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MORPHOLOGICAL EVIDENCE FOR MODERN HUMAN INFLUENCES IN LATE CENTRAL EUROPEAN NEANDERTALS

ABSTRACT: The long-standing debate on the role of Neandertals in the emergence of modern humans in Eurasia has been partially resolved by the genetic indications of relatively small, but not insignificant, Neandertal contributions to modern Eurasian populations. The relatively small contributions of Neandertals to modern humans likely stems from demographic factors limiting Neandertal population sizes. One of the issues not addressed by the genetic data was the impact of early modern human immigrant populations on the late Neandertals inhabiting Eurasia between ~35,000 and 45,000 years ago. East Central Europe, the area of focus for most of Karel Valoch's work, provides evidence of late Neandertals from the sites of Vindija (Croatia) and Šipka and Kůlna (Czech Republic). Analysis of the fragmentary Vindija specimens demonstrates an anatomical pattern reflecting reduction in facial size and prognathism. This pattern is consistent in all individuals but is projected onto a total morphological pattern that remains Neandertal. The Kůlna 1 maxilla and Šipka mandible also demonstrate aspects of this mosaic. These specimens provide anatomical evidence that reflects some impact of early modern biology during, or perhaps even slightly before, the early phases of modern human migration into Europe. This evidence further supports the interpretation that population dynamics between Neandertals and early modern people were complex and likely variable in differing parts of the ranges in which these populations overlapped.

KEY WORDS: Neanderthals – Central Europe – Assimilation – Vindija – Kůlna – Šipka

INTRODUCTION

In the late 1960s, two papers by eminent Czech scholars in *Current Anthropology* served to focus attention on the pattern of human evolution during the late Middle and Late Pleistocene in Central Europe. In 1969, Jan Jelínek reviewed the human fossil record, with a slight emphasis on the Neandertal and early modern human skeletal remains from then Czechoslovakia. In the previous year, Karel Valoch had published a similar paper dealing with the Palaeolithic archaeological record (Valoch 1968). These two papers emphasized to scholars not familiar

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with the record from this part of Europe the critical importance of the Central European record for understanding the emergence of modern Europeans and the role of Neandertals in that process.

Recently, the Central European fossil record has been conceptualized as having eastern and western components (Ahern *et al.* 2013). Kůlna, Šipka and other Moravian Neandertals fall in the eastern group, along with important Neandertal fossil remains from Slovakia (Šaľa, Gánovce), Croatia (Krapina, Vindija), Poland (Stajnia), Hungary (Suba-lyuk) and Romania (Ohaba-Ponor 1). Finds from Serbia (Mala Balanica) and Montenegro (Crvena Stijena) may represent Neandertals, but their attributions are not clear. The mandible from Mala Balanica seems too early to be considered a Neandertal *sensu stricto* (Rink *et al.* 2013), and its morphology is rather primitive compared to later Central European and other Neandertals (Roksandic *et al.* 2011, Ahern *et al.* 2013). An earlier review (Smith 1982, 1984) designated the fossil remains from Vindija, Šaľa, Šipka and Kůlna as late Neandertals, reflecting variable degrees of "transitional morphology" between earlier Neandertals and early modern humans in East Central Europe. New dating and new morphological studies necessitate a reassessment of this designation and the interpretations arising from earlier analyses.

NEANDERTAL FOSSIL SITES FROM EAST CENTRAL EUROPE

The earliest well-dated Neandertal sample from East Central Europe (ECE) comes from the sandstone rock shelter on the edge of the town of Krapina in northern Croatia. ESR dates from stratigraphic levels 1 (lowest), 5–6, and 7–8 are indistinguishable from each other and cluster around 130 ±10 kya (Rink *et al.* 1995). This places the site and its entire human fossil sample in MIS 5e (last interglacial) and confirms Gorjanović-Kramberger's (1913) estimate that the site formed over a relatively short (approximately 8,000 year) period. The ESR dating shows that all human skeletal remains from the site derive from the last interglacial. This is significant because there have been claims that some of the remains from the upper stratigraphic unit 8 were not Neandertals. In 1958, Škerlj argued that the Krapina 1 (or A) skull, a subadult partial calvaria, was not a Neandertal. Although this claim was countered (Smith 1976), the interpretation that the stratigraphy of the site extended into MIS 3 (Malez 1978) supported the possibility that transitional Neandertal-early modern human samples might be present at Krapina. A detailed comparative analysis of the Krapina 1 calvaria demonstrates that its morphology falls in the range of other Neandertal subadults (Minugh-Purvis *et al.* 2000), and this is commensurate with the ESR dating of the site.

A recent assessment of newer studies on the Krapina human skeletal remains reinforces the conclusion that the total morphological pattern of these remains identifies the entire sample as belonging to Neandertals (Ahern *et al.* 2013). This attribution is supported by the other ECE fossil human specimen from this time period, particularly the virtually complete, natural endocast from Gánovce (Slovakia), which is assigned to the end of the last interglacial on the basis of faunal and petrographic association (Vlček 1969). In addition to the endocast, natural moulds of a left fibula and partial radius were recovered (Jelínek 1969, Smith 1982). The endocast has a cranial capacity of 1320 cm^3 (Holloway *et al.* 2004), just slightly below the European Neandertal mean of 1350 cm^3 calculated by Cartmill and Smith (2009: 362). Gánovce exhibits a shape pattern comparable to Neandertal crania and has clear evidence of an occipital bun (Vlček 1969). The presence of this quintiessential European Neandertal structure also is evident in the subadult Krapina 2 (B skull) (Smith 1976) and the reconstruction of the Krapina 5 cranial vault (Caspari, Radovčić 2006). The documentation of bunning in these MIS 5e specimens is yet another feature that underscores their Neandertal total morphological pattern (Gorjanović-Kramberger 1906, Smith 1976, Ahern *et al.* 2013) and reinforces their similarity to Neandertal remains from Europe during the last glacial period (Smith 1982, 1984, Cartmill, Smith 2009).

