Comparative morphology and paleobiology of Middle Pleistocene human remains from the Bau de l'Aubesier, Vaucluse, France

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The discovery of later Middle Pleistocene human remains from the Bau de l'Aubesier, France reinforces an evolutionary model of the gradual accumulation of Neandertal-derived facial and dental features during the Middle Pleistocene of the northwestern Old World. The pronounced maxillary incisor beveling of Aubesier 4 helps to extend the antiquity of nondietary use of the anterior dentition. The interproximal "toothpick" groove on the Aubesier 10 molar increases the sample for these lesions. The pathological loss of the mandibular dentition of Aubesier 11 indicates advanced antemortem masticatory impairment, at a level previously undocumented before the Late Pleistocene. These remains support a view of later Middle Pleistocene humans able to support debilitated individuals despite the considerable use of their bodies to accomplish routine activities.

human paleontology | paleopathology | Neandertals | Archaic *Homo* | Europe

In 1975, the paleoanthropological record of the Middle Pleistocene was referred to as the "muddle in the middle" (1). Since that time, there have been major advances in our knowledge and perception of human biocultural evolution during the Middle Pleistocene. It has become increasingly recognized as the period in human evolution during which several important aspects of human biology and behavior evolved, including (among others) exaggerated encephalization, the controlled use of fire, temperate zone geographic dispersals, varieties of prepared core lithic reduction techniques, the development of effective (predatory and defensive) weaponry, and regional differentiation of human populations. At the same time, however, our paleoanthropological record for this period remains incomplete, and significant additions to it have the potential to enlighten further our perceptions of human evolutionary patterns.

In the context of this research, recent discoveries of later Middle Pleistocene human remains at the Bau de l'Aubesier in southeastern France, although limited anatomically, contribute to our perceptions of these later archaic humans. They provide additional information relevant to the regional differentiation of human populations during the Middle Pleistocene and the paleobiological patterns of these archaic human groups. In particular, it has been argued that there was a gradual evolution of a derived Neandertal morphological pattern through the Middle Pleistocene in Europe and that this represents a period of relative lineage stability combined with some degree of genetic isolation from other archaic human regional lineages in the cul-de-sac of Europe (2, 3). It also has been noted that few

of these Middle Pleistocene human remains exhibit serious pathological lesions (4, 5).

The Bau de L'Aubesier

The Bau de l'Aubesier is a large rock shelter in the Gorges de la Nesque, Monieux, Vaucluse, France (44° 05′ N, 5° 21′ E). Although previously investigated (6, 7), S.L. has excavated the site since 1987 and discovered Middle Pleistocene human remains in 1994 and 2000.

The upper portion of the Pleistocene deposits (13 m thick over >520 m²) consists principally of Late Pleistocene levels containing Middle Paleolithic archeological remains (Fig. 1). The lower portion of the site, with a thickness > 10 m, derives primarily from the Middle Pleistocene (levels G to K). Its succession of stratified deposits containing limestone éboulis, blocks, and slabs is interspersed with a nonsystematic matrix of fine interstitial calcareous sediment, much of which is brecciated in layer G. The archeological layer H-1, 55 cm thick, consists of a high density of faunal remains, lithics, wood charcoal, and ash in a highly organic sediment, and the lithics and faunal remains are burnt to different degrees. On the basis of the lithostratigraphy, there appears to have been a chronological hiatus between layer H-1 and the underlying I series.

The layers with human remains, I-2, I-3, and K-1, yielded high concentrations of large herbivore remains and flint artifacts, each a palimpsest of repeated phases of site occupation. Their lithic assemblages are typical Mousterian with abundant side-scrapers, Levallois flakes, and especially Levallois blades, similar to those from a growing number of late Middle Pleistocene Middle Paleolithic site levels containing laminar assemblages (8).

The fauna of level I includes *Ursus arctos*, *Dicerorhinus hemitoechus*, *Equus mosbachensis*, *Sus scrofa*, *Cervus elaphus*, *Dama dama*, *Capreolus capreolus*, *Megaceros giganteus*, *Bos primigenius*, *Hemitragus cedrensis*, and *Rupicapra rupicapra*, with *Bos* (43%) and *Equus* (31%) dominating. Well recognized in the Middle Pleistocene, *E. mosbachensis* in particular indicates an age no later than oxygen isotope stage (OIS) 6 (9); it is succeeded by *E. cf. taubachensis* in the overlying layer H-1, which could refer it to OIS 5e (9). The form of *C. elaphus* can be assigned to OIS
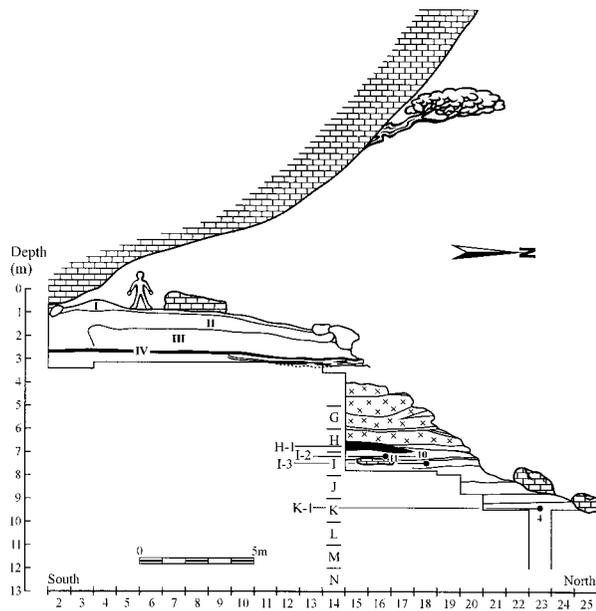
ANTHROPOLOGY

