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Review

Neandertals... 150 Years Later

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ABSTRACT

The place of Neandertals in modern human emergence has been a subject of debate since the first recognized Neandertal skeleton was discovered in 1856. This paper presents an overview of morphological, archaeological, and genetic evidence commonly used in discussions of Neandertals and their evolutionary significance. A brief historical sketch of the argument provides insight into the changing views on these interesting people. The major models proposed to explain modern human origins are also discussed.

Key words: *Neandertals, modern human origins, human evolution, Mousterian*

Introduction

Who were the Neandertals? What is their relationship to living human populations? How different are they from us? These are just some of the questions that have been asked by many since the 1856 recognition of the first Neandertal specimen. Today we know more about Neandertals than we do about any other human fossil group. What can we, after almost 150 years has passed since the discovery in the Neander valley, say about these interesting humans that once inhabited Europe and parts of Asia?

The Early Years

Ever since the discovery of Neandertal partial skeleton in the Kleine Feldhofer Grotte near Dusseldorf, Germany, in 1856, their place in human evolution has been hotly debated[1]. Following Hermann Schaaffhausen's initial description of the skeleton, one group of scientists argued that the Feldhofer remains represented a pathological but modern human. This was most strongly argued by one of the leading academic figures in Germany at the time, Rudolf Virchow. According to others, the remains were of an ancient type of human. A new taxonomic category, *Homo neanderthalensis*, was soon created by William King[2], but some scientists such as Schaaffhausen and T. H. Huxley saw Neandertals as a primitive race of *Homo sapiens*, rather than a distinct species. This was based on the original Neandertal's modern size brain that they felt precluded classification of the specimen as anything other than *Homo sapiens*. It is worth noting that the Feld-

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hofer remains were not the first fossils we today attribute to the Neandertals. They were predated by both a juvenile cranium from Engis (1829/30) in Belgium, as well as the adult Gibraltar cranium (1848). The significance of these finds, however, was not recognized until much later. Proof of the geological antiquity and the non-pathological status of Neandertals came from two important discoveries near the turn of the century. Two relatively complete skeletons from the Belgian cave site of Spy, discovered in 1886, as well as the discoveries at the Krapina rockshelter in Croatia (1899–1905), both in association with extinct fauna and Palaeolithic stone tools, proved the antiquity of the Neandertals. Dragutin Gorjanović-Kramberger, the discoverer of the Krapina fossils, used the fluorine dating technique in order to prove the contemporaneity of extinct fauna and Neandertal remains at Krapina[3]. Furthermore, these new fossil discoveries showed that pathology could not explain the morphology of the fossils. It became clear that Neandertals represent an ancient but normal population. Thus, by the beginning of the 20th century, the »Neandertal debate« turned entirely to the question of their role in human evolution. Numerous discoveries at the beginning of the 20th century allowed for a more detailed insight into the morphology and culture of these humans. Finds from Le Moustier, La Ferrassie, La Chapelle-aux-Saints, La Quina in France, and Monte Circeo in Italy provided the basis for enchanced scientific study. Unfortunately, Boule's reconstruction of the La Chapelle skeleton[4–6] (Figures 1 and 2), biased by both his misinterpretation of pathological changes on the skeleton and undoubtedly also by his rejection of the linear scheme for human evolution[7–9], influenced both popular and scientific views on Neandertals for a long time. Echoes of Boule's view of Neandertals as bestial, half-erected creatures can still be seen is some popular writings to this day.

Views on Neandertals in the first half of the 20th century can be placed into one of three main theories. Aleš Hrdlička's

Fig. 1. Neandertal skull from La Chapelle-aux-Saints.

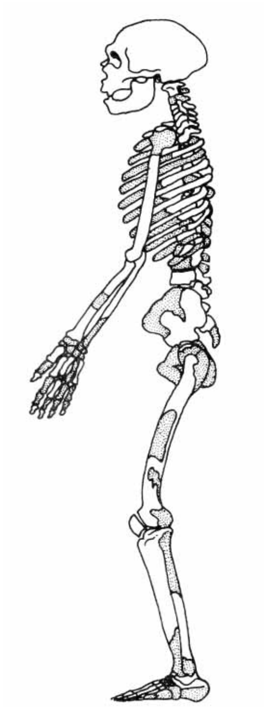

Fig. 2. Reconstruction of the La Chapelle-aux-Saints skeleton (after Boulle and Vallois, 1957).

Neandertal phase model posits that Neandertals represent an ancestral stage in the morphological shaping of modern peoples[10,11]. In contrast, the Pre-sapiens hypothesis, influenced strongly by Boule, gives them no role in modern human ancestry, but views them as an extinct side-branch[4–6,12,13]. F. Clark Howell is usually credited with popularizing the third view, according to which some Neandertal groups (earlier specimens such as Saccopastore, Steinheim, Ehringsdorf, Krapina etc) are ancestral to both later »classic« Neandertals, as well as to modern humans, while the »classic« Neandertals are too specialized in their adaptation and go extinct without contributing to the rise of modern human groups[14]. Elements of this so-called Pre-Neandertal hypothesis can be seen in some earlier publications. A more detailed review of the early ideas on the role of Neandertals in human evolution can be found in Spencer and Smith[15], Spencer[16], and Trinkaus and Shipman[17]. Most leading scientists of the era concured with one of these views. Franz Weidenreich, the main creator of the hypothesis that forms the core of what is today recognized as the Multiregional theory, agreed with Hrdlička with respect to the Neandertal role in modern human ancestry[18–20]. C. Loring Brace[21,22] adds a functional explanation to Hrdlička's model and draws attention to the importance of culture as an adaptation. This, however, is not a new concept in human evolutionary studies, as Darwin himself proposed stone tool manufacture as one of the main factors in hominid evolution. Models that dominate the anthropological literature today (Out of Africa, Multiregional model, Assimilation model) have their roots in one of these earlier models.

Morphology

There is an overwhelming quantity of literature dealing with Neandertal morphology. Here, I present an overview of the main characteristics that are commonly used to differentiate Neandertals from the preceding as well as from later human groups. Neandertal morphology is mainly a mixture of plesiomorphic (symplesiomorphic) characters, shared with the preceding late Middle Pleistocene humans, and apomorphic (synapomorphic) features in common with the later morphologically modern Upper Paleolithic people. Only rare features represent autapomorphies unique to Neandertals. It is the combination of these features found in high percentages in Neandertals, that distinguishes them as a group. For a review of commonly noted Neandertal characteristics see Wolpoff[23], Conroy[24], Klein[25], Smith[26], Trinkaus[27], and Aiello and Dean[28].