The Neandertal remains from Suba-lyuk, Ochoz, and Ohaba-Ponor are generally considered to derive from MIS 4, but the dating for all is far from certain. The best dated specimen in this time range in ECE is the relatively recently described Stajnia molar from Poland. It is radiocarbon dated to >49 kya and could be much older (Urbanowski *et al.* 2010). All of these specimens are rather fragmentary (a mandibular alveolar process and teeth for Ochoz, a few adult bones and a child's partial cranium and teeth from Suba-lyuk, and a pedal phalange from Ohaba-Ponor) and not particularly informative anatomically. Pap and colleagues (1996) emphasize the mosaic nature and variability of the Suba-lyuk remains, but all of these specimens align clearly with Neandertals (Smith 1984, Ahern *et al.* 2013).

The human remains from Šaľa (Slovakia) were long considered representatives of late Neandertals, with indications of evolutionary change toward early modern people (Jelínek 1969, Vlček 1969, Smith 1982). This was primarily based on the morphology of the Šal'a 1 frontal's supraorbital torus, which showed a degree of overall reduction and midorbital thinning commensurate with the late Neandertals from Vindija (Smith, Ranyard 1980). However, a reanalysis of the Šal'a biostratigraphy indicated a relative age for the specimen of MIS 5e, making it of comparable age to earlier Neandertals sites in ECE like Krapina and Gánovce (Sládek *et al*. 2002). Reanalysis of the Šal'a frontal (Sládek *et al*. 2002) revealed stronger similarities to earlier Neandertals than had previously been noted.

Three sites remain that may constitute relatively late Neandertals in ECE. These are the Šipka juvenile mandibular symphysis (Czech Republic), the Kůlna adult maxilla and cranial fragment (Czech Republic), and the Vindija G complex sample (Croatia). The Šipka mandible, recovered in 1880, is one of the earliest Neandertals to be recognized (Maška 1882) and played an important role in early arguments about the nature of Neandertals. Virchow (1882) used Šipka as an example, along with the original Neandertal remains from Germany, of a pathological modern human specimen incorrectly attributed to a primitive human form. However, by the early 20th century, Šipka was accepted as representative of Neandertals (e.g. Boule 1921, Hrdlička 1930). The mandible was from an eight-to-ten year old juvenile and recovered from a stratum (level 9) at the Šipla cave associated with fauna and artifacts suggesting an interstadial period (Pod hradem) during the last glacial advance (see discussion in Vlček 1969). Valoch (1965, 1968) supported this attribution on stratigraphic grounds as well as on the basis of the mandible's association with a typical Mousterian industry containing some 14% of Upper Paleolithic tools.

The Kůlna remains derive from a long stratigraphic sequence providing one of the best records of the late Pleistocene in Europe (Valoch *et al*. 1969, Valoch 1988). In 1965, a right adult maxilla was recovered in level 7a at the site, and subsequently a right parietal fragment and three deciduous molars were also found in the same level (Valoch 1988). Level 7a contained a Middle Paleolithic lithic industry characterized by Valoch (1967) as Micoquian, which also contained 6% of Upper Paleolithic tool types. Level 7a was dated by ESR to 50±5 kya and by uncalibrated radiocarbon to ~45 kya (Rink *et al*. 1996).

The site of Vindija is located in the Hrvatsko Zagorje region of northern Croatia. Like Kůlna, the site represents a long stratigraphic section, spanning much of the late Pleistocene. Unfortunately, Vindija was not excavated with the precision that Kůlna was, and this has led to considerable debate on the contextual integrity of some of the strata at the site. Most significant for this discussion is the G complex from the site, which comprises five strata designated G_5 (lowest) to G_1 (highest). During excavations extending from 1974 through 1986, the G complex yielded some 100 framentary skeletal remains of Neandertals, along with extensive fauna and Paleolithic artifacts (Malez *et al*. 1980). Level G_3 yielded the majority of these fossils and dates to between ~38 and 45.6 kya according to a variety of chronometric and biostatigraphic indicators (see review in Janković *et al*. 2011, Ahern *et al*. 2013). Direct AMS radiocarbon dating of two human specimens yielded dates of >42 kya (Krings *et al*. 2000) and 38.31 kya (Serre *et al*. 2004) from G_3. Faunal evidence is commensurate with this age estimation (Janković *et al*. 2011), and lithic artifacts from G_3 are late Mousterian (Karavanić, Smith 1998, 2011). Level G_1 is a distinct reddish-brown clay that caps the G complex. This level is relatively thin and in some portions of the cave lies directly above level G_3. In other areas a sedimentologically distinct stratum (level G_2) separates G_1 and G_3. Some eight diagnostic human remains are found in level G_1, including a frontal bone (supraorbital torus), mandibular, and zygomatic specimens that exhibit distinctly Neandertal features (Wolpoff *et al*. 1981, Smith, Ahern 1994, Cartmill, Smith 2009). G_1 dates to 32.4 kya on the basis of direct AMS radiocarbon dates (uncalibrated) for two human specimens, with error ranges of ± 800 on Vi 208 and ± 1800 on Vi 207 (Higham *et al*. 2006).

Higham and colleagues (2014) have recently published a series of improved accelerator radiocarbon dates documenting the end of the Mousterian and the Neandertals in Europe. This dating argues for the disappearance of the Mousterian, Châtelperronian, and the Neandertals between 39.26 and 41.03 cal kya. As the Vindija G_1 dates are unclaibrated, they fall well below this range. However, calibrating these dates results in values of 37,733 ± 2,224 (Vi 207) and 36,903 ± 1,145 (Vi 208), which fall just slightly more recent than the reported range. The fact that the dates may actually be "slightly older" (Higham *et al*. 2006: 555) could push them into this range. Certainly, there is no reason to doubt that the Vindija specimens represent very late Neandertals in Europe.