Fig. 1. Stratigraphic profile of the Bau de l'Aubesier. The positions of the Aubesier 4, 10, and 11 are indicated, as well as the H-1 black combustion horizon.

6. *D. dama* is present from level J and higher, indicating a post-Holsteinian (post-OIS 9 or 11) age for these levels (9). *H. cedrensis* corresponds to an age in OIS 7, 6, or 5e (9).

Thermoluminescence dating was performed on six heated flint samples from layer H-1, following the experimental procedures previously described (10, 11). To evaluate the external γ-dose rate, because it contributes $\approx$50% to the total accumulated dose, five $CaSO_4$ dosimeters were implanted in the same or adjacent squares for 1 year, and α- and γ-spectrometry was performed in the laboratory on samples of the fine component of the sediment. In principle, the results obtained with dosimeters reflect the actual environmental γ-dose rate more accurately, because the sediment is a mixture of large and small components. However, the γ-spectrometry revealed the presence of a disequilibrium in the ^{238}U decay chain, and the α-spectrometry indicated the loss of ^{226}Ra. Therefore, the external γ-dose rate, as measured with the dosimeters, might not have been true for the entire period of burial in the site. Two models have to be used to allow the calculation of minimum and maximum age estimates for layer H-1, because the timing of the (re-)occurrence(s) of the disequilibrium cannot be established. The minimum age is determined assuming the occurrence of a single, recent ^{226}Ra loss. The external γ-dose rate is thus calculated on basis of the concentration of ^{230}Th (full natural uranium chain) and corrected for the relative contribution of the fine sediment to the total external γ-dose rate from all components. Assuming a constant loss of ^{226}Ra since deposition, the maximum age can be calculated by using the external γ-dose rate as measured by the dosimeters.

The results of the two models for the six samples give an average minimum age estimate of 169 ± 17 thousand years (ka) and an average maximum one of 191 ± 15 ka for layer H-1. Using the 2-σ range of these age estimates, the flint samples were heated either in OIS 6 or 7. The biostratigraphic indicators for layer H-1 are somewhat younger than these results. The human remains from layer I2, I-3, and K-1 derive from slightly deeper in the stratigraphic sequence than later H-1, and they therefore date to the later Middle Pleistocene.

Fig. 2. Middle Pleistocene human dental remains from the Bau de l'Aubesier. From left to right: Aubesier 4 I^2 lingual, Aubesier 4 I^2 distal, Aubesier 10 M^{1-2} mesial, Aubesier 10 M^{1-2} distal. Scale in mm.

Materials

The Bau de l'Aubesier has yielded two series of human remains. From the Late Pleistocene Middle Paleolithic level IV, there are eight isolated deciduous and permanent teeth, which derive from Neandertals (12–15). These teeth are notable relative to other Neandertals by the modest dimensions of the permanent teeth, their dearth of hypoplastic lesions, and the presence of caries on two of them. The second series consists of two isolated teeth (Aubesier 4 and 10) and a mature mandible (Aubesier 11) from the Middle Pleistocene layers K-1, I-3, and I-2, respectively. It is these latter remains that are of concern here.