The most commonly noted Neandertal features are outlined in the following paragraphs. Neandertals have long and low crania with a cranial capacity on the high end of modern human range (Figure 3). Their frontal bone is low and exhibits a distinct supraorbital torus that forms a double arch above the orbits and thins laterally[29,30]. Further, the lateral orbital margin (frontal process of the zygomatic bone that connects to the zygomatic process of the frontal bone) is columnar-shaped, and the orbital and facial plates are not distinct as in modern populations[29–32]. The lambdoid region is flat, while the occipital bone bears a distinct posterior projection, the occipital bun. All Neandertal occipitals have suprainiac *fossae*, usually oval in form[33]. Neandertal mastoid processes are usually smaller or about the same in terms of projection as the juxtamastoid eminence, and the *incisura mastoidea* is closed anteriorly[34,35].

The mid-facial region is very prognathous, however, recent analyses[36] show that this prognathism is not extreme when compared to preceding populations. Greater projection in the upper facial region is a result of increased cranial capac-

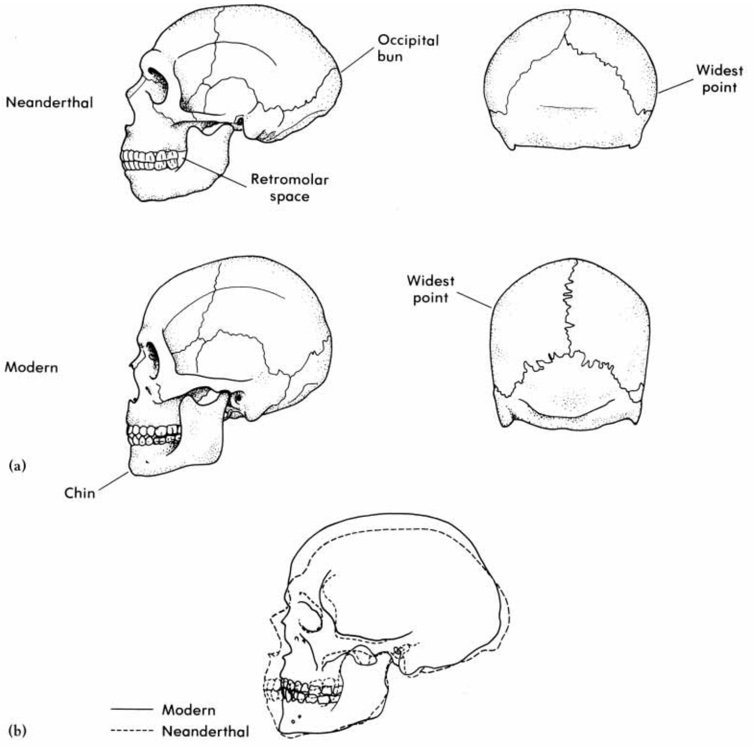

Fig. 3. Comparison of Neandertal and modern human crania (from Staski and Marks, 1992).

ity, as well as of robust nasal and supraorbital regions[29,36–38]. Facial prognathism, therefore, is not a Neandertal apomorphy, but it is the reduction in prognathism in modern humans that is the derived condition[36]. This is most likely connected to ontogenetic changes on the cranial base, possibly including sphenoid bone length[39,40]. The nasal cavity is very voluminous, and considering that the main function of the nose is heating and moisturizing inhaled air[41], and maintaining a constant brain temperature[42], Wolpoff[23] proposed this as the explanation for the Neandertal nasal morphology. Trinkaus[43] argues that this morphology is explainable bearing in mind Neandertal high activity levels in the light of termoregulatory demands. According to Dean[44], an important role is played by cooling of the arterial blood on the way to the brain. However, all the peculiarities of the Neandertal nasal morphology are not explainable solely by climatic adaptation[45], but like most other craniofacial features, results from numerous factors. Proposed Neandertal autapomorphies in the morphology of the nasal area[46,47] are shown to be present in both earlier populations, as well as in succeeding modern human groups[45,48,49].

In Neandertals, the lateral face is receding, while the maxilla lacks a canine fossa. Maxillary sinuses extend into the zygomatic body[32]. Some authors argue for a distinct morphology of the inner ear in Neandertals[50], although this is not seen in all Neandertal specimens[51]. The Neandertal mandible normaly lacks a true chin (*trigonum mentale*), although a *mentum osseum* is sometimes present, and the mandibular foramen is often horizontal-oval in shape[52–54] which might be related to the expansion of the sphenomandibular ligament[54]. This morphology, however, is present in both earlier, as well as in later human populations[54,55], and is most likely genetically controlled[54,30]. The mental foramen is usually posited inferiorly to the M1[53,56,57]. Maxillary incisors are shovel shaped and larger in size, both in crown and root dimensions[58,30], but not differing significantly in dimensions from those of early modern human populations of the early Upper Paleolithic[59,60]. Notable reduction in tooth size is seen later, at the Upper Paleolithic to Mesolithic boundary[59]. The unusual pattern of anterior tooth wear (labial tooth wear) in Neandertals is most likely related to paramasticatory activities (teeth-as-tools) (see[11,21,22,61]), although some authors suggest this is related to dietary factors[62]. Molars exhibit a high percentage of taurodontism, and according to Wu and Turner[63] and Bailey[64,65]. Neandertals tend to have a bridge connecting the protoconid and metaconid cusps, which is distinctive for these humans. There is a gap between M3 and the ascending ramus, known as the retromolar space[23,42,56,66]. It is most likely related to the mesial drift of the dentition and change in dimensions of the mandibular ramus[57]. On the internal side of the ramus, there is a developed medial pterygoid tubercle (the attachment of the *m. pterygoideum internus*)[67,68], but recent analyses[69] have shown that this trait is not autapomorphic as it is present in recent *Homo* groups. According to Smith and Paquete[30] and Rosas[57] there is an interrelation among various mandibular traits that is explainable by craniofacial growth. The *incisura mandibulae* in Neandertals is situated more medially at the border with the mandibular condyle[57,70–72], which is extending laterally (expansion of the *tuberculum subcondylum laterale*). This condition is also present in some earlier (pre-Neandertal), as well as in later early modern human groups[72–75]. Differences in the morphology of the mandibular ramus, especially more posterior placement of the lowermost point of the mandibular notch, and the lower positioning of the condylar process are genetically influenced according to Rak and colleagues[76].

