Unique Ramus Anatomy for Neandertals?

Milford H. Wolpoff[1*] and David W. Frayer[2]

[1]*Paleoanthropology Laboratory, Department of Anthropology, University of Michigan, Ann Arbor, Michigan 48109*
[2]*Department of Anthropology, University of Kansas, Lawrence, Kansas 66045*

KEY WORDS   mandibular evolution, Neandertal autapomorphy

ABSTRACT   The ramus of Neandertal mandibles is said to show a suite of uniquely Neandertal character states that demonstrate the independent course of Neandertal evolution. This is the latest of numerous attempts to define cranial and mandibular autapomorphies for Neandertals. We examine variation in the four presumably autapomorhic ramal features and show they are neither monomorhic within Neandertals (to the contrary Neandertals are at least as variable as other human samples) nor unique to Neandertals, since they regularly appear in populations predating and postdating them. Neandertals differ from other human populations, both contemporary and recent, but the question of whether this fact reflects a divergent evolutionary trajectory must be addressed by the pattern of differences. In this case, as in the other attempts to establish Neandertal autapomorphies, rather than showing restricted variation and increased specialization, the Neandertal sample shows that the range of human variation in the recent past encompasses, and in some cases exceeds, human variation today, even in the very features claimed to be autapomorphic. Am J Phys Anthropol 128:245–251, 2005.   © 2005 Wiley-Liss, Inc.

Fifty years ago, Weidenreich (1943) commented that:

It almost became a sport of a certain group of authors to search for the skeletal parts of Neandertal Man for peculiarities which could be claimed as "specialization," thereby proving the deviating course this form has taken in evolution... There is not one single peculiarity which has not been taken by some author to represent a unilateral specialization... Yet, evidence proving the correctness of such statements is lacking in all of the cases (p. 44)... There, indeed, is not one among the suspected peculiarities of the Neanderthal skulls which would stand firm against a thorough comparative scrutiny (p. 45).

Despite this warning, the following years have witnessed continued attempts to define cranial and mandibular autapomorphies (or presumed autapomorphies) for Neandertals. For mandibular anatomy, these have included the horizontal-oval (H-O) mandibular foramen, mental foramen position, mastoid tubercle, retromolar space, medial pterygoid tubercle, and absence of a chin (Rosas, 2001; Schwartz and Tattersall, 2000; Stringer et al., 1984). Yet the contentions of Weidenreich (1943) have held, and all studies thus far have failed to uniquely define Neandertals as a group, since these identical features are easily found in later modern European *Homo sapiens* samples and often elsewhere (Arensburg and Belfer-Cohen, 1998; Frayer, 1992; Heim, 1976, 1989; Mann et al., 1990, 2003; Smith, 1978; Trinkaus, 1993; Wolpoff and Caspari, 1996). This does not mean that the modern groups are Neandertals, but rather suggests that a significant Neandertal contribution to modern peoples, especially Europeans, cannot be excluded unless one proposes that these identical (mostly nonfunctional) morphologies evolved independently. The strong implication is that the Neandertals cannot have been a species apart from the rest of humanity (Wolpoff et al., 2001).

One recent, indeed ongoing, attempt to define unique Neandertal traits involves features of the superior aspect of the mandibular ramus that are said to "emerge as yet another element constituting the derived complex of morphologies . . . unique to Neandertals" (Rak et al., 2003, p. 194). As Rak et al. (2003, p. 199; and see Fig. 1) described the anatomy of this region in Neandertals:

In Neandertals . . . the coronoid process appears larger and more elevated than the . . . condylar process. A shallow notch lies between the processes, with its deepest point situated adjacent to the posterior one.

Two other ramal features are noted as Neandertal autapomorphies. One is the relationship between the notch's crest and the position where it joins the anterior border of the condyle (Rak et al., 2003, p. 201, and discussed in more detail in Rak, 1998). It is asserted that the unique Neandertal condition is for the notch crest to reach the condyle at or near its middle, while the modern (and plesiomorphic) condition is for the crest to reach the condyle at its lateral border (Fig. 1). The other feature is based on