Aubesier 4 consists of most of the crown and root of a moderately worn left I^2, and Aubesier 10 is a slightly worn right M^1 or M^2 with minimal marginal postmortem erosion (Fig. 2). The Aubesier 11 mandible (Figs. 3–5) is largely complete from the left C_1 alveolus to the right condylar margins, but it has lost most of the coronoid process and sustained minor damage to the symphysis and the right gonial region. There is little damage to
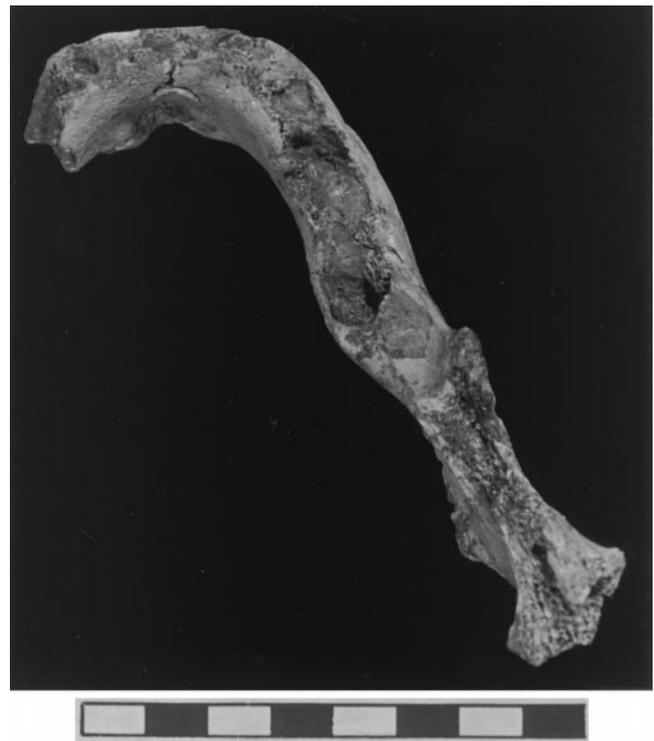

Fig. 3. Aubesier 11 mandible in superior view. Scale in cm.

Lebel *et al.*

Fig. 4. Aubesier 11 mandible in *norma lateralis* right. Scale in cm.

Table 1. Comparative dental labiolingual and buccolingual crown diameters (in mm) of the Aubesier 4 and 10 teeth, plus the means ± standard deviations (*N*) for samples of Middle and Late Pleistocene archaic *Homo*

Specimens and samples	I^2 Labiolingual	M^1 Buccolingual	M^2 Buccolingual
Aubesier 4 I^2	8.6		
Aubesier 10 $M^{1–2}$		12.0	12.0
Europe 300–500 ka	8.0 ± 0.3 (4)	12.4 ± 1.2 (9)	13.2 ± 1.3 (9)
Pre-Neandertals (300–100 ka)	8.5 ± 0.9 (20)	12.3 ± 0.9 (14)	12.7 ± 0.8 (14)
Neandertals (100–28 ka)	8.1 ± 0.7 (29)	12.0 ± 0.8 (32)	12.4 ± 1.1 (24)

Comparative data from primary descriptions of the original remains or personal measurements of the fossils are shown.

the alveoli or the remainder of the corpus; the only teeth remaining are the apices of the right C_1 and P_3 roots.

Based on dental wear compared with other Neandertal lineage specimens, it is likely that Aubesier 4 and 10 represent prime age adults. The age at death of Aubesier 11, although fully mature, is less certain; the advanced tooth loss and alveolar lesions, if associated with extensive antemortem dental attrition, could indicate an advanced age at death.

The Aubesier 4, 10, and 11 remains are compared principally to those of northwestern Old World (European and Near Eastern) temporal groups of archaic *Homo*. These have been divided into three temporal samples, during which the Neandertal morphological pattern emerged in this region. The first consists of remains between ≈500 and ≈300 ka B.P., the second of remains from between ≈300 and ≈100 ka B.P., and the third of Neandertals between ≈100 and ≈28 ka B.P. The first two samples are dominated by the large samples from Atapuerca–Sima de los Huesos (AT-SH) and Krapina respectively. Limited additional data are included for African Middle Pleistocene mandibles. Mandibular comparisons are limited to late adolescent and mature specimens.

Morphological Affinities of the Aubesier Human Remains

The Aubesier 4 I^2 (13) is notable for its labial bi-convexity and pronounced shoveling. The crown exhibits strongly marked marginal ridges corresponding to grade 6 shoveling of the Arizona State University Dental Anthropology System (ASUDAS) scale (16). These ridges meet lingually at an ASUDAS grade 5 tuberculum dentale. Labially, the tooth is

Fig. 5. Aubesier 11 mandibular alveolar arcade showing alveolar resorption, anterior apical abscesses, antemortem loss of the M_2, and worn root apices of the C_1 and P_3. Scale in cm.

strongly convex mesiodistally and superoinferiorly. The mesiodistal convexity is ASUDAS grade 4. This combination of strong shovel shape with a lingual tubercle and labial bi-convexity is a characteristic of Neandertal incisors and those of their Middle Pleistocene predecessors (17, 18). Although each of these characters can be found to some degree in other *Homo* samples, their combined presence appears to be unique to the Neandertal lineage (18). The Aubesier 4 labiolingual diameter (Table 1) is large for a later archaic *Homo*, being matched only by a few Neandertals and the relatively megadont Krapina sample.

The Aubesier 10 M^1 or M^2 crown presents little of morphological note, and its buccolingual diameter is well within the ranges of variation of later Neandertal lineage samples (Table 1). Its roots, however, exhibit marked taurodontism; the three roots are almost completely bridged and fused, such that the distances between the cervix and the clefts between the adjacent roots are 72.7%, 75.3%, and 79.2% of the maximum height of the root. Taurodontism has long been noted for many, but not all, Neandertals and their predecessors (19, 20). The degree of development of this feature in Aubesier 10 is exceptional even compared with most Neandertal lineage teeth (17, 21), but it matches the degree of taurodontism found in high frequency especially in the terminal Middle Pleistocene Krapina sample (22).

