must keep in mind we are dealing with a single site and that the cultural remains first and foremost reflect a specific function or activity, and so forth, and are not representative of the industry, or culture, as a whole. Most were accumulated as a result of short occupation episodes by smaller groups and were not long-term dwelling places of the whole population. An even worse mistake would be making generalizations about the biology, taxonomy, and phylogeny of people responsible for these archaeological (*sensu stricto*) assemblages, when in the vast majority of cases, no human remains were found in association with them (and even when they are, there is not clear authorship).

The so-called "transitional industries" include the Châtelperronian of France and northern Spain, Szeletian and Jankovichian of central and parts of eastern Europe, Uluzzian of Italy (Tuscany, Calabria, southern Adriatic area, Uluzzo Bay, etc), Streletskian of eastern Europe, Jerzmanowician of eastern Germany and Poland, Althmülian of southern Germany, Bohunician of the Czech Republic, Brynzeny and Kostenki Szeletian of Russia, and several other unnamed or site-specific assemblages from Poland, Slovakia, the Czech Republic, Romania, and so on, in which various elements of the Mousterian (or Middle Paleolithic) appear alongside the Upper Palaeolithic types or types produced using technology commonly associated with the Upper Palaeolithic. Many scholars recognize the origin of these industries in local Mousterian variants and see no abrupt change (Allsworth-Jones, 1990; Anikovich, 1992; Bordes, 1972; Cabrera Valdés et al., 1997; Churchill and Smith, 2000; Clark and Lindly, 1989; D'Errico and Zilhão, 1998; Gioia, 1988; Golovanova and Doronichev, 2003; Harrold, 1989; Kozłowski, 2004; Kozłowski and Kozłowski, 1979; Laplace, 1966; Otte, 1990; Palma di Cesnola, 1993; Pradel et al., 1966; Rigaud, 1989, 1997; Straus, 1997; Svoboda, 1993, 2004; Valoch, 1972). In a recent study of the Uluzzian, Riel-Salvatore (2010) suggests this industry was restricted to the southernmost part of peninsular Italy. According to this author, the Mousterian is rather distinct from the Uluzzian *sensu stricto*[20] but also from other contemporary early Upper Paleolithic industries (proto-Aurignacian). However, the question of whether late Neandertals or early anatomically modern humans were responsible for this industry is unclear (see Benazzi et al., 2011; Churchill and Smith, 2000; Riel-Salvatore, 2009; Riel-Salvatore et al., 2012). Indeed, it might have been a population encompassing biological elements from both groups. Except for documented associations of Neandertal remains and Châtelperronian artifacts from La Roche à Pierrot at St. Cesaire and Grotte du Renne at Arcy-sur-Cure (Hedges et al., 1994; Hublin et al., 1996; Leroi-Gourhan, 1958; Léveque and Vandermeersch, 1980; but see Bar-Yosef and Bordes, 2010; Higham et al., 2010), as well as the likely association of Neandertal remains with a "transitional" assemblage in level G_1 at Vindija (Janković et al, 2011), there are no diagnostic hominin fossils associated with any of these earliest Upper Palaeolithic finds (see Churchill and Smith, 2000).

These industries are either contempory with, or, in most cases, earlier than the Aurignacian, the industry seen by most as the handiwork of anatomically modern humans as they move into the region (Bailey et al., 2009; Mellars, 1996, 2006), although some authors argue for local origins (see Oliva, 1993; cf. Bar-Yosef, 2006). An additional problem is that the Aurignacian is often regarded as a single imported complex that can be recognized in the archaeological record by the appearance of certain tool types and automatically assigned to anatomically modern populations. However, more and more studies show that several tool types (especially bone tools) used as indicative of the Aurignacian are in fact commonly found in various aforementioned "transitional" industries (Allsworth-Jones, 1990; Janković et al., 2006, 2011; Miracle, 1998; Svoboda, 1993, 2004, 2006b; Valoch, 1972). Furthermore, the Early Aurignacian differs from the Late Aurignacian (Miracle, 1998). Finally, there are great differences between assemblages of the typical Aurignacian from Western Europe, and that of Central/Eastern Europe (Karavanić and Smith, 1998; Miracle, 1998; Oliva, 1993; Svoboda, 2004). All this makes it clear that there may be a different pattern of behavioral and most likely populational change in Western vs. Central/Eastern Europe

(Janković et al., 2006, 2011). Kozłowski (2004) recognizes several differences between these "transitional" industries according to the source from which they derived.[21] The industries that are characterized by the presence of backed points/blades, such as Châtelperronian, Uluzzian, and several site-specific industries in Poland, Slovakia, Moldova, and Romania, have no identifiable substrate and are quite widespread geographically. According to Kozłowski (2004), they arose independently of "Aurignacian" influence.