*Correspondence to: Milford H. Wolpoff, Department of Anthropology, University of Michigan, Ann Arbor, MI 48109.
E-mail: wolpoff @umich.edu
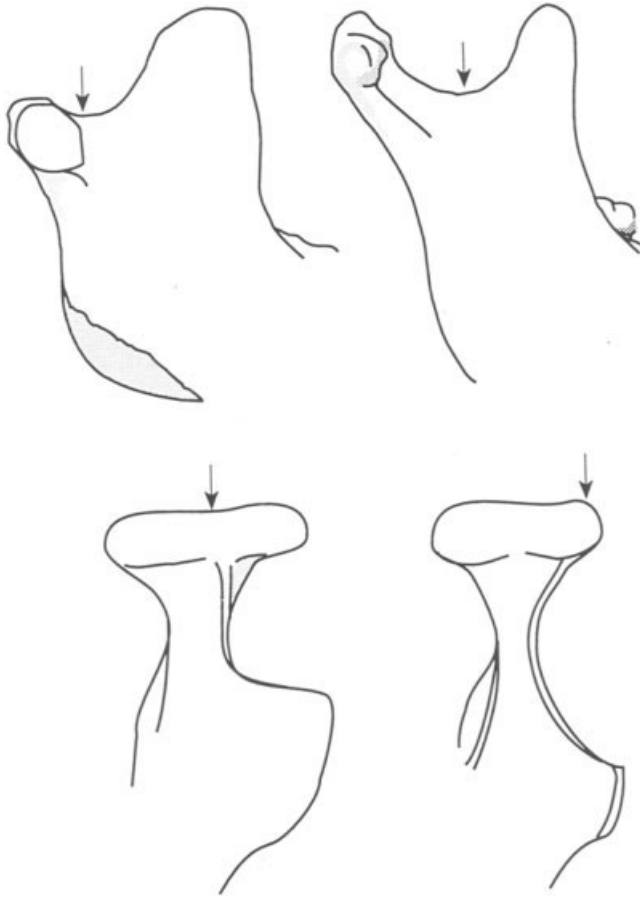
Fig. 1. Two nonmetric aspects of ramus form according to Rak (1998; reversed after his Fig. 1.). To avoid any possible misunderstanding, his figure caption is as follows (correcting for reversed positions): "**Top:** The ascending ramus of *Homo sapiens* (right) and *Homo neanderthalensis* (left). The arrow marks the deepest point of the mandibular notch. Note the symmetrical appearance of the two processes in *Homo sapiens* and their asymmetrical appearance in *Homo neanderthalensis*. In the latter, the coronoid process towers over the condylar process, and the notch's deepest point is close to the condylar process. **Bottom:** The relationship between the crest of the mandibular notch and the condyle. The arrow indicates the point where the crest meets the condyle. Note that in *Homo sapiens* (right), the crest extends to the lateral edge of the condyle, whereas in the Neandertal, the crest bisects the condyle and is perpendicular to the latter's long axis."

"tentative results of a study currently in progress" and concerns the position of the Neandertal condylar process "which is lower in absolute terms (closer to the occlusal plane) than in other hominids" (Rak et al., 2003, p. 202). In sum, the Neandertal character states (illustrated in Fig. 1) are:

1. The posterior position of the most inferior aspect of the ramal notch;
2. The ramal notch is shallow;
3. The central position of the notch crest on the long axis of the condyle where the crest joins the condyle; and
4. The low elevation of the condyle above the occlusal plane, compared with other hominids. The
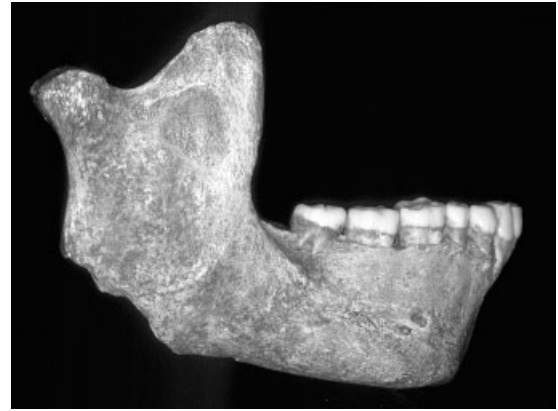
Fig. 2. Regourdou is shown in lateral view with toothrow horizontally oriented, as are all mandibles shown. It has a shallow ramal notch; the lowest point on it is in a posterior position; and the ramus is taller than the condyle. These are three traits characterized as "Neandertal" that can be seen in lateral view.

coronoid process extends more superiorly than does the condylar process, in this plane.

The phylogenetic importance of these new, distinguishing features is made clear by the two hypotheses presented in Rak et al. (2003, p. 200) and tested here:

1. The ascending ramus of Neandertals differs in morphology from that of other hominids
2. The degree to which non-Neandertals differ from each other in this respect is less than the degree to which they differ from Neandertals.

The underlying assumption is that Neandertals are a divergent European clade increasingly expressing unique features over time because of their adaptive specializations and genetic isolation.