The Aubesier 11 mandible presents a suite of characteristics that align it with late Middle Pleistocene members of the Neandertal lineage. Many of these features are associated with the emergence of midfacial prognathism, or the posterior movement of the lateral facial skeleton in the context of maintained anterior positioning of the midfacial (nasal and alveolar) region (23–25). Metric comparisons of the mandible are limited by its pathological alterations (see below), but the combination of characters preserved serves as a discrete trait reflection of overall mandibular proportions. Although many of these features have been considered to be Neandertal autapomorphies (26), they occur within other hominid samples and are variably present within the Neandertal lineage; it is their higher frequency in the later Neandertal lineage, rather than their presence, which appears to be distinctive (24, 25, 27, 28).

From anterior to posterior, Aubesier 11 exhibits a strongly retreating rounded anterior mandibular symphysis, the incipient presence of a mental trigone, a modest *planum alveolare*, an inferior lingual torus, the mental foramen at the level of the P_4/M_1 interdental septum extending to the M_1, the anterior marginal tubercle at P_4/M_1, a distinctive retromolar space in *norma lateralis*, the absence of lingular (horizontal-oval) mandibular foramen bridging, a prominent superior medial pterygoid tubercle, and an intersection of the mandibular notch crest with the middle third of the mandibular condyle.

Two of these features, the anterior symphyseal profile and the lingual torus, are plesiomorphous features and largely serve to distinguish Aubesier 11 from the majority of the later Neandertals. The lateral corpus, as best as can be estimated from the pathological condition of the specimen, appears to be relatively short and broad, in contrast to the higher and thinner ones of last glacial Neandertals. The absence of a lingular bridging of the mandibular foramen is an ancestral configuration (29), but it is found in approximately half of the more recent Neandertal lineage specimens (Table 2). The moderately posterior positions of the mental foramen and the anterior marginal tubercle relative to the dentition and the presence of a retromolar space align Aubesier 11 with the majority of the Neandertal lineage remains and separate it from the more anterior relative positions of these features in earlier African specimens; all three reflect midfacial prognathism (24, 26, 27). The hypertrophy of the superior medial pterygoid insertion on the posterior medial ramus, as reflected in its prominent tubercle, and the intersection of the mandibular notch crest with the middle third of the condyle also align Aubesier 11 with the Neandertal lineage, although their biological implications are less apparent. Indeed, except for a difference in retromolar space presence, Aubesier 11 is remarkably similar to the OIS 6 La Niche (Montmaurin) 1 mandible (30, 31).

These considerations therefore indicate that the Aubesier 4, 10, and 11 later Middle Pleistocene human remains are all fully compatible with, and reinforce the existence of, the emergence of a Neandertal craniofacial morphological during the second half of the Middle Pleistocene in the northwestern Old World. The I^2 crown, the M^{1-2} root, and the mandibular lateral corpus and ramus all exhibit features that are observed in their highest frequency in the late Middle and early Late Pleistocene archaic *Homo* of the northwestern Old World.

Paleobiological Aspects of the Aubesier Human Remains

The Aubesier 4 I^2 is notable for the high degree of beveling of its occlusal wear. Its beveling angle of 91° [measured between the occlusal plane and the chord joining its labial midline cervical and occlusal margins (32)] is associated with a wear quotient of 0.82 (labial chord/cervical labiolingual diameter). This beveling angle is elevated compared with recent humans with similar degrees of occlusal attrition, and it is high even relative to values for Krapina and last glacial Neandertal anterior maxillary teeth (33). It implies a pattern of attrition, and hence use, of the anterior dentition similar to that of recent humans and Neandertals but at least as pronounced as that which leads to the labially open incisor occlusion in older Neandertals. The reasonably well-preserved labial surface of the crown does not exhibit distinctive transverse scratches, such as would be made by a lithic implement.

The Aubesier 10 M^{1-2} exhibits a clear mesial interproximal "toothpick" groove [or abrasive noncarious cervical lesion (34)], broadest (2.3 mm) at its lingual end and tapering off buccally. It is shallow and polished, has sharp margins, and exhibits fine buccolingual wear striae within it. Such interproximal grooves have long been documented for Neandertals (35), occur in the Krapina and AT-SH samples (36, 37), and extend through the genus *Homo* (38). Aubesier 10 further documents this pattern among these archaic humans. Neither Aubesier 4 nor 10 exhibits any developmental or degenerative alterations of the crown or roots.

