10. Did Neanderthals make the Châtelperronian assemblage from La Grotte du Renne (Arcy-sur-Cure, France)?

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Abstract

Much debate has focused on the significance of the "modern" cultural elements found in European Late Middle Paleolithic (Châtelperronian, Uluzzian, and Szeletian) contexts. In light of evidence suggesting cultural interaction between the makers of these industries and the makers of the Aurignacian (presumably anatomically modern humans) it is imperative that the taxonomic affiliation of the hominins associated with these "transitional" industries be accurately identified. The fossil remains from the Châtelperronian levels (VIII-X) at the Grotte du Renne (Arcy-sur-Cure, France) comprise a series of isolated teeth, as well as a child's temporal bone. While the temporal bone has been analyzed (and identified as having Neanderthal affinity), most of the 29 teeth from these levels have not been described. The Châtelperronian dental remains from the Grotte du Renne comprise both permanent and deciduous teeth. Fortunately, most are well preserved and relatively unworn. Simple dental dimensions are not particularly helpful in attempts to differentiate between Neanderthals and anatomically modern humans. The dimensions of the postcanine teeth in these two groups overlap completely. However, Neanderthals are known to have larger anterior teeth (on average), especially relative to their postcanine tooth size. Not surprisingly, we find that the crown dimensions for the postcanine teeth from the Grotte du Renne fall within the ranges of both hominin groups. The crown dimensions of the anterior teeth, however, strongly suggest that they belong to Neanderthal individuals. The buccolingual measurements of all but one tooth fall outside the range of Upper Paleolithic modern humans and

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within the range of Neanderthals. Research by the first author has identified key dental morphological features that can be used to differentiate Neanderthals and anatomically modern humans. These key characters are found in the upper incisors, upper molars, P_4 and lower molars. Fortunately all but the upper molars are represented by the Châtelperronian remains at the Grotte du Renne. The strongly shoveled, labially convex lateral incisors with strong lingual tubercles, the asymmetrical P_4 with a strong, mesially placed metaconid and multiple lingual cusps, and the presence of the mid-trigonid crest on lower molars all point to a Neanderthal affinity of these individuals. In addition, the morphology of the deciduous teeth more closely resembles that of Neanderthals than it does that of anatomically modern humans. There is no single dental morphological character present exclusively in Neanderthals. Rather, it is the frequency with which certain characters occur and, more importantly, the combinations of morphological features that are important diagnostic tools. The distinctive combinations of features characteristic of Neanderthal teeth are all found in the Châtelperronian-associated teeth from the Grotte du Renne. Our analysis of both the permanent and deciduous teeth, therefore, is in agreement with the analysis of the temporal bone indicating the makers of the Châtelperronian at the Grotte du Renne were Neanderthals.

Introduction

The sites of Arcy-sur-Cure, located southeast of Paris in the Yonne department, consist of a network of caves carved out by the Cure River. These caves were excavated under the direction of André Leroi-Gourhan between 1946 and 1963 (Leroi-Gourhan, 1958, 1961). The Grande Grotte and the Grotte du Cheval are well known by Paleolithic art enthusiasts for their painted walls dating to between 24 and 32 ka. Other caves, the Grotte de l'Hyene, the Grotte du Renne and the Galerie Schoepflin, preserve evidence of Mousterian occupation, including fossils and/or artifacts.

The Grotte du Renne has been of particular interest because of the discovery of a Châtelperronian artifact assemblage, which is rich in bone tools and personal ornaments (d'Errico et al., 1998). Fourteen stratigraphic units were identified at the Grotte du Renne. The Châtelperronian artifacts are contained in three stratigraphic levels (VIII–X) that are sandwiched between an Aurignacian level (VII) and three Mousterian levels (XI–XIII). Gravettian levels (IV–VI) have also been identified (Figure 1). A child's temporal bone was recovered from the Châtelperronian level Xb, which has been dated by the ^{14}C method. If only the AMS dates are taken into consideration, the ages obtained are 33,820 ± 720 BP (OxA-3462), 34,450 ± 750 BP (OxA-8452/Ly-895) and 33,400 (OxA-9122/Ly-1055) (David et al., 2001). An older date of 38,300 ±1300 (OxA-8451/ly-894) may result from a sample inversion (David et al., 2001). Although there has been some controversy regarding dates in the Arcy sequence where conventional ^{14}C dates show evidence of contamination (David et al., 2001; White, 2001), palynological and chronostratigraphical information, together with information from other Châtelperronian sites, suggests that the Châtelperronian began at the start of the des Cottés Interstadial (Interstade des Cottés), and lasted about 5000 years, which places it generally between 38,000 and 33,000 ^{14}C years BP.