We tested these hypotheses for the four ramal traits, using the specimens Rak et al. (2003) cited in developing them and adding a number of other individuals. We examined and compared mandibles attributed to Neandertals, and compared these in turn with mandibles of earlier archaic samples of *Homo*[1] ("*Homo erectus*" according to some taxonomies) as well as with later, early Upper Paleolithic Europeans. In all cases, we seriated the specimens on the basis of the features examined, following exactly the descriptions provided (Rak, 1998; Rak et al., 2003; Fig. 1). This was done to examine the pattern of variation, establish its range, and compare samples across time. Most of our sample is confined to adults, but we used several subadult specimens, since Rak et al. (2003, p. 204) pointed out that "Neandertal ramal morphology is clearly

---

[1]We did not include the Atapuerca mandibles in this comparison. This large sample is earlier than the European Neandertals, but very similar to them in mandibular anatomy (Rosas, 2001), enough so for it to be argued that they be included in the Neandertal sample. We felt the most conservative approach for the hypotheses we are testing is to keep the Atapuerca remains out of either sample, and we restricted our comparisons to earlier remains.

Fig. 3. Amud 1 is geographically distant from Regourdou (Fig. 2), but shares all its notch features. In these specimens, the deepest point on notch is superior to the inferior rim of the lateral edge of the condyle.

Fig. 5. La Quina 5 has a deep ramal notch. The deepest point on the notch is level with the inferior rim of the lateral edge of the condyle, and is centrally rather than posteriorly located.

Fig. 4. Shanidar 2, courtesy of Erik Trinkaus, has a similarly placed posterior notch, but its expression is much deeper than Regourdou (Fig. 2) or Amud 1 (Fig. 3); the deepest point on the notch is level with the inferior rim of the lateral edge of the condyle. The mandible thereby deviates from the "Neandertal pattern" of Rak (1998).
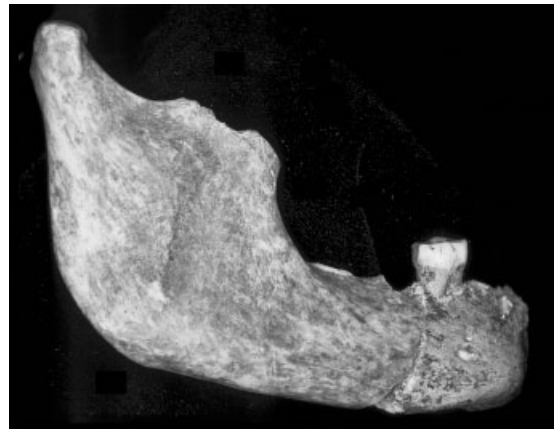

Fig. 6. While Vindija 226 is a rocker jaw and thereby difficult to align, it clearly has a deep, centrally located notch. The deepest point on the notch is well below the inferior rim of the condyle's lateral edge. The Coronoid process is broken, and its superior projection is unknown.

present in infant and juvenile specimens in our analysis."

We begin discussion with the first two traits, the position of the most inferior aspect of the ramal notch, and the depth of the notch. Regourdou (Fig. 2) is the specimen Rak et al. (2003) described as the most extreme Neandertal for all the conditions they regard as autapomorphic for the group, including these. Certain other Neandertal specimens are similar, e.g., Amud 1 (Fig. 3), from a different region of the world. In both cases, the notches are posteriorly located and are deepest near the condyle (and the condylar process is markedly lower than the coronoid; we discuss this below). However, not all Neandertal specimens are identical for this pattern. Some specimens, such as Shanidar 2, have a similar posterior placement for the deepest point on the notch but the notch is deeper (Fig. 4), and La Quina 5 has