The controversy surrounding G_1 stems from the association of these remains with an assemblage containing both Mousterian and early Upper Paleolithic artifacts. This industry has been attributed to artifical mixture of specimens from different levels (see Zilhão 2009 and references therein). While there is certainly some of this occurring, it is not clear that G_1 represents a primarily artifically admixed sample (Karavanić, Smith 1998, 2011, Ahern *et al*. 2013). The contextual association of Paleolithic artefacts with the Neandertal fossils is not the focus of our discussions here, and whether or not some Upper Paleolithic items were introduced artifically does not impact the anatomical assessment of the fossil human remains nor the direct dates derived from the fossil human material. Interestingly, the new dating discussed above not only pushes the terminus of Neandertals back in time, it also provides for a 2.60 to 5.40 ky overlap between the earliest modern Europeans and the late Neandertals (Higham *et al*. 2014). This temporal overlap is certainly sufficient for extensive gene flow between late Neandertal and early modern European populations. Higham *et al*. (2014: 309) note that this "*...potentially overlapping time may have acted as a stimulus for puntative Neandertal innovative and symbolic behavior in the millennia before theit disappearance*."

THE VINDIJA NEANDERTALS AND THE NATURE OF LATE PLEISTOCENE HUMAN EVOLUTION

Among the three late Neandertal ECE sites (Šipka, Kůlna, and Vindija), by far the largest fossil hominin sample comes from Vindija. The Vindija specimens have been described and discussed extensively (for recent reviews see Smith *et al*. 2005, Janković *et al*. 2006, 2011, Cartmill, Smith 2009, Ahern *et al*. 2013). Primary descriptions of the fossils (Smith, Ranyard 1980, Wolpoff *et al*. 1981, Smith *et al*. 1985, Smith, Ahern 1994) detail the anatomy and diagnostic freatures of the specimens. Here we revisit the anatomy of key facial and anterior vault anatomy that is crucial to the interpretation of the Vindija hominins' place in later Pleistocene evolution and their role in understanding the relationship between late Neandertals and early modern humans in ECE and in general. In our opinion, that role has changed to some degree over the past quarter century. However, the basic anatomical observations detailed in the references cited above are still valid. It is the framework in which the anatomy is interpreted that has changed.

In 1981, Wolpoff and colleagues noted several features of the Vindija sample that made it an excellent example of intermediacy between other Neandertals and early modern Europeans. These included aspects of facial reduction as seen in the maxillae and mandibulae, reduced facial progrnathism, a tendency toward anterior dental reduction, and possibly higher anterior cranial vaults. In the context of knowledge about the nature and timing of modern human origins in 1981, it was concluded that Vindija occupied a critical role in demonstrating "... that the Upper Pleistocene hominids of south central Europe represent an *in situ* evolutionary series, unbroken by the influx of fully developed modern types. " We see the origin of modern Europeans, at least as documented in south central Europe, as a product of the evolutionary transition from Neandertals giving renewed support to Hrlička's concept of the Neanderthal phase of man' as it was originally applied in Europe" (Wolpoff *et al*. 1981: 543). As is discussed in detail elsewhere (e.g. Smith 2002, Smith *et al*. 2005, Cartmill, Smith 2009), such an argument was defendable at that time as there was no compelling evidence that modern humans had emerged any earlier elsewhere.

In the latter half of the 1980s, things began to change. Results of the application of dating techiques such as thermoluminescence and electron spin resonance became available that showed modern humans were indeed older in the Near East than in Europe and that Neandertals existed at rather late dates, after modern people emerged. This roughly coincided with the first world-wide study of human mitochondrial DNA variational patterns which, among other things, argued for an African origin of all modern humans (Cann *et al*. 1987). The next year Stinger and Andrews (1988) articulated what is widely known as the recent African origin model of modern human origins, promoting a monocentric, African biological origin for modern humans, and presenting what is essentially a model of total replacement of archaic humans (like Neandertals) throughout Eurasia by expanding populations of a new, modern human species. From the late 1980s through to the end of the first decade of the current century, the majority of evidence supported the recent African origin model, including studies of fossil human remains, genetics and archaeology (see discussions in Klein 2009, Cartmill, Smith 2009). By the late 1980s, the implications of this new evidence required a reassessment of the argument for regional continuity in parts of Eurasia, including Central Europe. Based on the general observation that evidence of archaic-to-modern continuity in various regions of Eurasia was reflected more in anatomical details rather than overall anatomical form, Smith and colleagues (1989) posited the assimilation model of modern human origins. This model recognized Africa as the likely source for the origin of modern people but also supported the idea of relatively small contributions of archaic Eurasians to the gene pools of incoming modern groups. The model became somewhat lost in the "battles" between the multiregional evolution and recent African origin models, but it did receive some attention (e.g. Aiello 1993). Initially, the role of the Vindija sample in the assimilation model did not differ significantly from the interpretation given in 1981, but it was noted that, as a part of the "transition" from archaic to modern humans, "...assimilation of new elements into existing gene pools..." would be expected (Smith *et al*. 1989: 62).

In 2010, Green and colleagues published the first Neandertal draft genome, which comprised some four billion base pairs derived from three small, non-diagnostic long bone fragments from the Vindija G complex. This genome showed that Neandertals shared a significant number of single neucleotide polymorphisms with Eurasia populations that were not present in African populations, and this result was interpreted as indicating a Neandertal contribution of 2–4% to Eurasian modern human gene pools (Green *et al*. 2010). Interestingly, there were strong indications of this result when an initial million base pair sequence of the Neandertal genome was published in 2006 (Green *et al*. 2006). Following closely on the heels of publication of the Neandertal draft genome, Reich and colleagues (2010) published a draft genome based on organic material from a single manual phalanyx of another non-modern human from the Denesova cave in the Altai mountains of Siberia. The Denisovan genome is relatively closely related to Neandertals but also revealed low level contributions to modern Melanesians as well. Subsequently, genetic evidence of small amounts of Neandertal influence on modern North Africans have also been demonstrated (Sánchez-Quinto *et al*. 2012). The original draft Neandertal genome from Vindija has now been supplemented by another high-coverage Neandertal genome from Denisova and a low-coverage sequence from Mezmaiskaya in the Caucasus region of Russia (Prüfer *et al*. 2014). All three genomes support low-level Neandertal genetic contributions to modern people, although the average percentage has been revised to between 1.6% and 2.1% (Prüfer *et al*. 2014). As one of us has argued elsewhere (Smith 2013), if ca. 2% of Neandertal genes are still present in living humans, might this not mean that the contribution to the earliest modern west Eurasians was even higher? After all, we know that there has been considerable genetic change within European populations over the last 10,000 years (Balter 2013, Brandt *et al*. 2013), and thus we might expect early modern humans to have a higher percent of Neandertals contribution.