The Aubesier 11 mandible is exceptional for its degree of pathological alteration of the alveolar bone (Figs. 3–5). The lingual corpus bone is largely intact from the symphysis to the right M_1, with minor alveolar resorption along portions of it. However, nowhere along its preserved length does the labial or buccal alveolar bone extend much above the apices of the dental sockets mesial of the M_2; the rounded edges of the preserved margins and the adjacent exposed trabecular bone indicate

antemortem resorption of the missing external cortical alveolar bone. The degree of external alveolar resorption had progressed to the stage that only for the left I_2 to right I_1 and the right M_1 can one discern mesiodistal concavities for the original dental sockets on the lingual side. In addition, the apices of the left I_2 and the right I_1 and I_2 sockets were enlarged radially into the underlying corpus (presumably from periapical abscesses). The right M_2 was lost antemortem, as is indicated by the bridging over of its socket. The right M_3 socket is a large, smooth-sided cavity, at least twice the diameter of the original M_3 roots, with a fenestration through the lingual alveolar bone. And finally, the apices of the right C_1 and P_3 roots are present in their sockets, but the exposed superior surfaces, ≈11 mm and ≈8 mm respectively below their adjacent lingual alveolar margins, exhibit antemortem occlusal wear. It is possible that these two teeth were broken traumatically with subsequent wear on the remaining roots; alternatively, extensive occlusal attrition may have promoted extensive alveolar resorption, and the teeth continued to wear on the remaining roots.

From this pathologically altered condition, for at least the portions of the dental arcade preserved (left C_1 to right M_3), it is likely that few, if any, of the teeth remained in functional occlusion (not counting the C_1 and P_3 root tips). Based on their lingual alveolar indications of socket margins, it is possible that the left I_2 to right I_1 and the right M_1 were in place at death, but the absence of the external alveolar bone could be attributed to extensive periodontal-endodontal lesions, whose presence would have made mastication painful and mechanically ineffectual. It is not possible to determine how long before death these abnormalities occurred, but the complete closure of the M_2 socket suggests that the process had commenced some time before death. However, the minimal alterations of the morphology of the inferior corpus and ramus from that expected for a late Middle Pleistocene European archaic human mandible suggest that the process did not greatly precede death.

Discussion

Phylogenetic Implications. It is apparent from the suite of Neandertal lineage features present in the Aubesier Middle Pleistocene human remains that they provide further evidence for the gradual emergence during the second half of the Middle Pleistocene and the early Late Pleistocene of Europe of the derived (at least in frequency) Neandertal morphological pattern. This pattern is evident in the Aubesier 4 crown morphology, the Aubesier 10 root configuration, and several features (mental foramen and anterior marginal tubercle position, retromolar space, superior medial pterygoid tubercle, and mandibular notch crest position) of the Aubesier 11 mandibular lateral corpus and ramus.

At the same time, taken in the context of the variable frequencies of all of these traits within Neandertal lineage samples and other hominids groups, plus the clear presence of this pattern by the late Middle Pleistocene and initial Late Pleistocene of western Asia (21, 25, 39), it is unlikely that the Neandertal morphological complex evolved in isolation in Europe. It is more probable that these features increased in frequency through a combination of genetic drift and isolation by distance across the northwestern Old World, as one aspect of the general regional differentiation of hominid craniofacial morphology as the genus *Homo* became increasingly geographically dispersed during the Middle Pleistocene (40).

Paleobiological Implications: The Teeth. The Aubesier 4 I^2 occlusal beveling reinforces a pattern of considerable use of the anterior dentition for nonmasticatory purposes. This degree of beveling is well documented for more recent Neandertal lineage specimens (21, 33, 41), and labial wear striae have been documented for anterior teeth from AT-SH (42), Krapina (43), and several Neandertal specimens (12, 21, 44, 45). Sufficiently worn non-

Table 2. Discrete traits of the Aubesier 11 mandible and comparative African Middle Pleistocene and Neandertal lineage Middle and Late Pleistocene archaic *Homo* samples

Aubesier 11 samples	Mental foramen at M₁	Mental foramen at P₄/M₁ or M₁	Anterior marginal tubercle at M₁	Anterior marginal tubercle at P₄/M₁ or M₁	Retromolar space present	Mandibular foramen lingular bridging	Mandibular notch crest at mid-condyle	Superior medial pterygoid tubercle
Aubesier 11	P_4/M_1-M_1	P_4/M_1-M_1	P_4/M_1	P_4/M_1	Present	Absent	Present	Present
Africa Middle Pleistocene	0.0% (7)	35.7% (7)	0.0% (5)	20.0% (5)	0.0% (6)	0.0% (4)	0.0% (3)	0.0% (3)
Europe 300–500 ka	73.3% (15)	93.3% (15)	53.3% (15)	86.7% (15)	57.1% (14)	0.0% (10)	44.4% (9)	50.0% (8)
Pre-Neandertals 300–100 ka	60.0% (10)	100% (10)	50.0% (8)	75.0% (8)	80.0% (10)	50.0% (11)	75% (4)	79.4% (7)
Neandertals 100–28 ka	53.8% (26)	92.3% (26)	45.0% (20)	65.0% (20)	74.1% (27)	42.9% (21)	37.5% (16)	81.3% (16)

Comparative data from primary descriptions of the original remains or personal observations of the originals or high quality resin replicas are shown; sample sizes are in parentheses.