Postcranial differences between Neandertals and modern human populations are usually explained by the extreme robusticity of the former group (Figure 4). Results of the analysis by Lovejoy and Trinkaus[77] suggest that Neandertals were twice as strong as modern humans. The most notable differences in postcrania are discussed in the following paragraphs. Neandertals exhibit low values of both brachial and crural indices, which can be explained by Allen's[78] rule[42,79–83], as well as by biomechanical functional demands[27]. *Claviculae* are elongated, suggesting broad shoulders and deep chests, while the *scapulae* have a high percentage of dorsal grooving on the axilliary border[84,85]. This relates to the attachment area of *m. teres minor*, a lateral rotator of the arm, and could reflect a differential habitual loading position, resulting from such activities as the use of heavy thrusting spears while the arm is bent in the elbow[86,87]. Although most modern humans exhibit the ventral grooving pattern on the axillary scapular border, some Neandertals (e.g. some of the Krapina specimens and Shanidar 3), as well as the early Upper Paleolithic modern humans (e.g. Predmosti XIV, Barma Grande 2, Doni Vestonice XV, all of the Skhul and Qafzeh specimens) exhibit a bisulcate pattern[85,88–90]. Neandertal glenoid *fossae* tend to be shallow and oriented in a more superior position. *Radii* are curved and have elongated necks. Radial tuberosities (the attachment area of *m. biceps brachii*)

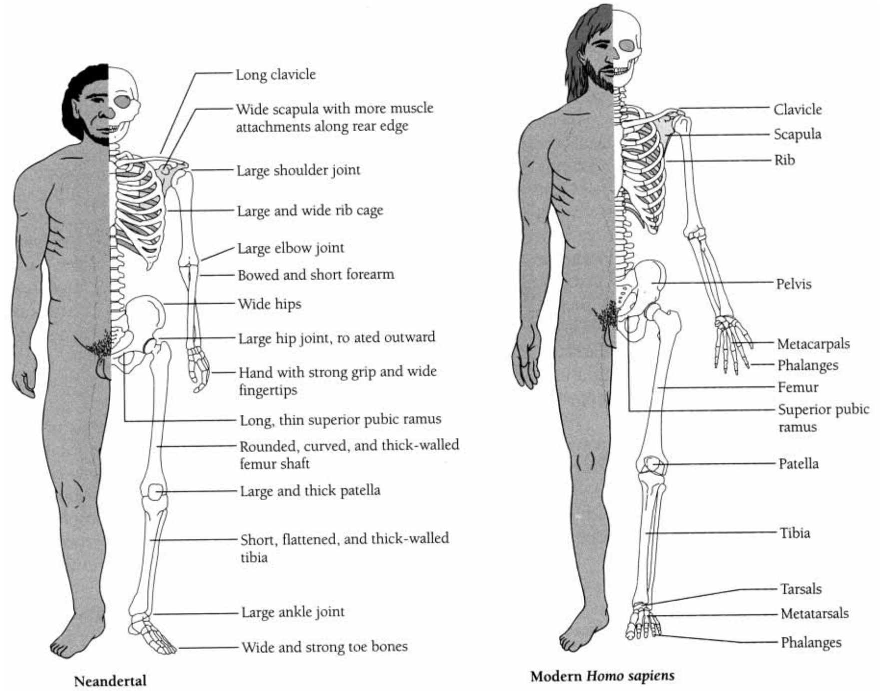

Fig. 4. Comparison of a Neandertal and modern human (after Stringer and Gamble, 1993).

tend to be oriented more medially, while the trochlear notch is generally oriented more in the anterior direction[27,52,53,91]. This is also explainable as advantageous during the arm loading in flexed elbow position[86]. Neandertal *humeri* are very robust, however, the reduction of this robusticity can be seen from later Neandertals, through the early Upper Paleolithic humans, to the later Upper Paleolithic people[92].

Differences in the hand bones between Neandertals and modern humans have been noted numerous times[27,52], this having been explained behaviorally[93]. Neandertal distal and proximal halluceal phalangeal rows are equal or sub-equal in length, while in most modern humans the distal phalange is two-thirds the length of the proximal one[27,94,95]. There is also some difference in the shape of the 1st carpometacarpal joint. According to some authors, these reflect differences in grip patterns[94,95], where Neandertals were adapted to forceful transverse grip and modern humans to the oblique power grip. As Neandertals and the morphologically more modern populations of the Levantine area both have the same, Mousterian industry (contra[96,97]), the significance of these morphological differences remains to be explained.

Neandertal pelves are characterized by an elongated superior pubic *rami* and somewhat laterally rotated superior part of the *ilia*[27,53,98–102]. These differences are most likely due to the biomechanical differences in habitual locomotion[103] and structural demands in short, heavy built people[104]. Femoral diaphyses are round in cross-section and lack the pilasters on their posterior surface that characterize modern human *femora*. Femoral heads are large, as are most muscle markings, especially for *m. gluteus maximus*, while the proximal part is rounded (in modern populations it is usually flattened anterioposteriorly)[27,43]. Femoral medial and lateral condyles face more posteriorly[27]. The *tibia*, *fibula* and *patella* are also robust, and the same is observed for the foot bones[27,43]. Proximal foot phalanges are robust and relatively short, while the first tarsometatarsal joint is convex. The talar neck is relatively short, while the lateral malleolar surface is large[105].

Neandertal postcrania clearly show marked robusticity observable in muscle attachment areas, however, like in many other metric trends, early Upper Paleolithic populations fall closer to Neandertals (or are intermediate in values) than to living human populations[92,106]. According to Trinkaus[43], lower limb morphology shows adaptation to a long-term persistence hunting strategy. Average Neandertals would reach around 167 cm in height and weight about 80.8 kg, according to Ruff and colleagues[37]. Although their brains were large, their cranial capacity means are on the high end of living populations (about 1.520 cm^3). This might reflect the fact that today's cold adapted peoples (e.g. the Inuit) tend to have a greater average cranial capacity. There is no discernable difference in cranial organization between Neandertals and living humans[107]. Life expectancy of Neandertals was late 30s to early 40s[108].

Most of the aforementioned differences in morphology can be explained either functionally or adaptively (cold adaptation). Many of the Neandertal characteristic features appear within the late Middle Pleistocene groups that date to OIS 11–9 (Vértesszöllös, Petralona, Arago, Steinheim, Swanscombe, Atapuerca), while by OIS 7, presence of most of these features is well established (e.g. in fossils like Ehringsdorf, Fontéchevade, Biache-saint-Vaast, Pontnewydd, La Chaise[35,56,57,71,109–111]). Therefore, we can observe increase in the incidence of these characteristics through time from about 500–400,000 years ago, to the time of OIS 6 and the appearance of the full-blown Neandertal gestalt. This »shift« in trait frequencies makes any sharp division between the preceding humans and Neandertals necessarily an artificial one.