In late 2014, two early modern human genomes were published. A modern left femur shaft from the site of Ust'-Ishim (western Siberia), directly dated to between 43.21 and 46.88 cal kya, yielded the first (Fu *et al*. 2014); and a left tibia from the modern Kostenki 14 skeleton (European Russia), directly dated between 36.20 and 38.70 cal kya, provided the second (Seguin-Orlando *et al*. 2014). Both genomes reveal percentages of Neandertal DNA that fall in the ranges originally published for recent Eurasians (Green *et al*. 2010) but slightly above the 1.6-2.1% contribution range published in 2014 by Prüfer and colleagues. The Ust'-Ishim femur reflects 2.3 ± 0.3% admixture with Neandertals, and Kostenki 14 yielded a very similar 2.4 ± 0.4% admixture with Neandertals. Both samples, however, preserved Neandertal DNA in longer segments indicating a relatively short time since Neandertal biological contribution to early modern human gene pools (Fu *et al*. 2014, Seguin-Orlando *et al*. 2014). That these percentages of Neandertal contribution in relatively early moderns are only marginally higher than the percentages in recent humans is surprising and suggests that these Neandertal genetic contributions must have been under very strong positive selection.

Including the results on these early modern humans, the current genetic evidence supports assimilation's claim, originally based on anatomical evidence, that archaic human contributions to early modern human gene pools were relatively common but also relatively small. These contributions were not, however, insignificant as they included aspects of the modern human immune system (Abi-Rachel 2011), skin and hair pigmentation (Vernot, Akey 2014) and perhaps susceptibility to certain diseases (Sankararaman *et al*. 2014). Sankararaman and colleagues found that Neandertal DNA in modern humans tends to be found most commonly in regions of the genome with the most variability, making them a prime target for natural selection.

One thing that has not been demonstrated by the Neandertal genomes is any clear evidence of early modern human contribution to late Neandertal populations. This has led to speculations about the nature of Neandertal-early modern interbreeding that would explain this seeming discrepancy. It is highly unlikely that gene flow would have occurred in only one direction, so where, besides the genes, might there be evidence for early modern human influence on late Neandertal populations? From our perspective, it is necessary to turn again to the morphology to find evidence of this interbreeding in late Neandertals. Of course, just as was the case with morphological evidence indicating interbreeding in general, some will not be convinced until the genetic evidence for this is isolated. Still there are morphological indications of interbreeding, and these indications are to be found in Vindija and other late ECE Neandertals.

VINDIJA NEANDERTAL MORPHOLOGY REVISITED

Although gene flow into the Vindija late Neandertals was suggested as a possible explanation as early as 1989, the publication of the initial Neandertal genome led to specific suggestions that the Vindija morphological pattern was likely the result of early modern human biological impacts on this late Neandertal sample (Janković *et al*. 2011, Karavanić, Smith 2011, Ahern *et al*. 2013). This interpretation is based on the original descriptions and discussion of the Vindija specimens' anatomy (Smith, Ranyard 1980, Wolpoff *et al*. 1981, Smith *et al*. 1985, Smith, Ahern 1994, Ahern *et al*. 2004). Thus it would seem advisable to quickly revisit the anatomy of the pertinent elements in the Vindija sample: the maxillae, mandibles, and frontal bones. The descriptions discussed in the following section are all derived from the original discriptive publication on the Vindija human remains unless otherwise indicated.

Vindija Maxillae. Two half maxillae (including the median palatine suture and one side of the nasal aperture) are preserved in the sample, both deriving from level G_3 (*Figure 1*). In the original descriptions, Vindija (Vi) 259 is shown to be an adult with the M^3 sockets clearly present, while the larger Vi 225 preserves only the mesial part of the M^2 socket. Still Vi 225's size relative to Vi 259 and its adult-sized post-canine to prosthion length strongly indicate that Vi 225 is also from an adult. Overall, both specimens are relatively small compared to other Neandertals, particularly in terms of alveolar height and nasal breadth. In revisiting the morphometrics of these specimens, these measurements were taken again on the original fossils. The nasal breadths (determined by doubling the measurement from the lateral-most extent of the nasal rim to the midline) resulting from the re-measurement of these specimens (*Table 1*) were essentially identical to the original measurements. The same was not true of the alveolar height measurements, and the values given in *Table 1* are slightly larger than the original values (Wolpoff *et al*. 1981) and were reconstructed using the more complete Krapina maxillae as reference models. As was reported in 1981, the presence of a canine fossa cannot be established on either specimen due to incompleteness.

FIGURE 1. The Vindija 259 maxilla in facial view. Note the presence of the midsaggital plane and the lateral rim of the pyriform aperture.

TABLE 1. Comparative Measurements on Neandertal and Modern Human Maxillae (in mm). All individuals measured by FHS. Altendorf is a robust German Neolithic sample housed at the University of Tübingen.

Specimen/Sample	Nasal Breadth	Alveolar Height
Vindija 225	28.5	19.6
Vindija 259	26.2	21.2
Kůlna 1	30.0	30.4
European Neandertal Mean (n, σ)	33.3 (8, 1.5)	26.1 (10, 3.0)
Upper Paleolithic Europe Mean (n, σ)	24.5 (10, 1.4)	18.7 (8, 2.6)
Altendorf Mean (n, σ)	23.0 (20, 1.5)	17.1 (20, 1.7)

The Vindija nasal breadths and alveolar heights were compared to the Neandertal and Upper Paleolithic Europe data using z-scores (*Table 2*). Results reveal a somewhat mixed pattern but show that in three of the four comparisons, the Vindija specimens fall closer to the Upper Paleolithic Europe sample than to other Neandertals. The Altendorf data are given in *Table 1* to demonstrate that these values continue to reduce over time within modern samples in Europe, but there was no reason to compare them using z-scores.

Vindija Mandibles. A total of seven mandibles are included in the Vindija G complex sample. Five were

TABLE 2. Z-scores for Maxillary Measurements. Symbol Key: Vi (Vindija), N (Neandertal), UPE (European Upper Paleolithic), K 1 (Kůlna 1).