an equally deep notch (Fig. 5), but its most inferior point is more centrally placed than in the previous three. Vindija 226 (Fig. 6) has a more central inferior point and an even deeper notch; the La Ferrassie 1 notch is also centrally placed and quite deep (Fig. 7). The condyle of this specimen has been flattened with osteoarthritis, so the notch is deeper than it appears, and this is also the case for Krapina 59. The most inferior point on the ramal notch of Krapina 59 (Fig. 8) is the most centrally located of all Neandertals illustrated here, but the notch is shallower than that of the Vindija and La Ferrassie specimens. In their combination of features, Vindija 226 and La Ferrassie 1 exhibit a ramal morphology that Rak et al. (2003) described as modern (Fig. 1), and Krapina 59 (Fig. 8) has an even more centrally located position for the lowest point on the ramal notch. Indeed, these three resemble the condition found in some early Upper Paleolithic European mandibles. For example, Dolní Věstonice 16 (Fig. 10) from the Central European Pavlovian, and the Au-
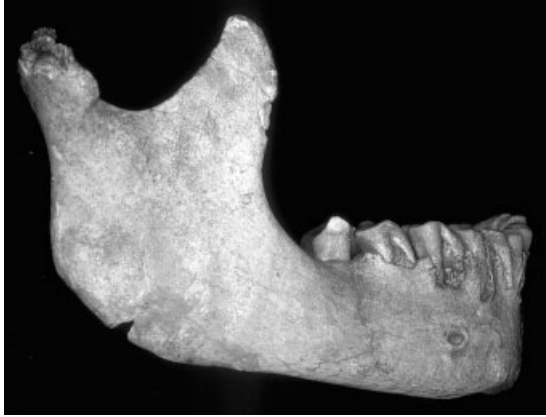
Fig. 7. La Ferrassie 1 has a deep (well below the lateral inferior border of the condyle), centrally located notch. Without arthritic flattening of the condyle, heights of condylar and coronoid process above toothrow would be about same; in this Neandertal, the coronoid process did not dominate the condylar process.
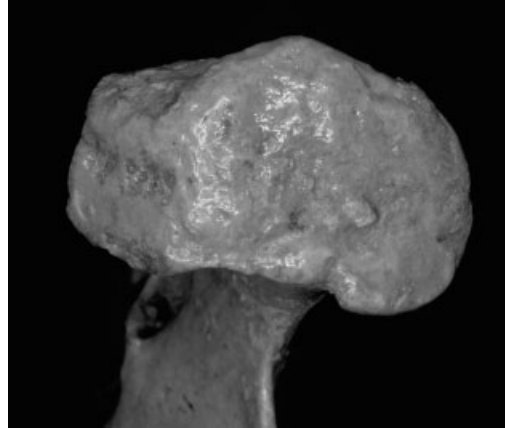
Fig. 9. Mandibular condyle of Krapina 59 ("J" mandible), seen in superior view. Surface of the condyle shows evidence of degenerative joint disease and is vertically flattened.

Fig. 8. Krapina 59 ("J" mandible). Without arthritic flattening of the condyle (Fig. 9), heights of the condylar and coronoid process above toothrow would be about same. The ramal notch in this mandible is most centrally located of any Neandertal illustrated here.
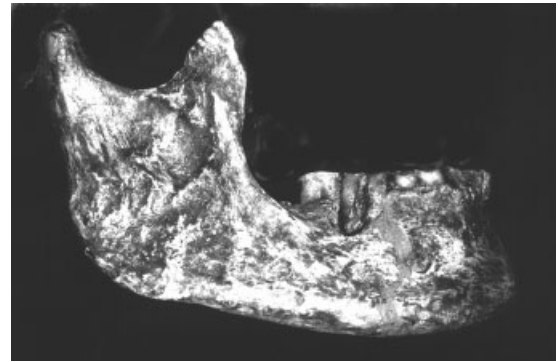
Fig. 10. Dolní Věstonice mandible 16, photo by Erik Trinkaus, with permission of Archeologický ústav (Brno), Akademie věd České republiky. This Pavlovian-associated specimen is quite similar to La Ferrassie (Fig. 7) in depth of notch, position of its most inferior point (slightly more anterior), and relative height of coronoid process. The most posterior tooth in this view is second molar.

rignacian-associated Vindija 207 (Fig. 11), both have centrally located ramal notches. The notch in the Vindija specimen is shallower; its most inferior point is just at the base of the inferior edge of the lateral condyle. Yet, other post-Neandertals such as the Aurignacian-associated Stetten 1 (Fig. 12) have a deep, far more posterior location for the deepest point on the notch, and are more like the Neandertal condition of specimens such as La Quina 5 (Fig. 5) than any other early Upper Paleolithic European mandible. Stetten 1 is also similar to the extreme expression of the Neandertal condition in its very high coronoid process (discussed below).

Late Pleistocene European samples show variation in the depth of the notch and in the position of its most inferior point. Some Neandertals resemble the later Europeans (Heim, 1976), and some later Europeans resemble the most extreme of the Neandertals. The comparison of La Ferrassie 1 (Fig. 7) and Krapina 59 (Fig. 8) suggests that the two ramal notch features vary independently. This is also evident in the two mandibles from Tabun (Fig. 13); the notch depth is shallower relative to the base of the condyle in mandible 2 (the "modern;" but see Quam and Smith, 1998; Stefan and Trinkaus, 1998), while its most inferior point is more posterior in mandible 1 (the Tabun "Neandertal") than more centrally located in mandible 2. Amud (Fig. 3), the other Levant "Neandertal" mandible with a complete ramus, has an even shallower ramal notch, and a very posterior position for its most inferior point.