Lebel *et al.*

European archaic *Homo* anterior maxillary teeth are rare, but at least the African Broken Hill 1 I¹s exhibit a degree and pattern of anterior dental wear suggesting nondietary dental use similar to that seen in the European Neandertal lineage.

The mesial interproximal wear groove on Aubesier 10 appears most likely to have been produced by some form of a tool to remove debris from between the teeth, because the large adjacent interproximal facet (7.1 mm wide) reflects close approximation of the adjacent mesial tooth and would have made stripping material between the teeth difficult. The groove serves to reinforce a pattern of dental care, despite the absence of documented dental caries in Eurasia before the last glacial.

Paleobiological Implications: The Mandible. In the Aubesier 11 mandible, the combination of apical abscesses, M₃ socket enlargement and lingual fenestration, rounding of exposed trabeculae and generalized alveolar bone loss implies pervasive and active periodontal-endodontal lesions throughout the dental arcades with all of the teeth being lost antemortem or mechanically unstable at the time of death. Although Aubesier 11 was still chewing, as indicated by the C₁ and P₃ root wear, the individual's ability to masticate tough or hard food items must have been severely compromised. The probable associated pain would have further impeded the process.

Significant antemortem tooth loss is documented for last glacial Neandertals [e.g., La Chapelle-aux-Saints 1, Guattari 1, and Shanidar 5 (21, 46, 47)], and alveolar bone loss and apical abscesses are commonly noted among the Neandertals (21, 41, 47–49). However, no hominid specimen dating before the last glacial with significant antemortem masticatory impairment has been previously documented. Broken Hill 1 experienced dental caries and tooth loss (50), but retained sufficient occlusal surface for mastication. The AT-SH 700/888 skull (AT-SH cranium 5 and mandible) sustained maxillary and mandibular dental apical abscesses and associated maxillary lesions after dental trauma, but without apparent dental loss (4). Arago 21 lost a P⁴ antemortem (51), and Ehringsdorf 6 exhibits anterior alveolar lesions and resorption (52).

Aubesier 11 is therefore unique among Middle Pleistocene (or earlier) hominids in its degree of antemortem masticatory impairment. This reduction in the ability to chew food implies significant behavioral adjustment to maintain Aubesier 11 alive for some period. This behavior could have involved selective allocation of softer food items, extensive manual preparation of food, and/or extensive cooking of food. Evidence for fire in the Middle Pleistocene of Europe before ≈150 ka B.P. is scattered and scarce. It consists mostly of evidence of burned bones and charcoal within archeological levels, with only scarce evidence for constructed hearths (53–57). Significant evidence for the concentrated use of fire comes in particular from layer H-1 of the Bau de l'Aubesier, the "black combustion horizon" overlying the hominid layers yielding Aubesier 10 and 11. It contains an abundance of charcoal, burnt bones, heated lithics, and other archeological remains, but there is no evidence of constructed hearths. It is therefore apparent that the ability to make and maintain fire was present around the time of Aubesier 11, but the degree to which it was closely controlled and used for culinary activities, as opposed to thermoregulation and illumination, remains uncertain at present.

Paleontological cases of serious lesions are rare among Middle Pleistocene (and earlier) human remains. In the Middle Pleistocene, the Salé 1 cranium exhibits evidence of a congenital torticollis (58), the Berg Aukas 1 femur had abnormal development of the hip region (59), and the Singa 1 cranium exhibits biparietal diploic expansion and unilateral labyrinthine ossification (60). Among the Neandertals, Shanidar 1 persisted through multiple traumatic injuries and hyperostotic disease (21, 61), whereas other Neandertals experienced varying degrees of

ANTHROPOLOGY

traumatic and degenerative lesions (47, 62), in addition to alveolar ones. Aubesier 11 is therefore not unique but remains unusual for a Middle Pleistocene human in its degree of impairment of a vital function.

Combined with other evidence of the survival of pathological individuals during the Middle Pleistocene, the Aubesier 11 lesions provide support for an important social component in the persistence of individuals during this time period. At the same time, the nondietary use of the anterior dentition, combined with pronounced appendicular hypertrophy (63–66), indicates that these Middle Pleistocene humans were using their bodies extensively to accomplish routine activities, albeit technologically aided in so doing.

Summary

The Aubesier 4, 10, and 11 human remains therefore provide further support for the gradual increase in frequency of derived Neandertal features in the northwestern Old World during the Middle Pleistocene, most likely as a product of isolation by distance from contemporaneous Africa and eastern Asian human populations. At the same time, these remains reinforce several paleobiological aspects of these human populations, including their frequent nondietary use of the anterior dentition and the prolonged survival of individuals with serious impairments. These human populations therefore had achieved a level of sociocultural elaboration sufficient to maintain debilitated individuals and to provide the motivation to do so. However, they also were using their biology to accomplish daily activities, reflecting behavioral patterns and a level of technological development significantly different from those of Upper Paleolithic and recent humans.