Comparison	Nasal Breadth	Alveolar Height
Vi225 – N	-2.04	-2.16
Vi225 – UPE	2.85	0.35
Vi259 – N	-2.96	-1.63
Vi259 – UPE	1.21	0.96
K1 – N	-2.20	1.43
K1 – UPE	3.93	4.50

described in 1981, the sixth four years later (Smith *et al*. 1985), and the seventh by Ahern and colleagues in 2004. All are clearly adult as indicated in the descriptions, except possibly for Vi 306 and Vi 11.52. Vi 306 preserves only the symphyseal area and lacks teeth, but the overall form and size of the sockets indicate that all permanent incisors and canines were erupted (Smith *et al*. 1985), suggesting adult status. Vindija 11.52 cannot be definitively considered adult (Ahern *et al*. 2004), but this specimen is not included in the comparisons reported here.

The Vindija mandibles are comparable in size to the Krapina mandibles (Wolpoff *et al*. 1981: 508) and exhibit characteristically Neandertal features (Smith 1982, 1984). One of the two major mandibular features suggesting "transitional" morphology concerns the symphyseal angle, which can be measured in three of the Vindija specimens. These are Vi 206 (which preserves the symphysis, right corpus [with the permanent canine and all three molars] and anterior ramus), Vi 226 (preserving the symphysis, left corpus [with only M1] and a complete ramus), and Vi 231 (preserving the symphysis, left corpus [with the P3 and all three molars] and the anterior ramus). As measured from the alveolar plane (see Cartmill, Smith 2009: 486), the Vindija symphyses are more acute (*Table 3*), suggesting more vertical symphyses than is common for other Neandertals (*Figure 2*). Again using z-scores to standardize comparisons supports this interpretation. Two of the three Vindija specimens fall closer to the Upper Paleolithic European sample than to other Neandertals (*Table 4*). The third mandible (Vi 231) falls almost exactly in between the Neandertal and EUP means.

The more vertical symphyses are consistent with the indications of reduced facial size in the Vindija Neandertals compared to other Neandertals. As described by Enlow and Hans (1996), facial growth involves growth that both elongates the face and results in greater projection (prognathism). For Neandertals, this would mean that if facial size were reduced, one would expect facial prognathism to be reduced as well (see discussion in Cartmill, Smith 2009). This would result in a more vertical symphysis, as seen in the Vindija sample.

FIGURE 2. The Vindija 231 mandible oriented to the alveolar plane. The relatively vertical mandibular symphysis is evident in this view.

TABLE 3. Comparative Symphyseal Angle Measurements on Neandertals and Early Modern Humans.

Specimen/Sample	Symphyseal Angle
Vindija 206	87°
Vindija 226	85°
Vindija 231	89°
European Neandertal Mean (n, σ)	98.7° (16,5.7)
Upper Paleolithic Europe Mean (n, σ)	78.2° (10,6.7)

TABLE 4. Z-scores for Symphyseal Angles. Symbol Key: Vi (Vindija), N (Neandertal), UPE (European Upper Paleolithic).

Comparison	Z-score
Vi 206 – N	-2.01
Vi 206 – UPE	1.31
Vi226 – N	-2.40
Vi226 – UPE	1.02
Vi 231 – N	-1.70
Vi231 – UPE	1.61

The second feature of interest in the mandible involves the morphology of the anterior symphyseal face. In Vi 206 (*Figure 3*) and Vi 231, for example, a weak but distinct *mentum osseum* is evident at the symphyseal base, as is an incipient *incurvatio mandibulae*, as defined by Weidenreich (1936). This is a concavity below the alveolar processes of the mandibular incisors that terminates in the mentum osseum. The development of this feature in both specimens can be described as incipient, but it is clearly visible on both. The Vi 306 symphysis exhibits both of these features as well, but they are less well-defined than on Vi 206 and Vi 231.

Vindija Frontal Bones and Supraorbital Tori. There are several frontal bone fragments in the Vindija sample. For two of these, Vi 261 (including Vi 277/278) and Vi 284 (including Vi 230, 255, 256), there are distinct indications of a relatively steeper frontal squama than in most other Neandertals (Malez *et al*. 1980, Smith, Ranyard 1980, Wolpoff *et al*. 1981, Ahern *et al*. 2004). Unfortunately, this feature is very difficult to quantify, but it is consistent with indications that changes in facial morphology affect vault form (Bastir *et al*. 2007, 2010, Bastir, Rosas 2013). Fortunately, patterns in the adult supraorbital tori are more easily observable and quantifiable.

FIGURE 3. The Vindija 206 mandible (lingual view). Note the incipient *incurvatio mandibulae* and *mentum osseum* of the symphysis.

The Vindija supraorbital sample comprises a total of ten specimens. One, Vi 227, is unquestionably from an infant; and two others, Vi 224 and Vi 279, do not exhibit the histological features that identify fully adult status for Neandertal supraorbital tori (Smith, Ranyard 1980, Wolpoff *et al*. 1981). These specimens were thus excluded from the analysis given here, because including subadult toral measurements could make the sample appear more "gracile" than it actually is. Two other specimens, Vi 305 (Smith *et al*. 1985) and Vi 308 (Smith, Ahern 1994) are adult but do not preserve the portions of the torus needed for the analysis performed here. This leaves a total of five adult tori (Vi 202, 260, 261, 262, and 284) that preserve enough of the torus to take thickness measurements (anterior- posterior chords) at the midorbit and lateral regions as detailed by Smith and Ranyard (1980). It has previously been demonstrated that the overall torus dimensions at Vindija exhibit size reduction compared to the earlier Krapina sample (see *Table 5*) but that the differences did not attain statistical significance (Smith, Ranyard 1980). Also it bears repeating that the Vindija sample has been claimed to be dominated by subadults and females (e.g. Stringer, Bräuer 1994). However, only demonstrably adult tori were used in our analysis (see above), and a study by Ahern and colleagues (2002) demonstrated that sex and other biases had low probabilities of impact on the Vindija torus sample.