The range of variation in these later Pleistocene samples is also found in their Middle Pleistocene forebears. This is certainly the case for the Atapuerca SH mandibles, whose nonmetric variation resembles the Neandertals in great detail (Rosas, 2001). In earlier *Homo*, some mandibles attributed to *"Homo erectus"* have a centrally placed, deep notch as Rak et al. (2003) ascribed to this taxon and also to modern *Homo sapiens*: an example is the Turkana juvenile WT ER-15000 (Fig. 14). However, Mauer (Fig. 15) has a posteriorly placed, very shal-

low notch, and Ternifine 3 (Fig. 16) has a posteriorly placed, deep notch with a high coronoid process.

Thus, the so-called Neandertal autapomorphic condition of a shallow ramal notch with a posterior position for its lowest point is found in populations preceding the Neandertals and in those following them, and in each of these three samples (as well as Atapuerca), the so-called Neandertal autapomorphic condition is part of a much larger range of variation. We do not contend that these samples are the same in the mean expression of the two traits, but rather that the Neandertals are neither homogeneous nor unique, and their notch anatomy cannot be considered an autapomorphy.

A third feature proposed as unique in Neandertals is the manner in which the notch crest reaches the condyle (Fig. 1). In recent *Homo sapiens*, the common pattern is for the crest to join the condyle at its most lateral aspect, as Rak (1998) described. Rak

(1998) proposed that in Neandertals, this crest reaches the condyle in a centrally located position (Fig. 1). However, Trinkaus (1995) noted that relative to the articular head, there is not a clear distinction between Neandertals and subsequent populations, and Jabbour et al. (2002) and others showed that while the more central position of the crest is more common in Neandertals, it is not difficult to find Neandertal specimens that show (what Rak (1998) described as) the "modern" morphology. In our seriation, we noted that the lateral placement typifies Vindija 226, La Quina 9, and one side of Zaffaraya 2, where the notch crest joins the condyle at its outside edge. Others such as La Ferrassie 1 are intermediate in this anatomical character, and some Neandertal mandibles are indeed as Rak (1998) described. The point is that the Neandertals are not monomorphic for this feature, and it cannot be considered a Neandertal autapomorphy, both be-
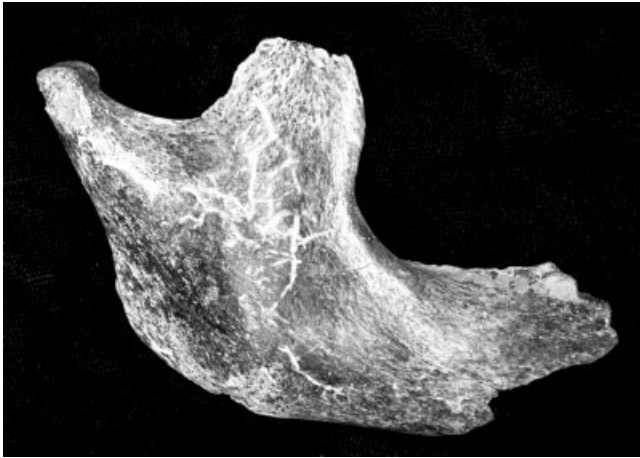
Fig. 11. Vindija 207, an Aurignacian-associated mandible with a shallow ramal notch, at level of the lower lateral condylar border, and a centrally placed most inferior point.