1. Butzer, K. W. & Isaac, G. L. (1975) *After the Australopithecines* (Mouton, The Hague, The Netherlands).
2. Trinkaus, E. (1982) in *The Transition from the Lower to Middle Palaeolithic and the Origin of Modern Man*, British Archaeological Reports S151, ed. Ronen, A. (British Archaeological Reports, Oxford, U.K.), pp. 301–314.
3. Stringer, C. B. & Hublin, J. J. (1999) *J. Hum. Evol.* **37,** 873–877.
4. Pérez, P. J., Gracia, A., Martínez, I. & Arsuaga, J. L. (1997) *J. Hum. Evol.* **33,** 409–421.
5. Trinkaus, E., Formicola, V., Svoboda, J., Hillson, S. W. & Holliday, T. W. (2001) *J. Archaeol. Sci.*, in press.
6. Moulin, F. (1904) *Bull. Soc. Préhist. France* **1,** 14–20.
7. de Lumley, H. (1969) *Gallia Préhist. Suppl.* **5,** 1–463.
8. Bar-Yosef, O. & Kuhn, S. L. (1999) *Am. Anthropol.* **101,** 322–338.
9. Guérin, C. & Patou-Mathis, M., eds. (1996) *Les Grands Mammifères Plio-Pléistocènes d'Europe* (Masson, Paris).
10. Aitken, M. J. (1985) *Thermoluminescence Dating* (Academic, London).
11. Mercier, N., Valladas, H., Valladas, G., Reyss, J. L., Jelinek, A., Meignen, L. & Joron, J. L. (1995) *J. Archaeol. Sci.* **22,** 495–509.
12. de Lumley, M. A. (1973) *Etud. Quatern.* **2,** 1–626.
13. Trinkaus, E., Lebel, S. & Bailey, S. E. (2000) *Bull. Mém. Soc. Anthropol. Paris* **12,** 207–226.
14. Trinkaus, E., Smith, R. J. & Lebel, S. (2000) *J. Archaeol. Sci.* **27,** 1017–1021.
15. Lebel, S. & Trinkaus, E. (2001) *J. Archaeol. Sci.*, in press.
16. Turner, C., Nichol, C. & Scott, G. (1991) in *Advances in Dental Anthropology*, eds. Kelley, M. & Larsen, C. S. (Wiley–Liss, New York), pp. 13–31.
17. Patte, E. (1962) *La Dentition des Néanderthaliens* (Masson, Paris).
18. Crummett, T. (1995) in *Aspects of Dental Biology: Palaeontology, Anthropology, and Evolution*, ed. Moggi-Cecchi, J. (International Institute for the Study of Man, Florence, Italy), pp. 305–313.
19. Gorjanović-Kramberger, D. (1906) *Der Diluviale Mencsh von Krapina in Kroatien* (C. W. Kneidel, Wiesbaden, Germany).
20. Keith, A. (1915) *The Antiquity of Man* (Williams and Norgate, London).
21. Trinkaus, E. (1983) *The Shanidar Neandertals* (Academic, New York).
22. Kallay, J. (1970) in *Krapina 1899–1969*, ed. Malez, M. (Jugoslavenske Akademije Znanosti i Umjetnosti, Zagreb, Croatia), pp. 165–176.
23. Trinkaus, E. (1987) *J. Hum. Evol.* **16,** 429–443.
24. Franciscus, R. G. & Trinkaus, E. (1995) *J. Hum. Evol.* **28,** 577–595.
25. Stefan, V. H. & Trinkaus, E. (1998) *J. Hum. Evol.* **34,** 443–468.
26. Rosas, A. (2001) *Am. J. Phys. Anthropol.* **114,** 74–91.
27. Trinkaus, E. (1993) *Riv. Antropol. (Rome)* **71,** 259–274.
28. Stefan, V. H. & Trinkaus, E. (1998) *Bull. Mém. Soc. Anthropol. Paris* **10,** 293–324.
29. Smith, F. H. (1978) *Am. J. Phys. Anthropol.* **48,** 523–532.
30. Billy, G. & Vallois, H. V. (1977) *L'Anthropologie* **81,** 273–312.
31. Tavoso, A., Crégut-Bonnoure, E., Guérin, C., Pernaud-Orliac, J. & Cammas, R. (1990) *C. R. Acad. Sci. Paris* **310,** 95–100.
32. Ungar, P. S. & Grine, F. E. (1991) *J. Hum. Evol.* **20,** 313–340.
33. Ungar, P. S., Fennell, K. J., Gordon, K. & Trinkaus, E. (1997) *J. Hum. Evol.* **32,** 407–421.
34. Levitch, L. C., Bader, J. D., Shugars, D. A. & Heymann, H. O. (1994) *J. Dent.* **22,** 195–207.