For our analysis here, we calculated the browridge thickness index (BTI) for the Vindija tori and the tori/browridges of the comparative samples. The BTI is calculated by dividing the midorbital thickness measurement by the lateral thickness measurement for a torus/browridge and multiplying this by 100. The resulting values are given in *Table 5* and show that the Vindija tori exhibit a higher degree of mid-orbital thinning than do the Krapina or other European Neandertal samples. The form of the supraorbital region is still clearly a torus in the Vindija specimens, in that there is not a distinct separation between a superciliary arch and supraorbital trigone as is typical for modern humans (including Upper Paleolithic European specimens) (see discussion in Smith, Ranyard 1980, Cartmill, Smith 2009). Still, the Vindija sample consistently does approach the modern human pattern more than other Neandertals, through the process of midorbital thinning.

To emphasize the intermediate, or at least partly intermediate, status of the Vindija tori, z-scores were calculated for the BTI of each of the adult Vindija tori listed in *Table 5*. These z-scores (see *Table 6*) basically reinforce the morphological and metric observations that the Vindija tori are fundamentally more like other Neandertals as compared to modern, even early modern, specimens. All of the Vindija values fall closer to the Neandertal means but, except for Vi 262, always below the mean. However, the consistent pattern for the adult Vindija torus sample is of a closer relationship to the

TABLE 5. Comparative Data on Neandertal Supraorbital Tori and Early Modern Human Brow Ridges.

Specimen/Sample	Lateral Thickness	Midorbital Thickness	Browridge Thickness Index
Vindija 202	11.3	9.5	84.1
Vindija 260	11.0	8.5	77.2
Vindija 261	10.5	8.3	79.0
Vindija 262	10.0	8.6	86.0
Vindija 284	10.6	8.6	81.1
Vindija Mean (n, σ)	10.7 (5,0.5)	8.7 (5,0.6)	81.5 (5,4)
Krapina Mean (n, σ)	12.5 (11,1.6)	10.7 (13,1.8)	85 (11,8)
European Neandertal Mean (n, σ)	12.5 (9,1.5)	11.1 (9,0.7)	86 (9,8)
Upper Paleolithic Europe (n, σ)	8.1 (11,1.4)	5.4 (11,1.7)	71 (11,5)

early modern morph than that demonstrated by other Neandertals. Again, that similarity is not likely to be the result of any sample bias in the Vindija supraorbitals. It is interesting to note that supraorbital tori do hold on as aspects of the morphology of the earliest modern humans in Africa and the Near East (Cartmill, Smith 2009), so it is not surprising that this aspect of the Vindija morphology retains more similarity to other Neandertals than do other aspects of the anterior skull.

TABLE 6. Z-scores for Browridge Thickness Index Comparisons. Symbol Key: V (Vindija), N (Neandertal), UPE (European Upper Paleolithic). The Neandertal sample here does not include Krapina.

Comparison	Z-score
V202 – N	-0.24
V202 – UPE	2.62
V 260 – N	-1.10
V260 – UPE	1.24
V 261 – N	-0.75
V 261- UPE	1.60
V 262 – N	0.00
V262 – UPE	3.00
V 284 – N	-0.98
V 284 – UPE	2.02

Vindija Postcrania. Postcranial elements possessing diagnostic anatomy are relatively rare at Vindija. Several were described by Wolpoff and colleagues (1981) and more recently recognized pieces are discussed by Ahern and colleagues (2004). There are also several undiagnostic long bone fragments, such as the three from which the first Neandertal draft genome was extracted (Green *et al.* 2010). Even the specimens with diagnostic anatomy are difficult to conclusively attribute to Neandertals, although there is nothing anatomical that indicates any specimen is definitely not from a Neandertal. Two specimens that exhibit characteristically Neandertal features are the Vi 209 scapular fragment and the Vi 13.8 radial shaft. The latter specimen exhibits an orientation of the radial tuberosity that is found far more commonly in Neandertals than in modern samples (Ahern *et al.* 2004). The Vi 209 scapula preserves a complete glenoid fossa and enough of the axillary boarder to show that the axillary sulcus runs on the dorsal side of the axillary crest (Wolpoff *et al.* 1981), constituting what Stewart (1962) designated the "Neandertal type."

Wolpoff and colleagues (1981) also noted that the glenoid fossa of the Vi 209 scapula was relatively narrow for a Neandertal, falling in the low range of modern human breadth/height indices and more than a standard deviation above the mean for eight Krapina and other Neandertal scapulae. More recently, DiVincenzo and colleagues (2012) have provided a more detailed comparative analysis of the Vi 209 glenoid fossa in comparison to those from other late Pleistocene humans in western Eurasia. Their data essentially confirm the relationships suggested in 1981. These authors interpret their results as follows:

> The Vindija SGF (scapular glenoid fossa) and those of the later Near Eastern Neanderthals (Kebara and Shanidar) approach the modern condition and are somewhat segregated from both northwestern European (Neandertal and La Ferrassie) and early Mediterranean Neanderthals (Krapina and Tabun). Although more than one scenario may account for the pattern seen in the Neanderthals, the data is consistent with palaeogenetic evidence suggesting low levels of gene flow between Neanderthals and modern humans in the Near East after ca. 120–100 ka (thousands of years ago) (with subsequent introgression of modern human alleles into eastern and central Europe; DiVincenzo *et al.* 2012: 274).

In addition to Vi 209, body size estimates can be made on two additional Vindija specimens that preserve articular surfaces, the proximal row manual phalange Vi

300 and the fifth metacarpal Vi 203. In 1995, Trinkaus and Smith compared the estimates for these three specimens with those for other Neandertals. While noting the limitations of the comparisons due to the fragmentation of the Vindija postcrania, Trinkaus and Smith demonstrated that the Vindija dimensions fell only slightly below the means for other Neandertals and concluded that it was "…more reasonable to consider their facial anatomy, both the dimensions of their supraorbital tori, maxillae, and mandibular corpora and (especially) the morphologies of those regions, as indicating evolutionary change relative to earlier Neandertals" (Trinkaus, Smith 1995: 206) as opposed to this resulting from smaller body size. The key now is to identify what the nature of that evolutionary change was.