Biological Variation

Neandertal and adjacent populations' biological variation across space and time can be informative about the patterns of selection, gene flow, and genetic drift. Under a scenario where Neandertals were completely isolated from adjacent humans until some very limited hybridization with invading modern humans (cf. Currat and Excoffier, 2011), we would expect the pattern of biological variation within Neandertals to be independent of the biology of adjacent populations. In other words, there should not be a west to east cline of Neandertal features with Western European fossils exhibiting the highest frequency of Neandertal features and with an increase of more modern features as one moves farther to the east. Furthermore, Neandertals should not accumulate more and more modern features over time, if they had been completely isolated.

Heterogeneity within Neandertal populations is well known in terms of morphology as well as ancient DNA (i.e., Degioanni et al., 2011; Fabre et al., 2009; Hambücken, 1998; Vandermeersch and Garralda, 2011; Voisin, 2004). However, a more detailed approach to Neandertal morphology shows that more than being heterogeneous, their morphology displays a west to east cline (Voisin, 2006). Neandertals from Western Europe present more pronounced characters than Neandertals from the Near East.[22] Recent works on the shoulder are consistent with this hypothesis (Di Vincenzo et al., 2012; Voisin, 2011). In other words, Western Neandertals could be viewed as "hyper-Neandertal" and Eastern ones could be viewed as "hypo-Neandertal." Moreover, modern humans from Central Europe (as well as from the Near East) display some Neandertal traits that do not exist in modern humans from Western Europe (Voisin, 2006).

In terms of temporal variation within Neandertals, the case for Neandertals evolving in the direction of modern humans (cf. Smith, 1984; Smith et al., 1989) is less compelling than it once was. This explanation made sense when some more gracile and modern-like fossils were thought to be later in time than more "classic" or "hyper-Neandertal" fossils in the region. However, revised dating of some "transitional" fossils has moved them from being potentially late Neandertals to being much earlier (e.g., Ša'la, see Sládek et al., 2002). Furthermore, one of the most "classic" or "hyper-Neandertal" specimens from Central Europe, Feldhofer 1, has been dated to be quite late (Schmitz et al., 2002). Finally, the Hähnofersand frontal's new Holocene date (Terberger et al., 2001) has made its robust morphology irrelevant for understanding Neandertal–early modern human admixture. What remains, however, is the temporal sequence formed by the Krapina and Vindija samples. This sequence formed the core of past arguments about temporal change in Central Euorpean Neandertals (Smith, 1982, 1984; Smith and Ranyard, 1980; Wolpoff, 1980) with such specimens as Ša'la 1 used to illustrate that the temporal pattern was likely region-wide. As was the case then, fossil sample sizes remain small aside from those from Krapina and Vindija. So, although the Krapina-Vindija sequence hints at a localized temporal change in Central European Neandertals in the direction of modern humans, it does not demonstrate it.

The current evidence regarding temporospatial variation in Central European Neandertals is inconsistent with a scenario whereby Neandertals were fully isolated from extra-European populations, although such a scenario is not clearly falsified. A more conclusive testing of this hypothesis must await more fossils or, at least, improved techniques for analyzing temporospatial variation when samples are very small and not randomly distributed through space and time.

Appearance of Modern Humans and the Disappearance of Neandertals

The oldest, directly dated fossil in Central Europe that exhibits sufficient modern features to not be called a Neandertal is the Oase 1 mandible, dating to 34.3 + 1.0/–0.9 ka ^{14}C BP (Figure 5.2; Trinkaus et al., 2003b). The Oase 2 specimen yielded a date of > 28.9 ka ^{14}C BP. Recent direct dates of the Muierii and Cioclovina specimens place them approximately 4,000–5,000 years younger than Oase 1. All of the early Romanian fossil dates reported here used ultrafiltration pretreatment, which offers greater accuracy over standard AMS dating (Bronk Ramsey et al., 2004). Unfortunately, other early modern human remains from Central Europe have not been directly dated yet using this improved technique. The Mladeč Chamber D remains have been directly dated to 30.7–31.5 ka ^{14}C BP, but these dates are not ultrafiltration ones and thus may not be comparable to the Romanian dates. Nevertheless, it appears that anatomically modern humans are present in eastern Central Europe by ~30–35 ka ^{14}C BP.