Having noted the main differences in morphology of Neandertals and modern humans, we are left with questions concerning the significance of these. How much of a real difference is this difference? What does it mean, if anything, for the taxonomic status of Neandertals? What are the possible explanations? Functional explanations for the Neandertal morphology have been suggested by many scholars (for instance, see Brace,[21–22], Smith[53,61], Trinkaus[27] and Wolpoff and colleagues[112]). Coon[42] held that Neandertal mid-facial prognathism can be explained by nasal projection and that it reflects cold adaptation, while Smith[61] suggested this as an adaptation to paramasticatory activities. The teeth-as-tools hypothesis as an explanation of Neandertal midfacial morphology was suggested early in the last century[10,113], and later accepted by many scholars[21,22,61,114]. It is well established that Neandertals used their teeth in activities other than food processing, as we can see from microwear studies[112], high instances of temporomandibular joint pathologies[27,53], and the unusual manner of anterior tooth wear[53,115].

Explanation of Neandertal facial morphology has been the subject of the two competing models. Rak[116] proposed a model, which centers around the placement of the infraorbital plate in a more parasagittal orientation, which would, in turn, better resist the rotational torsion during the anterior tooth loading. In Neandertals, the zygomatic root is positioned above the M2 or M3, while in modern humans it is located more anteriorly, above the M1 or M2[117]. In Trinkaus' model, changes in the infraorbital region are seen as a secondary consequence of the reorganization in the position of dental and masticatory muscle regions[117]. Demes[118] believes that the elimination of the angles between the infraorbital plate, the maxillary walls, and the zygomatic body reduces and redistributes stresses more evenly. Maureille and Houët[119] argue that the absence of the canine *fossa* and the alignment of the infra-orbital and maxillo-zygomatic surface in a more oblique plane should be considered a Neandertal apomorphy.

Occipital bunning and the long and low cranial form provide a more horizontal orientation of the posterior cranium, adding to the biomechanical efficiency of the nuchal musculature, which would be beneficial in counteracting stresses produced by anterior dental loading[61]. Adaptive changes are seen in the mastoid region, where the mastoid process and juxtamastoid eminence are divided by a broad sulcus, the attachment place of the digastric muscle (which retracts the mandible). It is possible that the morphology of the occipital region is a result of the ontogenetic difference in brain growth[120]. In addition, at least a part of the morphology may not be a result of the functional adaptation, but of genetic factors[57,61] and genetic isolation of small populations under heavy selective pressures[79].

Another important morphological region that has been argued to have an important role in reduction of the stresses put upon the Neandertal face due to anterior tooth loading is the supraorbital area. Endo[121] proposed that having a more vertical forehead is advantageous in dissipating stresses, however in Neandertals who are characterized by receding frontal squama, supraorbital tori will compensate for a lack of a more vertical forehead. According to Moss and Young[122], however, the supraorbital torus is functionally related to maintaining the integrity of the cranium between neural and orbital tissues (a prognathic face and receeding forehead). The results of Vinyard and Smith's[31] analysis demonstrated the association between the robusticity of the supraorbital region and craniofacial size in modern humans that was previously demonstrated in non-human primates by Ravosa[123]. The supraorbital torus is a primitive trait that is present in human evolution for a long time, and there is no sudden reduction in its robusticity even at the Middle-to-Upper Paleolithic boundary, although there are some changes in the overall pattern and shape[124].

Somewhat different demands are put on the lateral part of the torus including the lateral orbital wall[31,32]. Paramasticatory activities produce stresses affecting the lateral part of the torus and frontal process of the zygomatic bone[31,32,61,125,126], while other peculiarities of the zygomatic region are explainable as a result of the maxillary sinus expansion and adaptation to climate[32].

In conclusion, craniofacial reorganization in Neandertals is a result of numerous factors, including biomechanical demands and changes in facial dimensions[11,21,22,61,116–118,123,127], environmental adaptations[42,79], as well as the genetic and ontogenetic factors[57,61,120]. Changes in one part of the cranium necessary affect the morphology of other parts.

Postcranial morphology in Neandertals is explainable to a large extent by climatic adaptations[42,79–83,91,114,128–130]. This is not contradicted by the fact that the Levantine Neandertals exhibit similar body proportions, bearing in mind that Neandertals first appear in Europe and only later inhabit the eastern parts of their geographical distribution[131,132]. Also, some of the cold adaptations are not as pronounced in the Levantine Neandertals[133]. Other details of Neandertal anatomy can be seen as a continuation of long-term evolutionary trends seen in earlier European hominids[23,27,35,53,57,61,111,117,132], or influenced by isolating mechanisms[79]. In addition, newer genetic studies make us wonder how much of these »Neandertal characteristics« can be explained with the aforementioned models, and how much of these are governed by certain genetic mechanisms such as regulatory genes.

Time, Culture, and Lifeways

Neandertals are usually recognized to have inhabited Europe and parts of Western Asia (Figure 5) from about 200,000 to 30,000 years ago. As noted before, they evolve from local European populations, therefore making the onset of this time range somewhat arbitrary. After they appear in their full blown form on the European continent, they spread to the parts of Western Asia where they co-exist with early morphologically modern human groups. Interestingly, both groups produce indistinguishable stone tool culture. The fact is that evolutionary changes work in a mosaic pattern with some traits appearing before others. Therefore, some authors recognize specific fossils possessing certain Neandertal traits as Neandertals[23,134], while others include them within the variation range of earlier hominids and assign them to such taxa as *Homo antecessor*[135] or *Homo heidelbergensis*[136]. Some of the aforementioned Neandertal traits are recognizable in fossils like Fontéchevade, Swanscombe, Saccopastore, Salzgitter-Lebenstedt, Ehringsdorf, Steinheim, Petralona, Arago, and Vértesszölös[57,134,137,138]. These include the presence of suprainiac *fossae*, certain occipital characteristics, occipital bunning, retromolar spaces and some other mandibular features. One of the earliest finds everyone agrees represents Neandertals is the skeletal collection from Krapina in Croatia, dating to the OIS 5e (about 130,000 years ago)[139]. Likewise, the youngest Neandertals come from the Croatian site of Vindija, which is dated to about 28 or 29,000 years ago[140] and the site of Zaffaraya in Spain[141]. Late surviving Neandertals are also reported from the Caucasus region[142]. Speaking in terms based on the Alpine glacial sequence, which is not

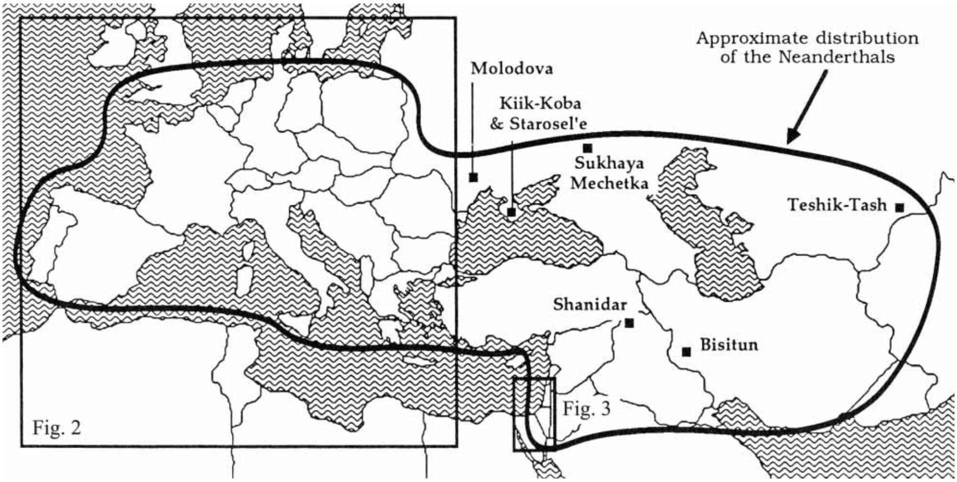

Fig. 5. Geographic distribution of Neandertals (from Klein, 1989).