EXPLANATION OF THE VINDIJA LATE NEANDERTAL MORPHOLOGICAL PATTERN

As the analyses cited above demonstrate, the arguments that the consistent pattern of craniofacial form documented for the Vindija Neandertals in the previous section can be explained by sample bias relating to developmental age of the specimens, sex ratio in the sample, or small body size are not substantiated. Furthermore, the probability that these changes represent indigenous evolution in late Pleistocene Europe, without influences via gene flow from modern populations, seems equally unlikely in the light of current knowledge of the pattern of modern human origins in, and its spread from, Africa. So how is it possible to explain the Vindija morphological pattern with these constraints in mind? One possibility is that these changes are simply a parallelism, not reflecting any biological connection to the emergence of modern European morphology. Disproving the possibility of parallelism in paleoanthropological samples is extremely difficult at best, but the question is how robust an expanation this would be in this case. In other words, how likely is it that craniofacial and some postcranial changes would occur independently in this region of ECE and mimic the changes reflecting modern human biology? When it was claimed, incorrectly, that multiregional evolution was arguing for the independent emergence of modern humans in different regions of the Old World, this was argued to be highly unlikely (Howells 1993). That same argument of unlikelihood, in our opinion, applies to the Vindija case. It is much more parsimonious to consider this pattern as reflecting some real, biologically significant factor impacting on the Vindija late Neandertals than to evoke the vague spectre of parallelism.

When the Vindija-based Neandertal gemone was presented, one notable aspect was the lack of genetic evidence for gene flow from early modern gene pools into Neandertals (Green *et al*. 2010), and none has been identified in the subsequent two Neandertal genomes (Prüfer *et al*. 2014). Given the nature of human interbreeding as repeatedly demonstrated in more recent contexts, unidirectional gene flow seems highly unlikely. We argue that one compelling area of evidence for early modern human impacts on late Neandertal biology in ECE is provided by the Vindija morphological pattern just summarized in the previous section (see also Ahern *et al*. 2013, Smith 2013). Given the geographic position of ECE and the Vindija site, this interpretation is much more plausible than parallelism, and reflects again the need for both morphologically-based and genetically-based perspectives on the pattern of human evolution.

THE ROLE OF MORAVIAN LATE NEANDERTALS IN ECE MODERN HUMAN ORIGINS

The Šipka Neandertal mandible unfortunately was destroyed in the fire at Mikulov Castle on the Czech-Austrian border at the end of World War II (Vlček 1969), so only casts remain (*Figure 4*). Based on analysis of casts, the anatomy of the Šipka specimen has been studied by Jelínek (1965, 1969), Vlček (1958, 1969) and Smith (1982, 1984). All of these analyses acknowledge the problems inherent in examining the features of this specimen. Apart from the absence of the actual fossil, the most significant limiting factors are the fact that the specimen only preserves the mandibular symphysis, that the anterior face of the symphysis is missing except for toward the base, and its juvenile status. Still, there is much that can be documented on the specimen. Šipka's permanent incisors are small. Its I_1 and I_2 dimensions fall 1.4 and 2.6 standard deviations, repectively, below the Krapina means and are smaller than any other ECE Neandertals (Smith 1982: Table 2). Furthermore, although the symphysis was apparently somewhat receding, there does appear to be an *incurvatio mandibulae*, defining a weak mental eminence. In the latter two features, Šipka appears to be quite similar to the Vindija mandibles. Furthermore, Šipka appears to exhibit a weak outline of a mental trigone. This suggests that as the symphysis becomes more vertical the features of a fully modern chin structure begin to emerge.

The Kůlna parietal fragment appears to exhibit similar curvature to that seen in western European Neandertals (Jelínek 1981), but the maxilla, Kůlna 1 (*Figure 5*), reveals a more complex pattern. As described by Jelínek (1966), the Kůlna maxilla has a relatively narrow nasal opening (see *Table 1*) and evidence of a canine fossa (see also Vlček 1969, Smith 1982). Z-scores reflect the relatively narrow nose but also show the alveolar height to be 1.36 standard deviations above the Neandertal mean, and over four standard deviations above the Upper Paleolithic European mean (see *Table 2*).Thus this specimen, which is likely a few thousand years older than Vindija and perhaps Šipka as well, may reflect the very beginning of the trend toward facial reduction in ECE late Neandertals.

FIGURE 4. The Šipka subaduct mandibular symphysis (cast).

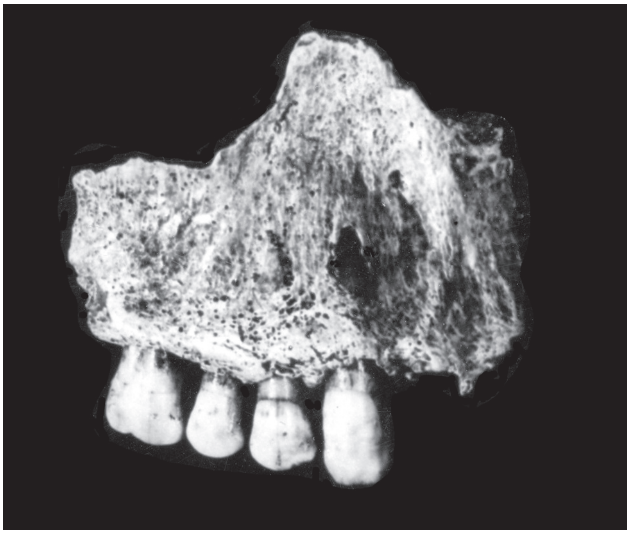

FIGURE 5. The Kůlna 1 maxilla.

THE TIMING OF EARLY MODERN HUMAN APPEARANCE IN EUROPE AND THE ECE LATE NEANDERTAL MORPHOLOGICAL PATTERN

If the morphological pattern documented for the Vindija, Šipka, and Kůlna ECE late Neandertal sample reflects the biological impact of early modern humans, one might expect evidence of modern people in Europe as early as 50 kya. Does such evidence exist? The answer is not completely clear. Evidence of early modern people in Euope could take one (or more) of three forms: genetic indicators, morphology, or behavioral indicators.