Before the redating of numerous remains to the Holocene, the western Central European "early modern human" sample played an important role in interpretations of the appearance of modern humans in Europe (cf. Churchill and Smith, 2000; Conard and Bolus, 2003). The *kulturpumpe* model's presumption, that the earliest Aurignacian = anatomically modern humans, was based, in large part, on the presumed > 30 ka age of the Vogelherd human remains (Conard and Bolus, 2003). At this point, only a few fragmentary remains from western Central Europe are still thought to be Aurignacian in age, and direct dates are not yet available for any of these. Because of their fragmentary nature and lack of direct dates, it is currently not possible to provide a reasonable estimate for the appearance of anatomically modern humans in western Central Europe.

Equally as important as the date of the appearance of modern humans is the date of the last Neandertals in Central Europe. The Vindija G_1 specimens Vi-207 and Vi-208 provide the youngest dates of any Neandertals in the region at 30.6–34.2 ka ^{14}C BP (Higham et al., 2006). In western Central Europe, the Kleine Feldhofer Grotte fossils appear to be the youngest (c. 38.6–41.1 ka ^{14}C BP; Schmitz et al., 2002). All of the other Neandertal fossils from western Central Europe have not been successfully directly dated. While approximate chronology is known for most of them (Table 5.2), none exists (beyond "Pleistocene") for either the Untere Klause or Zeeland Ridges specimens. Those with approximate dates all appear to be > 46 ka.

So, based upon dates of available specimens, the oldest modern humans in eastern Central Europe are 30–35 ka ^{14}C BP. While the oldest date of appearance in western Central Europe is far less clear, it seems likely that at least some of the few Aurignacian-associated human fossils in this area date to ~28–30 ka ^{14}C BP, if not slightly older. The last Neandertals in eastern Central Europe date to ~30–34 ka ^{14}C BP and in western Central Europe to ~38–41 ka ^{14}C BP. Because the focus of this paper is on biology, we have not made any estimates of appearance and disappearance based on the presence or absence of particular archaeological industries. Although such evidence is more common in the record than fossils, we caution against the typology of such industries, not to mention a priori equating any of them with a particular "type" of human.[23] Furthermore, none of the available dates, of fossils or otherwise, are likely to be the *actual* dates for either the appearance of modern humans or the disappearance of Neandertals in the region, since taphonomical biases make finding the actual oldest or actual youngest very improbable (Martin, 1993; Surovell and

Brantingham, 2007; Surovell et al., 2009). In reality, modern humans likely appeared in Central Europe perhaps as many as a few thousand years before the last Neandertals and a few thousand years later than what the fossil record currently indicates. Thus, although the period of overlap in the region appears to be ~4,000 years based on dated specimens, it was likely longer.

Neandertal-Modern Admixture

Available genomic information clearly demonstrates admixture between Neandertals and modern humans (Hawks, this volume), with approximately 1–4% of living Eurasian ancestry derived from Neandertals (Green et al., 2010). The resolution of this evidence is such that it is presently not possible to tell the details of temporospatial patterning of such admixture. Thus, fossil anatomy remains as the best source of such insights.

There is a continuum of possible degrees of admixture that could be reflected in the Central European fossil record. These range from a complete replacement of Neandertals in the region (i.e., no admixture) to a high level of gene flow between Neandertals and modern humans. There are two lines of evidence that we can draw upon to test hypotheses of admixture for the region. First is evidence of gene flow from modern humans to Neandertals. The presence of characteristically modern human features in the last Neandertals in the region would indicate such gene flow. This gene flow could have taken place before a migration of modern humans into Europe (via exchange of mates between adjacent populations without a major population movement), and/or it could have taken place following a migration of modern humans into the region. In the case of the former, modern features may be present in Neandertal fossils that predate the earliest appearance of modern humans. In the case of the latter, there should not be such evidence and modern features should be limited to Neandertal fossils that postdate the appearance of modern humans. However, given the difficulties in determining when modern humans actually appeared in Central Europe, knowing which Neandertal fossils predate and which postdate this event is far from straightforward. Second is evidence of gene flow from Neandertals into modern humans. The presence of characteristically Neandertal features in the earliest and post-Neandertal modern humans would be indicative of such gene flow. The admixture may have taken place in Central Europe or it may have taken place exclusively outside of the region before the modern human population entered.