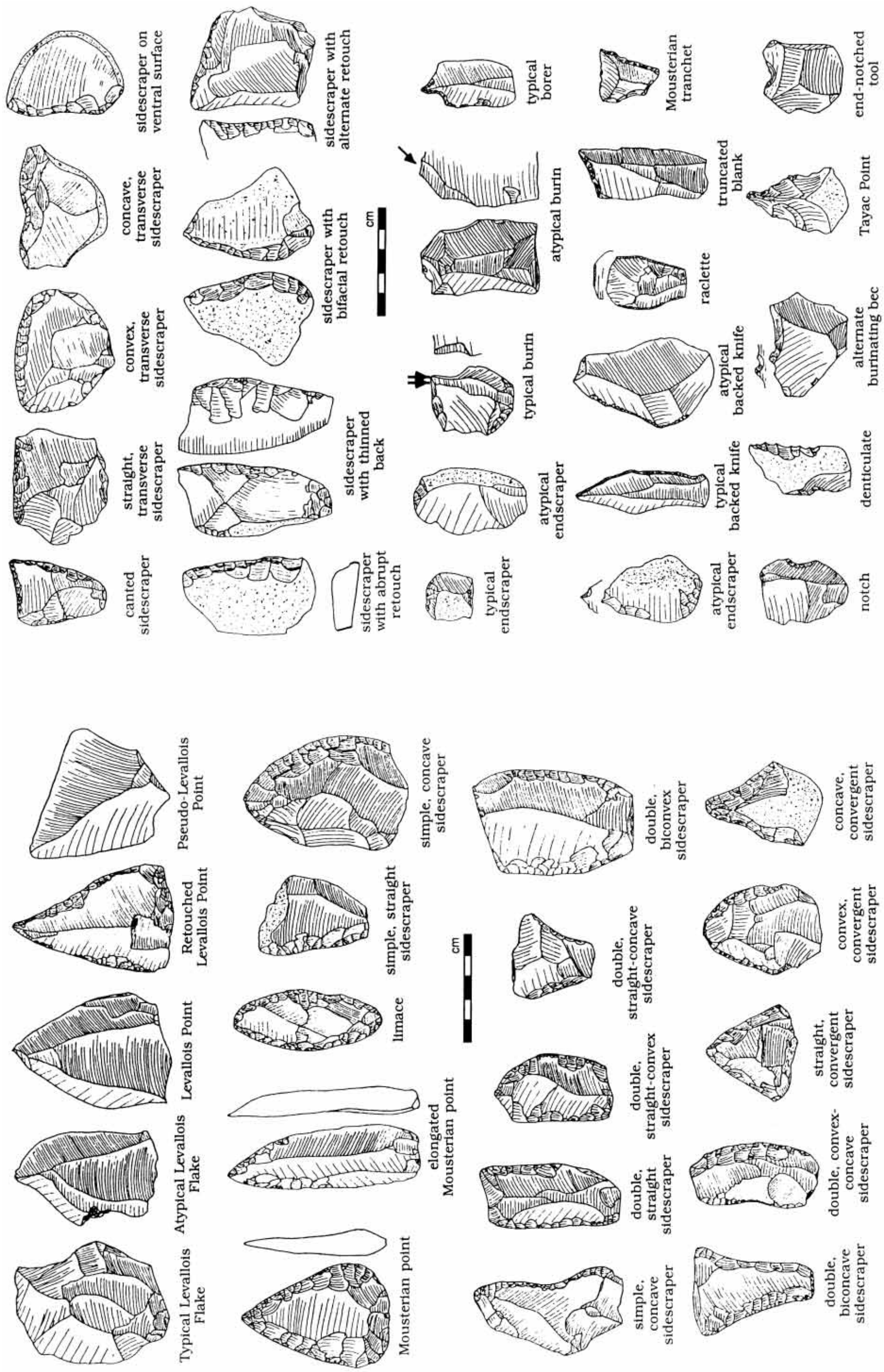

Fig. 6. Mousterian tools (from Klein, 1989).

widely used in more recent literature but dominates earlier publications, Neandertals belong to the time range starting with the Riss-Würm interglacial, to the beginning of the Würm 2 stadial.

As previously noted, Neandertal fossils come from sites in Europe and parts of Asia, while some possibly Neandertal artifacts dated to about 40,000 years ago come from the European Arctic region[143]. Most Neandertal finds are found in association with stone artifacts. The stone tool culture commonly associated with Neandertals is the Mousterian (Figure 6), named after the site of Le Moustier in France. This stone tool industry is characterized by a large number of side scrapers and tools made on flakes[144]. The use of the so-called Levallois technique of producing standardized flakes (Figure 7) is so common that, although this technique developed within the preceding Acheulean complex, we recognize it as one of the characteristics of the Mousterian. Bordes[144,145] recognizes four different facies of Mousterian culture: 1) Mousterian of Acheulean tradition, 2) typical Mousterian, 3) denticulated Mousterian, and 4) Quina-Ferrassie Mousterian (Charentian). In addition, each of these facies can be defined as being Levallois type, according to the percentage of use of this technique within the site or within an individual layer. Bordes[145] believes that different Neandertal tribes are responsible for the production of each of these different facies. Although Bordes' typological division of the Mousterian is still much in use, his »tribal explanation« of the Mousterian subdivision has been heavily criticized. Lewis and Sally Binford[146] believe that it is the function that determines the type of Mousterian industry, while Dibble[147] argues that there is no basic difference among Bordes' types, but that in the course of use and re-use (resharpening), tools change their appearance. Further analyses of individual sites and layers within sites will help clarify this question. Neandertals lived in smaller, mobile groups[25,71,148], and mostly used raw materials within a few kilometers from the site[25,149], although there are studies showing raw material acquisition from more distant sources[150,151].