It has generally been accepted that the Aurignacian in Europe represents a behavioral indicator of early modern humans (see Klein 2009). Using calibrated radiocarbon dating, a case can be made that the beginnings of the Aurignacian in Europe is about 40 kya, or 41 kya for Proto-Aurignacian according to Zilhão (2013), or to perhaps 5-6 ky earlier according to Higham and colleagues (Higham 2011, Higham *et al*. 2012; see also Higham *et al*. 2014). If claims that modern humans produced the Châtelperronian are true (Bar-Yosef, Bordes 2010), then the date might go back a few thousand years more. However, there are good reasons not to accept the disconnect between Neandertals and the Châtelperronian (see discussion in Zilhâo 2013), so the Aurignacian is the best cultural proxy for the presence of modern people. It bears mention that, despite the fact that associating modern people with the earliest Aurignacian is suggested by the current evidence (Hublin 2013), the origin and authorship of the earliest Aurignacian is not clear (see Cartmill, Smith 2009). However, assuming the Aurignacian-modern human association is valid, an age somewhere between approximately 46 kya and 40 kya for early moderns would seem defensible, as is the overlap range between late Neandertals and early modern Europeans recently suggested by Higham and colleagues (2014).

In this context, a cultural complex with which Karel Valoch's name is closely associated might provide some additional information. The Bohunician is an Initial Upper Paleolithic industry found only at a limited number of open-air sites in the Czech Republic and is known only on the basis of stone tools (Valoch 2000). Bone does not preserve at these localities, and thus there is no preservation of associated fauna (except for some teeth) nor of the humans responsible for the lithics. Recent dating places the Bohunician between 40 kya and 48 kya, perhaps inclining more to the earlier date (Richter *et al*. 2009). Valoch excavated the critical Bohunician sites at Stránská skála and Brno-Bohunice (Valoch 1976, 2006). For him, the Bohunician represented a technological evolution from the indigenous Middle Paleolithic (Valoch *et al*. 2009). He saw clear similarities with the Boker Tachtit. industry in the Near East and held that both were "...likely to have been produced by people of the same type, most probably the Neanderthals" (Valoch 2000: 625). However, as Valoch clearly notes for the Bohunician, there are no fossil human remains associated with either industry. Bar-Yosef (2006) suggests these may be modern humans and that it was these Boker Tachtit, presumably modern, people who brought the Upper Paleolithic to Europe. In the same vein, Tostevin and Škrdla (2006) do not see close technological connections between the Bohunician and the indigenous Middle Paleolithic but rather connect it directly to Boker Tachtit. Clearly, establishing who made the Bohunician would be a valuable contribution to understanding the emergence of initial indications of Upper Paleolithic level behavior in ECE.

From the standpoint of biological indicators, there are now two modern human genomes from Russia indicating the presence of early modern people between 36 kya and 45kya (Fu *et al*. 2014, Seguin-Orlando *et al*. 2014). Unfortunately, the 45 kya date is from a western Siberian specimen, so that the earliest possible date on modern genetic material in Europe (European Russia) is 38.70 cal kya (Seguin-Orlando *et al*. 2014). However, fossil human remains that are clearly modern are found in ECE by approximately 39 kya based on calibration of radiocarbon dates associated with the Oase skeletal remains from Romania (see discussion in Ahern *et al*. 2013). Two other sites have recently been claimed to evince an even earlier presence of modern human morphology. In 2011, Higham and colleagues presented dating for the Kent's Cavern 4 (KC4) maxillary fragment placing in between 41.4 and 44.2 kya (calibrated). The maxillary fragment, discovered in 1927, is considered modern (Keith 1927, Higham *et al*. 2011), but its contextual relationship to the dates reported is questionable. White and Pettit (2012) detail the problems with the excavations at the site, which include rather imprecise methods of excavation and lack of precise stratigraphic control of the specimen's location in the deposits. Thus, while the dates may well be accurate, it is not clear whether they date KC4. Also in 2011, Benazzi and colleagues argued that two deciduous molars, dated to 43-45 kya (calibrated) from the Grotta del Cavallo (Italy), represent modern humans. These teeth are associated with the Ulluzian which, like the Châtelperronian, is an Initial Upper Paleolithic industry. Along with the Ust'-Ishim femur, the Cavallo teeth represent the currently available skeletal evidence for modern humans in Europe in excess of 40 kya.

The dating range for level G_3 at Vindija extends from 38 kya to perhaps greater than 42 kya, while the Kůlna level 7 dates are older – at ~50 kya. Although the dates for early moderns, even including Grotta del Cavallo or Ust'-Ishim, do not extend as far back as the oldest range of the ECE late Neandertal date range, there is enough overlap to indicate that modern human biology could have impacted on these late Neandertal groups. The fact that the Kůlna maxilla does not appear to exhibit the full suite of features indicated by the later Vindija sample suggests that the initial influences on ECE late Neandertals were not extensive, and it may well be that the initial numbers of early modern humans in ECE were very small and have simply evaded detection. The Vindija G complex sample, however, falls temporally in the span when modern people were quite likely to have been already entering ECE.

The morphological pattern of the late ECE Neandertals is commensurate with the low level of gene flow suggested to characterize Neandertal-early modern human interactions in western Eurasia by the assimilation model of modern human origins (Smith *et al*. 2005, Cartmill, Smith 2009, Smith 2013, Ahern *et al*. 2013). As detailed elsewhere (Smith 2013) the reasons for the relatively low Neandertal contribution to early modern humans are likely related to the rarity of Neandertals on the landscape: there are biological and cultural indicators suggesting that Neandertal population levels and density were quite low. The continuation of modern gene flow into Neandertal populations ultimately increased substanially, and eventually, of course, Neandertals were completely genetically and demographically swamped by modern people. By 35 kya (or perhaps slightly older), there are no morphologically definable Neandertals left in western Eurasia. The ECE late Neandertal sample represents, in our opinion, the initial stages of that process – a time when modern genes and people were just beginning to enter Europe, and the complex population dynamics that characterized their interaction over the next several millenia, ultimately resulting in the morphological disappearance of Neandertals, were just beginning.

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