In the case of the Central European record, the Vindija G_1 fossils are the only ones that clearly postdate the appearance of modern humans in the region. However, the closest penecontemporary modern human fossils are more than 400 km away (Oase), and the potentially younger Mladeč remains are more than 350 km distant, Thus, it is unclear if the Vindija G_1 Neandertals or their immediate ancestors would have had any contact with modern humans. Anatomically, the small, fragmentary G_1 sample does not exhibit any clearly modern features (Ahern et al., 2004; Janković et al., 2006, 2011; Smith and Ahern, 1994; Smith et al., 1985; Wolpoff et al., 1981). The lack of clearly modern features, however, cannot falsify a hypothesis of admixed ancestry for the last Neandertals in Central Europe. As discussed above, the larger Vindija G_3 sample does exhibit some modern-like features (Ahern et al., 2004; Janković et al., 2006, 2011; Smith and Ahern, 1994; Smith et al., 1985; Wolpoff et al., 1981). This sample, which dates to approximately 38–45.6 ^{14}C ka, predates the oldest Central European modern human fossils, although this may be an artifact of sampling. So, although we contend that the modern-like features of the G_3 Neandertals are due to gene flow with modern humans, unfortunately we do not have the chronological resolution to determine whether this gene flow was before or after a modern human population migration into Europe.

Regarding evidence of gene flow from Neandertals into modern human populations, there are clearly Neandertal (or at least Neandertal-like) features present in the earliest modern humans as well as later populations (Cartmill and Smith, 2009; Frayer, 1992; Trinkaus, 2007; Wolpoff, 1999).[24] Although not ubiquitous among pre-Gravettian modern humans in Central Europe, their presence in this sample is in marked contrast with their absence in the earliest modern humans in Africa and their low frequency among the Skhūl-Qafzeh Middle Paleolithic humans. Furthermore, Wolpoff and colleagues (2001) report a similar degree of difference between the Mladeč male crania and Neandertals and between the former and the Skhūl-Qafzeh male crania. Although the homology of some of these traits has been debated (especially in the case of occipital morphology), the most parsimonious explanation of the presence of these Neandertal-like traits in the earliest Central European modern humans is admixture.[25]

That some Neandertal traits, albeit at lower frequencies, even persist into Gravettian populations in Central Europe is telling, given that these peoples postdate the oldest known Central European modern human remains (Oase) by approximately 10,000 years and the youngest known Central European Neandertals (Vindija G_1) by approximately 6,000 years. As Trinkaus (2005, 2007) points out, such a time gap means that these remains are not nearly as informative about the pattern of modern human origins as the pre-Gravettian fossils. That the gestalt of the Central European Gravettian fossils is decidedly modern cannot be taken, a priori, as lack of genetic continuity between Neandertals and Upper Paleolithic modern Europeans. Even if the Gravettian fossils lacked any evidence of Neandertal ancestry, such evidence could not refute a hypothesis of Neandertal–early modern admixture/continuity. However, the fact that some Neandertal features persist in the Eastern Gravettian fossils speaks to at least some degree of admixture in their ancestry (Frayer, 1992; Trinkaus, 2007). The "tropical" limb proportions (Table 5.5) in this population may reflect an even more recent (than the first appearance of modern humans in Europe) migration from lower latitudes. Alternatively, it might reflect a shift in locomotor mechanics from earlier populations, including earlier Upper Paleolithic ones, for which we know little about limb proportions. What the Gravettian limb proportion evidence cannot tell us is that the *first* modern humans in Europe came from Africa.