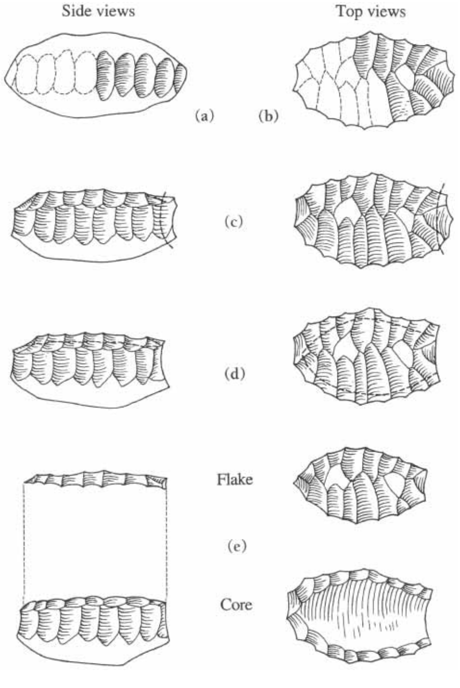

Fig. 7. Levallois technique (from Feder and Park, 1989).

One of the reasons Neandertal fossils are so complete compared to the preceding human fossils is the fact that they were the first humans to deliberately bury their dead. While some scholars[152–154] have tried to explain this by other (taphonomic) factors, it is agreed among most scholars that Neandertal burial is an indisputable fact, although the reasons for this treatment of the dead is a matter of debate[25,142,150,155–168]. Burials at such sites as La Chapelle-aux-Saints, La Ferrassie, Spy, Amud, Kebara, Dederiyeh, and Teshik Tash are just some of the examples. The Shanidar 4 burial is often cited as being an example of funerary practices that are more than just disposal of the deceased. According to Leroi-Gourhan[160] and Solecki[162], a high concentration of flower pollen in the grave suggests flowers as grave goods. Furthermore, it is quite possible that Neandertal burials are underrepresented in the literature, considering the fact that most of the finds come from the early 20th century, when the excavation techniques and methods were not as detailed and strict as they are today.

Neandertal life was hard. This is known from a high incidence of injuries and pathological changes seen on their bones. Some of the skeletal remains, such as Shanidar 1[27] from Iraq and Krapina in Croatia[169] exhibit trauma of extreme magnitude. In case of Shanidar 1, the individual was probably blind in one eye, missing a forearm, and displaying various other antemortal pathologies[27], while one Krapina skull shows a healed injury at the lambdoidal region that would have rendered the individual unconscious for days or weeks. If we explain these as signs of care for the injured, it shows us a very different picture from that portrayed by Boule. On the other hand, adding to the picture of Neandertal bestiality are the claims for cannibalism. These started with Gorjanović-Kramberger's explanation for the fragmentary nature of the Krapina remains[52] and were further developed by Ullrich[170], White and Toth[171] and Defleur and colleagues[172] among others. Other authors suggest alternatives such as taphonomic factors[173] or even a pattern of secondary burial[174,175]. Even if episodes of cannibalism happened, it tells us nothing about Neandertal »humanness«, as reported cases of anthropophagy come from both prehistoric specimens such as Bodo and Klassies River Mouth[176,177], as well as from the numerous reports throughout human history up to the present day[178].

Although some scholars suggest that Neandertals were mostly scavengers[179] or opportunistic hunters at best[180], more and more evidence is showing that they were successful hunters[181]. Evidence from faunal remains coming from various sites[182–184], as well as stable isotope analyses[185–188] show they obtained their protein intake almost exclusively from animal sources, which would not be possible for a terrestrial scavenger.

Possession of a fully modern language and developed speech abilities have been proposed to distinguish early modern humans from Neandertals and may have added to the latter's demise[189]. The »evidence« for much of the supposed differences in speech abilities comes from the reconstruction of the La Chappelle vocal tract[190–194]. Later analyses, however show the fallacy of this reconstruction[195–197]. Cranial base angulation has also been argued to influence speech capability[198], however Arensburg and colleagues[199,200] show that these are not connected, and Ross and Ravosa[201] show that the basicranial angle is related to relative brain size. Furthermore, as Frayer[202] has shown, the basicranial angle of Neandertals is within the values of modern human populations. Various studies have shown that there is no discernable difference in brain organization between the Neandertal and modern human groups[107,203,204], thus providing no basis for the speech argument. In addition, the discovery of the 60,000 year old Neandertal hyoid bone from the Israeli site of Kebara (KMH2)[168] shows that its morphology is indistinguishable from that of modern humans[102,199]. There is no anatomical basis for the supposed speech/language advantage of Upper Paleolithic populations. Speech and language development should be considered as a trait evolving in the hominid lineage for a long time.

Continuity? Archaeological, Morphological, and Genetic Data

The formula of Neandertals equal Mousterian, modern humans equal Upper Paleolithic industries has been a part of the archaeological and anthropological literature for a long time. This has influenced theories on the tempo and mode of morphological change. The change in the archaeological material (i.e. the appearance of Upper Paleolithic industries) was associated with the appearance of morphologically modern humans that supposedly replaced Mousterian-producing Neandertals in a relatively short time span. This picture changed considerably with the discovery of Neandertal skeletal remains in direct association with the Upper Paleolithic Châtelperronian industry at St. Cesaire and Arcy-sur-Cure in France[205–207]. This industry is most likely derived from the preceding Mousterian[208]. A similarly interesting and complex situation is seen in Central and Southeastern Europe, where Szeletian, another early Upper Paleolithic industry, shows continuity from the preceding Mousterian culture[209]. At Vindija cave, Croatia, Neandertal remains from the G1 layer have been found in direct association with a characteristically Upper Paleolithic bone point (Aurignacian or Olschewian), while other artifacts showing Upper Paleolithic traits are common in that layer[210–213]. The G1 layer has been dated to between 28 and 29,000 years ago, a time when early modern humans were already present in Europe for at least a few thousand years[140]. On the other hand, the Levantine hominids, both Neandertal and anatomically more modern humans are associated with Mousterian industries[168,214–218], adding to the complexity of the picture.

There are two competing models that have tried to explain the archaeological side of the Middle to Upper Paleolithic transition. According to the human revolution model, the transition is seen in archaeological material, and associated with changes in symbolic behavior, cognitive capabilities and the appearance of fully modern language[25,179,219,220]. Climatic changes are also seen as having a significant role[221]. This explanation is in agreement with the model in which morphologically modern newcomers replace the Neandertals. McBrearty and Brooks[222], however, argue that the »modernity« in behavior is the result of evolutionary development starting within the Middle Stone Age of Africa. Further, there is no abrupt and sudden behavioral change seen in archaeological record at the Middle to Upper Paleolithic boundary[145,223,224]. Various authors have shown that the initial Upper Paleolithic industries of various geographic regions, such as the Szeletian and Jankovichian of Hungary, Altmühlian of southern Germany, Jerzmanowician of eastern Germany and Poland, Bohunician of Czech Republic, Brynzeni and Kostenki-Szeletian of Russia, Châtelperronian of France, and Uluzzian of Italy, reflect elements of the preceding Mousterian and are most likely a result of a local development[151,209,225–231]. Mousterian influences are lost in the later industries, such as the Aurignacian and Gravettian, although the population responsible for the production of Aurignacian or Aurignacian-like tools is still unknown[225]. It is probably best to consider this industrial complex as a number of local industries and not a homogenous phenomenon.