35. Siffre, A. (1911) *Bull. Soc. Préhist. Française* **8,** 741–743.
36. Frayer, D. W. & Russell, M. D. (1987) *Am. J. Phys. Anthropol.* **74,** 393–405.
37. Bermúdez de Castro, J. M., Arsuaga, J. L. & Pérez, P. J. (1997) *Am. J. Phys. Anthropol.* **102,** 369–376.
38. Ungar, P. S., Grine, F. E., Teaford, M. F. & Pérez-Pérez, A. (2001) *Arch. Oral Biol.* **46,** 285–292.
39. Trinkaus, E. (1995) *Paléorient* **21,** 9–23.
40. Wolpoff, M. H. (1999) *Paleoanthropology* (McGraw–Hill, New York).
41. Heim, J. L. (1976) *Arch. Inst. Paléontol. Hum.* **35,** 1–331.
42. Bermúdez de Castro, J. M., Bromage, T. G. & Fernández Jalvo, Y. (1988) *J. Hum. Evol.* **17,** 403–412.
43. Lalueza, C. & Frayer, D. W. (1997) *Int. J. Osteoarchaeol.* **7,** 133–149.
44. Martin, H. (1923) *L'Homme Fossile de La Quina* (Octave Doin, Paris).
45. Patte, E. (1960) *L'Anthropologie* **64,** 512–517.
46. Sergi, S. (1974) *Il Cranio Neandertaliano del Monte Circeo* (Accademia Nazionale dei Lincei, Rome).
47. Trinkaus, E. (1985) *Am. J. Phys. Anthropol.* **67,** 19–41.
48. Lalueza, C., Pérez-Pérez, A., Chimenos, E., Maroto, J. & Turbón, D. (1993) in *La Mandíbula de Banyoles en el Contex dels Fossils Humans del Pleistoce*, ed. Maroto, J. (Centre d'Investigacions Arquelolgiques de Girona, Girona, Spain), pp. 135–144.
49. Egocheaga, J. E., Trabazo, R., Rodríguez, L., Cabo, L. L. & Sierra, J. (2000) *Bol. Cien. Nat. Real Inst. Estud. Astur.* **46,** 219–263.
50. Carter, J. T. (1928) in *Rhodesian Man and Associated Remains*, ed. Bather, F. A. (British Museum of Natural History, London), pp. 64–65.
51. Dastugue, J. & de Lumley, M. A. (1976) in *La Préhistoire Française*, ed. de Lumley, H. (Centre National de la Recherche Scientifique, Paris), pp. 612–622.
52. Vlček, E. (1993) *Fossile Menschenfunde von Weimer-Ehringsdorf* (Konrad Thiess, Stuttgart).
53. Přichystal, A. & Strnal, M. (1995) in *Stránská Skála Hill*, ed. Musil, R. (Moravian Museum, Brno, Czech Republic), pp. 149–152.
54. Kretzoi, M. & Vértes, L. (1965) *Curr. Anthropol.* **6,** 74–87.
55. de Lumley, H. (1966) *Bull. Mus. Anthropol. Préhist. Monaco* **13,** 29–51.
56. Perlès, C. (1976) in *La Préhistoire Française*, ed. de Lumley, H. (Centre National de la Recherche Scientifique, Paris), pp. 679–683.
57. Michel, D. (1989) in *Nature det Fonction des Foyers Préhistoriques*, eds. Olive, M. & Taborin, Y. (Musee de Préhistoire d'Ile de France, Nemours, France), pp. 131–134.
58. Hublin, J. J. (1991) Thèse de Doctorat d'Etat (Univ. Bordeaux, Talence, France).
59. Trinkaus, E., Ruff, C. B. & Conroy, G. C. (1999) *Am. J. Phys. Anthropol.* **110,** 379–391.
60. Spoor, F., Stringer, C. B. & Zonneveld, F. (1998) *Am. J. Phys. Anthropol.* **107,** 41–50.
61. Crubézy, E. & Trinkaus, E. (1992) *Am. J. Phys. Anthropol.* **89,** 411–420.
62. Berger, T. D. & Trinkaus, E. (1995) *J. Archaeol. Sci.* **22,** 841–852.
63. Hublin, J. J., Tillier, A. M. & Tixier, J. (1987) *Bull. Mém. Soc. Anthropol. Paris* **14,** 115–141.
64. Ruff, C. B., Trinkaus, E., Walker, A. & Larsen, C. S. (1993) *Am. J. Phys. Anthropol.* **91,** 21–53.
65. Carretero, J. M., Arsuaga, J. L. & Lorenzo, C. (1997) *J. Hum. Evol.* **33,** 357–408.
66. Trinkaus, E., Stringer, C. B., Ruff, C. B., Hennessy, R. J., Roberts, M. B. & Parfitt, S. A. (1999) *J. Hum. Evol.* **37,** 1–25.