Assimilation in the Late Pleistocene of Central Europe

As pointed out by Smith and colleagues (2005), the available evidence remains insufficient to falsify any but the most extreme of models of modern human origins. Nevertheless, we think that one explanation, the Assimilation Model (Smith et al., 1989, 2005), offers the best fit with the evidence from Central Europe. This model posits that modern morphology, as a complex, evolved first in East Africa, and that, as this modern population spread out, it admixed to varying degrees with indigenous archaic humans, such as Neandertals. Thus, the overall pattern of modern human origins should reflect this overwhelmingly African origin combined with the persistence of some regional features that characterized archaic populations outside of the modern human homeland (Cartmill and Smith, 2009; Smith et al., 2005). This explanation is consistent with the current genomic evidence, in that the vast majority of living human ancestry appears to have come out of Africa in the Pleistocene (Cann et al., 1987; Thomson et al., 2000; Underhill et al., 1997), but that there are some alleles outside of Africa that have deeper roots in these regions (cf. Hammer et al., 1998, 2011; Harding et al., 1997; Harris and Hey, 1999; Huang et al., 1998). Furthermore, the paleogenomic estimate of 1–4% of living Eurasian ancestry being from Neandertals (Green et al., 2010)[26] is also commensurate with the Assimilation Model. The "mostly Out-of-Africa" model, based in large part on the genetic evidence (Relethford, 2001a; Rogers and Harpending, 1992; Rogers and Jorde, 1995; Templeton, 2002, 2005), is for the most part the same as the Assimilation Model. As mentioned previously, Multiregional Evolution does encompass, at least in recent renditions (Caspari and Wolpoff, this volume; Hawks and Wolpoff, 2001a; Wolpoff et al., 2004), the scenario proffered by the Assimilation Model. In this respect, Assimilation is a more specific explanation and one that we think best fits the available evidence.

The Assimilation Model does allow for a certain range of possible degrees and patterns of admixture and other processes as part of its explanation of modern human origins. Furthermore, these may vary from one location to the next, even if our present fossil record does not offer the resolution to see such variation. The current evidence does allow us to examine, to a certain degree, the patterns of variation over time and from region to region (see "Biological Variation" section, above). The temporal pattern seems to indicate an increase in more modern-like features among Neandertals over time, although much of this hinges on the Vindija level G_3 sample that may actually postdate contact with modern humans (Cartmill and Smith, 2009). Although the temporal pattern is not very clear, the spatial pattern appears to indicate a west to east cline of decreasing frequency of "hyper-Neandertal" features (Voisin, 2006). A potential implication of this clinal variation, which may be accommodated within the Assimilation Model, is that there was a gradient of interfertility between Neandertals and early modern humans across the Neandertal range. Admixture between the two human groups may have been possible in the eastern part of the Neandertal range, like West Asia. In Central Europe the interbreeding may still have been possible but less frequent. In the western area of the Neandertal range, hybridization may have been trivial or perhaps even impossible (Voisin, 2006).[27] Such a pattern of gene flow corresponds to a speciation by distance (Ridley, 2004).[28] Moreover, this hypothesis is consistent with recent simulations about Neandertal/modern human interactions (Barton et al., 2012). An alternative explanation of the clinal pattern, which also would be consistent with the Assimilation Model, is that of isolation by distance without complete reproductive isolation of even western Neandertals upon a modern human spread into Europe. Although somewhat less frequent than in Central Europe, Neandertal-like features persist in early modern human fossils in Western Europe, as well (Trinkaus, 2007). One possible explanation for the Les Rois pre-Gravettian human sample from France is that it represents a hybrid population (Ramirez Rozzi et al., 2009). Also, certain aspects of the Gravettian Lagar Vehlo (Portugal) child's anatomy appear to reflect some Neandertal ancestry, as well (Duarte et al., 1999; Zilhão and Trinkaus, 2002; but see Tattersall and Schwartz, 1999). However, the presence of Neandertal features among early modern humans in Western Europe, or Central Europe for that matter, does not necessarily mean that the modern population admixed with Neandertal of the same region, as their ancestors could have interbred with Neandertals in other regions before arriving.