As we can see, this transitional period is complex and locally diverse, providing no sharp distinction either in morphological, or archaeological data. The same can be said for the appearance of symbolic behavior, however difficult to define it may be. Possible evidence of symbolism is seen within the sites of the Middle Paleolithic[232]. Objects like pierced or modified animal teeth and bones come from the Châtellperronian layers of Grotte du Renne

(Arcy-sur-Cure) and St. Cesaire[205,207,227,233], and some aspects of this so-called »behavioral modernity« are present at even earlier times. Use of pigment[145,181,234], burial (see references earlier in the text) and similar manifestations speak about similarities in thinking between Neandertals and Upper Paleolithic people. Objects such as Gravettian portable art, Solutrean stone points, Magdalenian cave paintings and so on, are those people tend to think about when talking about the artistic behavior. These however, happen much later in time during the Upper Paleolithic, and several thousands of years after the disappearance of the Neandertals. The population responsible for creating objects such as the animal figurines from the Aurignacian layers of the Vogelherd cave remains to be identified[225,].

In recent years, most of the debate on modern human origins concentrated around two competing models. According to the Out of Africa model (Single Origin Model, Replacement Model) (Figure 8) morphologically modern people evolve on the African continent, later replacing all local archaic human populations in other geographical regions with no, or with very limited genetic exchange[235,236]. In this model, Neandertals are seen as a separate species, *Homo neanderthalensis*[56,109,237–240]. This explanation has its roots in earlier models such as the Garden of Eden hypothesis[241] and the Noah's Ark hypothesis[242], and is present in earlier publications[13,243]. According to the Multiregional Continuity model (Figure 9), modern humans evolve out of the preceding local populations within each geographic region. Gene exchange is present at all times, preventing speciation. In this model, Neandertals are a part of a single polytypic species, *Homo sapiens*, sometimes distinguished from living humans on the subspecies level, as *Homo sapiens neanderthalensis*[244–247]. This model is recognizable in Weidenreichs' wri-

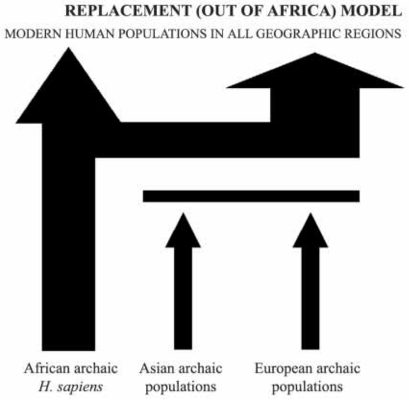

Fig. 8. Replacement model.

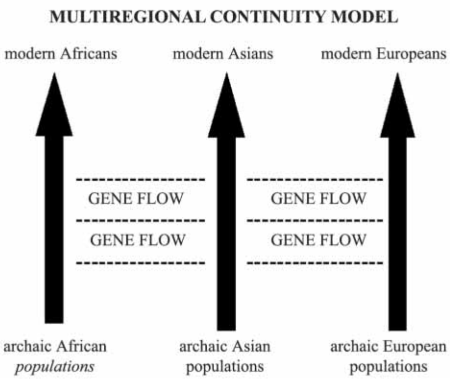

Fig. 9. Multiregional continuity model.

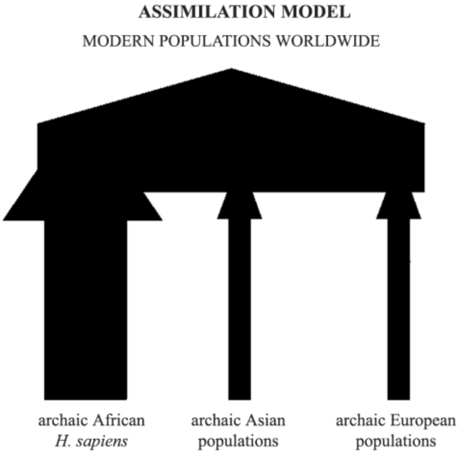

Fig. 10. Assimilation model.

tings[18–20], and discussions of the role of Neandertals in modern human ancestry seen in publications of G. Schwalbe[7], Gorjanović-Kramberger[52], A. Hrdlička[11], L. Brace[21,22], J. Jelinek[248] and others. The third, and somewhat intermediate explanation is the Assimilation Model (Figure 10). According to this model, most of modern human morphology evolved in a single region, most likely in Africa, but local populations in other geographic regions contribute to the newcomers by interbreeding. In this model, European Neandertals interbred with the Early Upper Paleolithic peoples, thus genetically contributing to the modern human gene pool[249–251], as seen in continuation of some of the morphological traits (discussed later in the text).

Morphological continuity from Neandertals, through the early Upper Paleolithic humans, to the populations of the Late Upper Paleolithic and Mesolitic is seen in continuation of certain evolutionary trends, such as reduction in size and change in morphology in facial and supraorbital region[29,57,66,124,213,252], dental dimensions and mandibular morphology[55,59,72–75,211,253–254], various other craniofacial traits[45,247,248,254–257], as well as in the postcranial elements[37,85,90,92,106]. Early morphologically modern people from Mladeč and Predmosti in Moravia exhibit certain »Neandertal traits« including a level of occipital bunning and lambdoidal flattening[26,248,254,257]. Late Neandertals from the Vindija Cave in Croatia show a more gracile morphology than the earlier specimens of the same region (Krapina)[112,211–213,22,258]. Other Neandertal traits such as the horizontal-oval mandibular foramen, also show continuity from late Neandertals to early modern human groups[54]. A horizontal-oval mandibular foramen is present in about 53% of Neandertals, in about 18% cases in early Upper Paleolithic Europeans, 7% of the Upper Paleolithic specimens, while in recent populations this trait is observes in less that 2% of cases[254]. Thus, it is a shift in trait distribution through time, not a shift in traits that we see in some morphological data. Again, no sharp distinction exists between Neandertals and early modern humans in certain morphological details. Dental dimensions in early Upper Paleolithic groups are closer to that of Neandertals, or intermediate between Neandertals and late Upper Paleolithic humans, while a more pronounced dental reduction is seen much later, during the Mesolitic[59]. Likewise, morphology of the supposedly modern people of Qafzeh and Skhul is different from both Neandertals and living humans. For instance, multivariate analysis of cranial form in the Skhul/Qafzeh hominids shows that some of them fall out of the normal modern human range[259,260] and closer to Neandertals[259]. This is also in agreement with a certain continuity in traits that is shown for the European region[26,90,211–213,246,247,252,256,258], East Asia[246,247,261], and Australasia[244,262]. Lagar Velho 1 (a burial of a child of about 4 years) from Portugal, dated to about 24–25,000 years ago[263] shows a mixture of Neandertal (femorotibial proportions, tibial condylar position) and modern human traits (presence of chin), while some traits are intermediate in their values (mastoid region). According to Duarte and colleagues[263], this is best explainable as a result of some genetic contact between the two groups, and the continuation of these traits in later times (Gravettian) when the Lagar Velho child lived and died. This explanation was greeted with much criticism by the replacement proponents[264].