Much debate has surrounded the significance of the Châtelperronian industry at Arcy-sur-Cure. Initially, conventional thought presumed that anatomically modern humans were the makers of the Châtelperronian, as well as of other early Upper Paleolithic-like assemblages. Doubts had already been raised about this view by Leroi-Gourhan himself, who claimed some teeth from Arcy could be non-modern (Leroi-Gourhan, 1958, 1961). After the discovery of a well-preserved partial Neanderthal skeleton clearly associated with the Châtelperronian at St. Césaire (Lévêque and Vandermeersch, 1980), attention turned to hypotheses regarding the explanation of Neanderthal remains with Upper Paleolithic artifacts. Several authors have supported the view that the cultural evolution of the very last

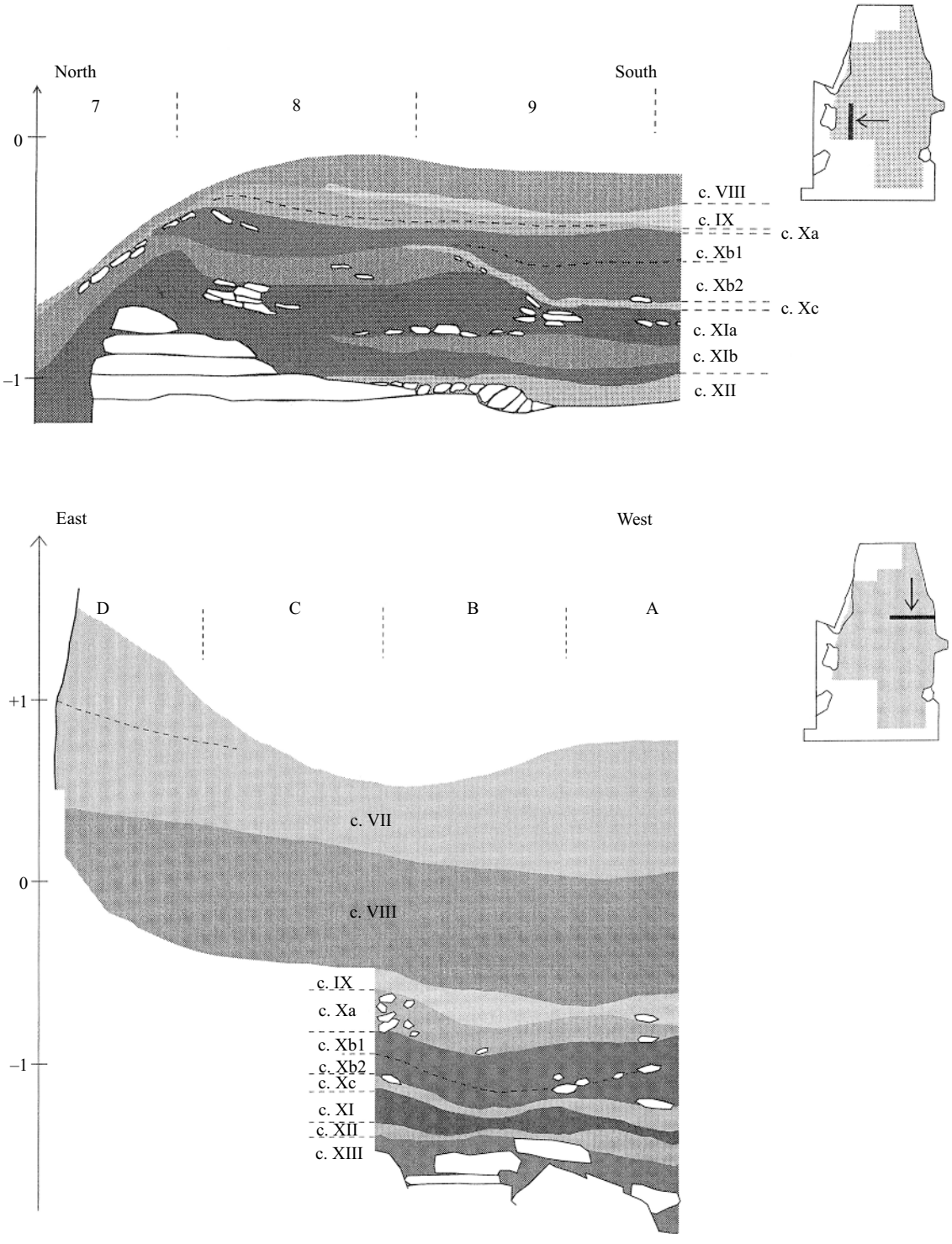

Figure 1. Profiles from the Grotte du Renne, Arcy-sur-Cure. A. Eastern aspect B. Northern aspect (Drawn by R. Humbert, taken from Connet, 2002 with permission).

Neanderthals could result from an acculturation process by the modern invaders (Demars and Hublin, 1989; Harrold, 1989; Hublin et al., 1996; Mellars, 2004). Alternatively, some have proposed an independent invention of some of the Upper Paleolithic cultural innovations by the last Neanderthals, in particular, the use of body ornaments (d'Errico et al., 1998).

Recently, the re-dating of several Upper Paleolithic sites (e.g., Vogelherd, Cro-Magnon) has led some to suggest that we do not know who the makers of any of the early or initial Upper Paleolithic assemblages were (Conard et al., 2004). One primary issue is that the human remains associated with such assemblages are generally poorly preserved, and in certain cases consist nearly wholly of teeth. For example, recently Henry-Gambier et al. (2004) claimed that the human remains associated with the early Aurignacian at Brassempouy are undiagnostic and could be either Neanderthal or anatomically modern. A critical analysis of the available data does not support this view, but rather confirms the anatomically modern nature of these remains (Bailey and Hublin, 2005).