Summary and Conclusions

New fossils, new dates, and new analytical techniques, over the last few decades, have improved our understanding of modern human origins dramatically. While many of these discoveries have been made regarding other regions, many have also been made about Central Europe. Most of the new Neandertal fossils from Central Europe are fragmentary and have not greatly changed our interpretations. However, the ~30–35 ^{14}C ka BP Oase early modern human remains, with their Neandertal-reminiscent features, in combination with the dismissal-by-direct-dating of almost all of the gracile, "hyper-modern" human remains from the early modern European sample, have fundamentally changed our understanding of the earliest modern humans and their admixed ancestry. New analyses of much of the Central European fossil record have also helped, especially in the case of the genomic analysis of aDNA from Vindija that demonstrates a Neandertal genetic contribution to living Eurasians.

Given the current evidence, we contend that Central European Neandertals were assimilated by early modern humans, contrary to either an overall in situ regional continuity or a complete replacement scenario. Although it is difficult to tell how much admixture took place in the region, the presence of more modern-like anatomy among late Neandertals and, more convincingly, the persistence of Neandertal features in early modern humans indicate that the degree of admixture exceeded that expected by interspecific hybridization. An improved fossil and archaeological record across the Neandertal-modern transition, further direct dating of fossils, more fossil genetic information, and the further application of additional analyses will help test this interpretation.

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Notes

1. In particular Cann et al., 1987.
2. See reviews in Relethford (2001a) and Cartmill and Smith (2009) for discussions of DNA studies on both extant and extinct humans.
3. Kleine Feldhofer Grotte, Mladeč, Krapina, Šal'a, Vindija, Kůlna, Peştera cu Oase, Muierii, and Cioclovina.
4. Although a tooth from Crvena Stijena (Montenegro) was originally published as Neandertal (Baković et al., 2009), its size and questions about its provenience may indicate otherwise (M. Roksandic, personal communication; R. Whallon, personal communication).
5. Part of the connecting highlands of eastern and western Central Europe.
6. Zeeland Ridges (Netherlands), Sarstedt, Hohlenstein-Stadel, Warendorf-Neuwarendorf, Hunas, and Ochtendung. A partial neonatal (or late-term fetal) skeleton from Sesselfelsgrotte preserves more of a single individual than any of the others, except for Feldhofer, but its young age (and fragmentary nature) makes interpretation difficult.
7. Interestingly, remains of the Barbary macaques (*Macacca sylvanus)* are found in earlier levels (Rosendahl et al., 2011).

8. The site of Crvena Stijena (Montenegro) contains a long Mousterian sequence topped by Aurignacian, Gravettian, and early Holocene deposits (Baković et al., 2009). Rare for a cave or rockshelter, a layer of volcanic ash from the Campanian Ignimbrite event is present in the deposits, marking the Middle/Upper Paleolithic boundary and dated to 39.3 ka (Morley and Woodward, 2011). During 2004, screening of slumped profile deposits (inferred to be from Basler's 1975 Middle Paleolithic levels), a single tooth was discovered (Baković et al., 2009). Baković and colleagues report that it is a Neandertal tooth but do not provide further clarification. Recent, unpublished analysis of the specimen by M. Roksanic indicates that the tooth is a left maxillary canine, and that, metrically, it falls below the Neandertal range and closer to Holocene modern humans (M. Roksandic, personal communication). Given the specimen's anatomy and that it was recovered from collapsed profile sediments, further interpretation of the Crvena Stijena tooth will have to await direct dating and/or genetic analysis (R. Whallon, personal communication).
9. Also known as Švédův stůl, after the name of the cave site.
10. The analysis of preserved faunal remains at Krapina indicates that the people living there exploited a wide variety of game, but it is also demonstrated that one of the animals well represented in the site is not the result of human activities (Miracle, 2007). The abundant cave bear remains at Krapina represent denning behavior after Neandertals abandoned the site. On the other hand, the extensive representation of rhinoceros remains do appear to be the result of human exploitation, probably mostly hunting, which further adds to the picture of Neandertals as top-level predators (Miracle, 2007).
11. A fragment of mandibular ramus (Vi 11.52) is labeled as coming from the older Level I, but this provenience is not certain (Ahern et al., 2004).
12. The G_1 assemblage also contains many Mousterian elements (Ahern et al., 2004).
13. Podbaba (Matiegka, 1924) and Silická Brezova (Vlček, 1957).
14. The eastern Central Europe cases involve skeletal remains that are intrusive into the levels they were initially reported from, and this intrusiveness was not recognized during excavation. This is true at both the Czech and Croatian sites (Table 5.1). At Velika Pećina, for example, there were skeletons from the Bronze Age discovered higher in the stratigraphic sequence, and it is likely that the Velika Pećina frontal belongs to this sample. It was originally thought to derive from level I at the site, associated with an undiagnostic Upper Paleolithic tradition and dated to ~34 ka (Smith, 1976a). The date for level I at the site is still valid for the early Upper Paleolithic in Central Europe, although it is an old, standard ^{14}C date and thus may be an underestimate of the actual age. It is important to note that the Velika Pećina specimen did play an important role, despite the dismissal of its early Upper Paleolithic age (Smith et al., 1999). The description of the specimen (Smith, 1976a) made it clear that its browridge morphology was distinct from that of the Neandertals and helped demonstrate the fundamental difference between even earlier modern Europeans and late Neandertals, while at the same time suggesting the existence of some continuity between them (Smith, 1982). Thus, work on Velika Pećina contributed to the arguments, later developed into the Assimilation Model (Smith et al., 1989), concerning the pattern of later human evolution in Europe.
15. Attempts at directly dating this specimen have, thus far, been unsuccessful.
16. The slightly younger dates from Mladeč 25c and collagen from Mladeč 9 (brown collagen) are likely due to contamination (Wild et al., 2006).
17. Also known as mylohyoid bridging.
18. However, not all Gravettian humans lacked robust postcrania. The female skeleton Dame du Cavillon (France, formerly Homme de Menton) is far more robust than recent European males (Chevalier et al., in prep a,b; Voisin et al., in prep a,b).
19. Single nucleotide polymorphism.
20. Especially in the use of bipolar technology, see also Palma di Cesnola (1993).
21. For example, Kozłowski (2004) contends that the blade technology seen in the production of Upper Paleolithic tool types of the Bohunician, as well as the material from Temnata Cave in Bulgaria and Korolevo in Ukraine, arose directly from the Levallois tradition. The Szeletian and Streletskian types of leaf points, and likely Jerzmanowician, are modelled on the preceeding Micoquian/Mousterian (also see Anikovich, 1992; Kozłowski, 1982).