Besides the continuity in certain morphological traits, the gap between the two groups (Neandertals and morphologically modern humans) is lessened by the fact that some of the proposed Neandertal apomorphies are in fact synapomorphies, as they are present in living populations.

Nasal morphology and the suggested upper respiratory tract »specialization«[46] has been shown to be within the variation range of modern people[48]. The same is true for the position of the mental foramen below the M1 and the presence of retromolar space[57,66], as well as the morphology of the mandibular notch[72–75]. Dental development of both groups is also similar[265].

Although numerous authors noted the accelerated ontogenetic development in Neandertals compared to modern humans[39,51,266–268], early Upper Paleolithic groups were closer in their ontogenetic development to Neandertals (or intermediate between the two groups) than to the living populations[266,269] making the taxonomic differentiation on the species level unjustifiable.

The potential usefulness of genetics in solving questions relating to hominid evolution was realized very early. For example, in 1967, V. Sarich and A. Wilson used the immunological analysis to determine the time of divergence of evolutionary line leading to African Apes from that leading to hominids[270]. In the last 15 years, analyses of DNA have been used to test the likeliness of models of the modern human emergence. In 1987, R. Cann and colleagues published their analysis of mitochondrial DNA, claiming that all living human populations share a recent female ancestor (ancestors within a relatively small group) that lived in Africa between 140,000 and 290,000 years ago[271]. Publication of their paper caused quite a stir, and reaction from both Multiregionalists and Replacement proponents soon followed. Most importantly, it catalyzed a number of new genetic studies dealing with paleoanthropological issues. Templeton[272] showed a number of errors in the original study, while Nordborg[273] allows for some genetic contact to have been maintained between archaic and modern groups.

Genetic studies are used more and more in questions concerning the Neandertal role in the modern human emergence. While the publication of mtDNA isolated from Neandertal specimens from Feldhofer[274,275], Vindija[276,277], Mezmaiskaya[142], La Chapelle-aux-Saints and Engis[277] show differences in sequences from modern humans, Relethford[278,279] shows that this might be explained by genetic drift and population size. In addition, the results of the analysis by Adcock and colleagues[280] shows that some of the mtDNA of past populations can be lost and therefore not shown in modern human samples. Furthermore, mitochondrial DNA is only a small part of the genome and the presence of Neandertal genes in other parts of the genome cannot be excluded on the basis of mtDNA results[280]. On the basis of the analysis of other parts of genome, including the mtDNA and Y chromosome, Templeton[281] concludes that, although the African population might have had the dominant role in forming of the contemporary human gene pool, there were at least three major migrations out of Africa, and at least one from Asia into Africa in the course of the last 2 million years. Splitting of evolutionary lines into distinct European, Asian, and African lines never happened, and all three represent a single evolutionary lineage with certain regional distinctions, resulting from isolating factors[271, 278,279,281–283]. Newer genetic analyses by Eswaran[284,285] appear to be specifically in agreement with the Assimilation Model of modern human emergence.

Comparisons of Neandertals with living humans will result certainly in numerous genetic, as well as morphological, differences and are as fruitless as the comparisons of Mousterian and Microsoft technology would be. We must bear in mind that almost 30,000 years have passed from the time when last recognizable Neandertal populations roamed the Eurasian continent. Only comparisons of »morphologically modern« groups that were contemporary with or close to the time of Neandertals can give meaningful results and provide some insight into the complex interrelationship between those groups. Comparisons of mtDNA extracted from several Upper Paleolithic specimens failed to show a clear continuity between Neandertals and early modern humans[277,285]. However, as Serre and colleagues[277] conclude, at least 50 early modern human samples would be needed to exclude 10% Neandertal contribution to the modern human gene pool, while in order to exclude a 5% contribution, we would need a sample of early modern human skeletal remains larger than the one we have at present time.

Conclusion

After considering the archaeological, morphological and genetic data, what is the most likely explanation of the role Neandertals played in the genesis of early modern humans? Based on the available evidence presented in this review, several main points can be made:

1. Early morphologically modern humans in Europe did not evolve directly from the preceding Neandertal populations.

2. The most likely place of origin for the most of modern human morphology is Africa and the emergence of the basic modern human anatomical pattern in Europe likely stems from the migration of modern people into that continent.

3. There is a shift in the ratio of some traits that show a high percentage in Neandertals from Neandertals, through early modern humans of the early Upper Paleolithic, to populations of the late Upper Paleolithic, Mesolithic and living human populations, and at least in the certain details of morphology (as discussed in the text) there is no sharp line showing a clear discontinuity (that is, there is a shift in percentage of traits, not a shift in traits).

4. Archaeological evidence also does not show a sharp distinction between the European Middle Paleolithic (Mousterian) and the industries of the earliest Upper Paleolithic (Szeletian, Châtelperronian, and some other local industries) in this region. The same is observed for the symbolic and/or artistic expression. Most commonly noted differences are seen in the later part of the Upper Paleolithic, and after the disappearance of Neandertals.

5. Recent genetic studies show that the available data do not disprove the possibility of some Neandertal contribution to the early gene pool of early modern humans.

6. The most likely explanation based on the evidence presented above is the Assimilation Model, in which Neandertals are seen as an extinct group of populations, not an extinct or separate species, and are expected to have contributed to some extent to the early modern human gene pool in Europe.

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NEANDERTALCI... 150 GODINA KASNIJE

SAŽETAK

Mjesto neandertalaca unutar evolucijskog razvoja modernih ljudi predmetom je rasprava od vremena prvog prepoznatog nalaza neandertalca godine 1856. U radu je iznesen pregled morfoloških, arheoloških i genetičkih saznanja koja pridonose rješavanju ovog pitanja. Kratak povijesni pregled rasprava omogućava uvid u razvoj ideja o položaju ove zanimljive ljudske populacije. Također je iznesen pregled glavnih modela o porijeklu morfološki modernih ljudi.