Fig. 12. Stetten 1, an Aurignacian-associated mandible, has a moderately deep, posteriorly located ramal notch and a high coronoid process.
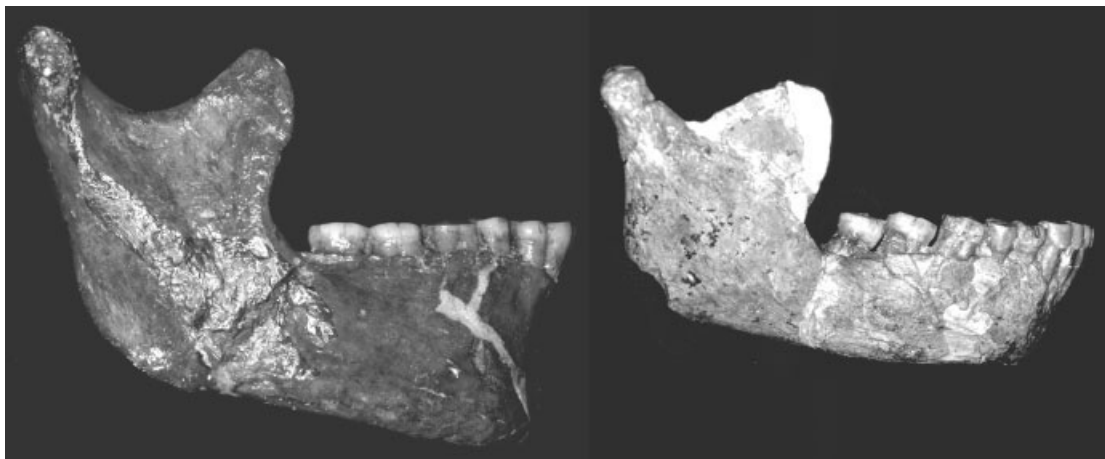
Fig. 13. Two mandibles from Tabun, 2 (left) and 1 (right), have many similar ramal features, including some not discussed in this paper, such as the expression of medial pterygoid tubercle, the retromolar space between the last molar and the anterior ramus edge, and shape of that edge. The ramal notch in Tabun 1 is deeper, but more posteriorly located. While many regard Tabun 1 as Neandertal and Tabun 2 as early "modern," we do not believe either description is necessarily correct, and further suggest that their comparison does not reflect idealized patterns in Figure 1. Specimens are shown at same approximate size; note the missing condylar head of Tabun 2.

Fig. 14. Cast of WT ER-15000, a juvenile with a dental age of 10–11 years that is the earliest of mandibles discussed here. Its ramus anatomy is similar to that found in later specimens, some Neandertal and some not.
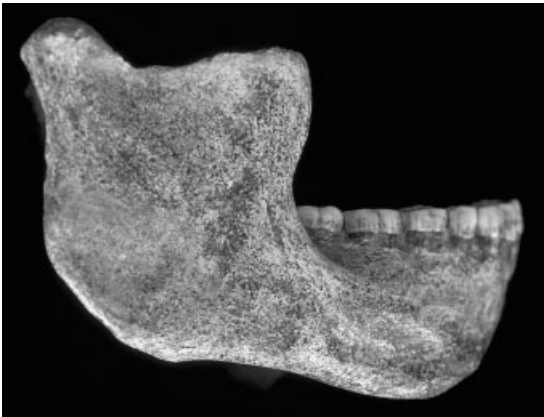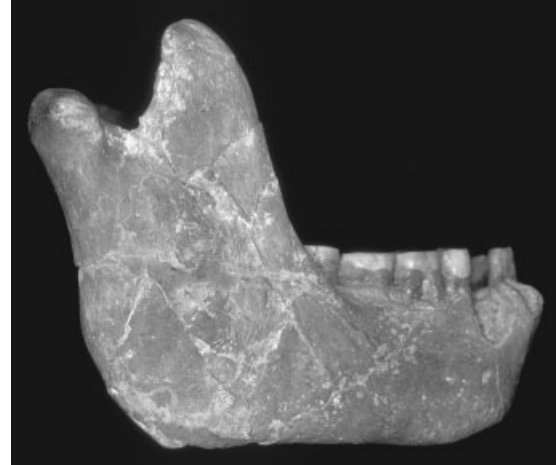

Fig. 15. Mauer has a very shallow, broad, ramal notch, with a difficult-to-define inferior point that appears to be in a posterior position.
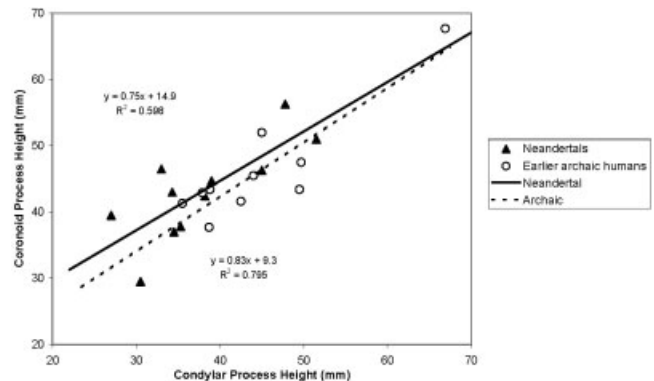

Fig. 16. Ternifine 3 is a mandible with a very tall ramus and a deep, posteriorly located ramal notch. The coronoid process is absolutely tall, and relatively tall compared with the condylar height, as it is in Regourdou (Fig. 2) and Stetten 1 (Fig. 12).