22. For example, occipital morphology, morphology of the mastoid process, height of the cranial vault, morphology of the scapula axillary border, clavicle morphology, radius shaft, stature, and so forth. For a list, see Voisin, 2006.
23. Also, the "transitional" industries and the early Aurignacian generally lack any associated diagnostic fossils except for Vindija G_1, where potential level mixing complicates their interpretation.
24. Trinkaus (2007) reports the following Neandertal craniomandibular features present in the pre-Gravettian modern humans from Central Europe: (1) long, flattened frontal bones (Oase 2, Cioclovina 1, and Muierii 1); (2) occipital bunning (Muierii 1, Mladeč 3, 5, and 6) and hemibunning (Cioclovina 1, Mladeč 1, Oase 2); (3) lack of an external occipital protuberance, a medially limited nuchal torus, and an oval suprainiac fossa (Cioclovina 1 and Mladeč 6 except the latter has a broad nuchal torus); (4) a prominent juxtamastoid eminence (Oase 2, Mladeč 1, 2, and 5); (5) mandibular foramen lingual-bridging (Oase 1); (6) an asymmetrical mandibular notch (Muierii 1); (7) medially displaced mandibular notch crest (Muierii 1); (8) prominent lingual tubercle, marginal ridges, and a central lingual ridge on maxillary canines (Mladeč 9); and (9) a large ratio for front to back dental proportions reflecting large anterior teeth (Mladeč 54).
25. Furthermore, the degree of frequency difference between Neandertals and Upper Paleolithic modern humans for most of these traits is not statistically greater than what can be sampled from a comparison of Amerindian trait frequencies in Amerindians and postcontact Euroamericans (Ahern, 2006a).
26. As well as a slightly higher degree of Denisovan contribution to Melanesians (Reich et al., 2010).
27. Howell (1952) proposed that western Neandertals and modern humans were infertile contrary to more eastward populations. For Howell, this situation was due to complete isolation and genetic drift in the west part of the Neandertal distribution area caused by the extension of glaciers during cold periods that stopped gene flow between east and west populations.
28. The most striking examples of this are ring species like the salamander *Ensatina* or the greenish warbler *Phylloscopus* (Irwin et al., 2001a, 2001b, 2005).

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