Fig. 17. Condylar and coronoid heights above the alveolar plane and perpendicular to it for archaic humans and Neandertals with both structures preserved (measurements in millimeters). We note that the condyles of several of 11 Neandertal mandibles (e.g., La Ferrassie in Fig. 7 and Krapina 59 in Fig. 8) have been flattened with osteoarthritis, and direct measurement from the alveolar margin to the top of the condyle is less than it would have been before this pathological alteration. Neandertal specimens are: Amud 1, Krapina 59, La Chaise BD-1, La Ferrassie, La Quina 5, Le Moustier, Montmaurin, Regourdou, Shanidar 1 and 2, and Tabun 1. The earlier archaic human sample includes: Arago 2 and 13, Dmanisi 2600 and juvenile 2735, juvenile ER 15K, Mauer, Ternifine 2 and 3, and Zhoukoudian G1 and H1. "Neandertal" and "earlier archaic human" are used here as descriptive terms; neither of these designations is meant as a valid taxonomic representation of the specimens listed, and neither describe nor reflect the validity of taxa.

cause of Neandertal variation and because all of the Neandertal variants are fount in recent and living humans (Jabbour et al., 2002, contra Stefan and Trinkaus, 1998, their Table 2).

A similar range of variation occurs in earlier archaic hominids, where the position that the notch crest reaches the condyle also ranges from central in Ternifine 2 to lateral in Mauer and ER WT-15000. We assume that this range of differing character states is the ancestral condition.

Finally, according to Rak et al. (2003, p. 202–203), the height of the condyle "governs the Neandertal ramus morphology," while the "coronoid process appears to be situated at approximately the same height in Neandertals and other hominids." Inspection of Figures 2–8 suggests that this assessment may not be accurate. To examine the question systematically, we measured the perpendicular height of these processes above the horizontally positioned alveolar margin. The measurement was taken from the alveolar margin and not the occlusal plane, because we wanted to avoid the effects of occlusal wear and include specimens with teeth lost postmortem. Still, a few specimens were affected by degenerative

joint disease (La Ferrassie 1, Krapina 59), and we did not include specimens such as La Chapelle-aux-Saints where premortem tooth loss resulted in periodontal resorption and a great reduction of corpus height. All measurements were taken on the original specimens except for Zhoukoudian G1 and H1, for which the originals no longer exist (cast measurements were used), and the Dmanisi mandibles that were measured from scaled photographs (Gabounia et al., 2002; Vekua et al., 2002).

In Figure 17, we show these heights for the 11

Neandertal and 10 earlier archaic human mandibles preserving the anatomy, in a bivariate plot of condylar and coronoid heights above the alveolar plane. The Neandertals do not stand apart from the earlier archaic humans, as the hypothesis of increasing Neandertal specializations predicts. The two distributions are mixed. This is evident from visual inspection and can be demonstrated in several other ways. For us, the most straightforward is the fact that the least mean square (LMS) slopes for the two distributions are quite similar and are within one standard error of each other: the LMS slope and standard errors for the Neandertal and archaic human samples are, respectively, 0.75 ± 0.22 and 0.83 ± 0.17. Moreover, these samples do not differ in the magnitude of the height of the condylar process, nor is there any other systematic difference in the relation of condylar and coronoid heights as reflected in these measurements. Neandertal ramal anatomy, in other words, does not set Neandertals apart from their ancestors.

The question we have addressed is not whether Neandertal ramal features differ from other samples; all populations vary and have their unique aspects, whether in unusual anatomies or in differing frequencies of anatomical variants. The question is whether Neandertals differ in a way that could be used to support the notion that they are a distinct clade, evolving for whatever reason in their own unique direction. Are there, in the words of Weidenreich (1943) cited above, "peculiarities which could be claimed as 'specialization,' thereby proving the deviating course this form has taken in evolution"? We believe the answer is no. The "distinctive" mandibular ramus features discussed here are not Neandertal autapomorphies. They are neither limited in their range of expression within Neandertals (to the contrary, Neandertals are at least as variable as other human samples) nor are they unique to Neandertals, since they appear in populations predating and postdating them. Weidenreich (1943) remains correct: Neandertals cannot be described as a divergent group, with restricted variation in unique features ("peculiarities") that reflect increased specialization over time (Hawks and Wolpoff, 2001). These ramal features are not useful in decisions about taxonomic placement (what is and what is not a Neandertal), and cannot be used to reject models of continuity or to designate Neandertals as a valid species apart from the rest of humanity. Rather than reflecting restricted variation and increased specialization, these features further elucidate what is already known from other studies of the anatomy and genetics of later Pleistocene hominids: the range of human variation in the recent past encompasses and in some cases exceeds human variation today, in spite of today's immensely larger population numbers (Hawks and Wolpoff, 2003).

LITERATURE CITED

Arensburg B, Belfer-Cohen A. 1998. Sapiens and Neandertals. In: Akazawa T, Aoki K, Bar-Yosef O, editors. Neandertals and modern humans in Western Asia. New York: Plenum Press. p 311–322.

Frayer DW. 1992. Evolution at the European edge: Neanderthal and Upper Paleolithic relationships. Prehist Eur 2:9–69.

Gabounia L, de Lumley M-A, Vekua A, Lordikipanze D, de Lumley H. 2002. Découverte d'un nouvele hominidé à Dmanissi (Transcaucasie, Géorgie). C R Palevol 1:243–253.

Hawks J, Wolpoff MH. 2001.The accretion model of Neandertal evolution. Evolution 55:1474–1485.

Hawks J, Wolpoff MH. 2003. Sixty years of modern human origins in the American Anthropological Association. Am Anthropol 105:87–98.

Heim J-L. 1976. Les hommes fossiles de La Ferrassie. Tome I. Le gisement. Les squelettes d'adultes: crâne et squelette du tronc. Arch Inst Paleontol Hum Mem 35:1–331.

Heim J-L. 1989. La nouvelle reconstitution du crâne Néandertalien de La Chapelle-aux-Saints: méthode et résultats. Bull Mem Soc Anthropol Paris New Ser 1:95–118.

Jabbour RS, Richards GD, Anderson JY. 2002. Mandibular condyle traits in Neanderthals and other *Homo*: a comparative, correlative, and ontogenetic study. Am J Phys Anthropol 119:144–155.

Mann AE, Lampl M, Monge J. 1990. Décomptes de périkmaties chez les enfants Néandertaliens de Krapina. Bull Mem Soc Anthropol Paris New Ser 2:213–220.

Mann AE, Monge J, Lampl M, Radovčić J. 2003. Patterns of crown variation in Neandertals and modern humans. In: Brůžek J, Vandermeersch B, Dolores Garralda M, editors. Changements biologiques et culturels en Europe de la fin du Paléolithique Moyen au Néolithique. Hommage à Jan Jelínek. Prague: Repro Služby. p 61–74.

Quam RM, Smith FH. 1998. A reassessment of the Tabun C2 mandible. In: Akazawa T, Aoki K, Bar-Yosef O, editors. Neandertals and modern humans in Western Asia. New York: Plenum Press. p 405–421.

Rak Y. 1998. Does any Mousterian cave present evidence of two hominid species? In: Akazawa T, Aoki K, Bar-Yosef O, editors. Neandertals and modern humans in Western Asia. New York: Plenum Press. p 353–366.

Rak Y, Ginzburg A, Geffen E. 2003. Does *Homo neanderthalensis* play a role in modern human ancestry? The mandibular evidence. Am J Phys Anthropol 119:199–204.

Rosas A. 2001. Occurrence of Neanderthal features in mandibles from the Atapuerca-SH site. Am J Phys Anthropol 114:74–91.

Schwartz JH, Tattersall I. 2000. The human chin revisited: what is it and who has it? J Hum Evol 38:367–409

Smith FH. 1978. The evolutionary significance of the mandibular foramen area in Neanderthals. Am J Phys Anthropol 48:523–531.

Stefan VH, Trinkaus E. 1998. Discrete trait and dental morphometric affinities of the Tabun 2 mandible. J Hum Evol 34:443–468

Stringer CB, Hublin J-J, Vandermeersch B. 1984. The origin of anatomically modern humans in Western Europe. In: Smith FH, Spencer F, editors. The origins of modern humans: a world survey of the fossil evidence. New York: Alan R. Liss, Inc. p 51–135.

Trinkaus E. 1993. Variability in the position of the mandibular mental foramen and the identification of Neandertal apomorphies. Rivista di Antropologia (Roma) 71:259–274.

Trinkaus E. 1995. Near Eastern late archaic humans. Paleorient 21:9–23.

Vekua A, Lordkipanidze D, Rightmire GP, Agusti J, Ferring R, Maisuradze G, Mouskhelishvili A, Nioradze M, Ponce de León MS, Tappen M, Tvalchrelidze M, Zollikofer CPE. 2002. A new skull of early *Homo* from Dmanisi, Georgia. Science 297:85–89.

Weidenreich F. 1943. The "Neanderthal man" and the ancestors of "*Homo sapiens*." Am Anthropol 45:39–48.

Wolpoff MH, Caspari R. 1996. An unparalleled parallelism. Anthropol (Brno) 34:215–223.

Wolpoff MH, Hawks J, Frayer DW, Hunley K. 2001. Modern human ancestry at the peripheries: A test of the replacement theory. Science 291:293–297.