Similar to Brassempouy, the fossil sample associated with the Châtelperronian assemblage at the Grotte du Renne consists mainly of teeth. As a result, the taxonomic affiliation of the fossils, as well as their association with the Châtelperronian artifacts, has been questioned. In addition to isolated teeth, the fossil sample consists of some skeletal remains including an infant's temporal bone. The six teeth originally recovered from the Châtelperronian levels were described as "paleoanthropic" and indistinguishable from those from lower Mousterian levels by Leroi-Gourhan (1958). More recently, Hublin et al. (1996) showed that the infant's temporal bone from Level Xb had a clear Neanderthal affinity. Coming after the Saint-Césaire discovery, this provided support that Neanderthals, not modern humans, were responsible for the assemblage.

Recently the association between the temporal bone and the Châtelperronian artifacts has been questioned by Connet (2002). This author suggests that the temporal bone derives from a part of the cave where there is the potential for disturbance resulting from the sloping of the deposits away from the cliff wall in an area where a Mousterian fossil could have "moved up" in the stratigraphy. If this were the only human fossil associated with the assemblage, it could indeed be problematic. However, subsequent to Leroi-Gourhan's original 1958 publication an additional 25 teeth mostly, but not exclusively, from level Xb have been recovered. With this expanded dental sample we observe not one, but several individuals associated with the Châtelperronian assemblage of Arcy. When plotted on a map of the site (Figure 2), it is apparent that the teeth are not limited to any particular area. An equal number of teeth come from the horizontal deposits more than one meter thick in the back of the shelter and from the thinner deposits of the slope. Although it is possible to argue, as did Connet (2002), that the latter witnessed some disturbance in relation with processes of site formation, this argument does not apply to the former.

There are two primary questions that need to be addressed with regard to the Châtelperronian dental sample from the Grotte du Renne. First, is it possible to identify the taxonomic affinity of the sample based solely on isolated teeth? And second, if the teeth are diagnosable as Neanderthal, are those teeth that exhibit *diagnostically Neanderthal* characters limited to the areas of the site where vertical displacement is a viable and likely explanation? The expanded fossil sample, as well as recent work on Neanderthal dental morphology, provides us with an opportunity to address this issue in a novel way.

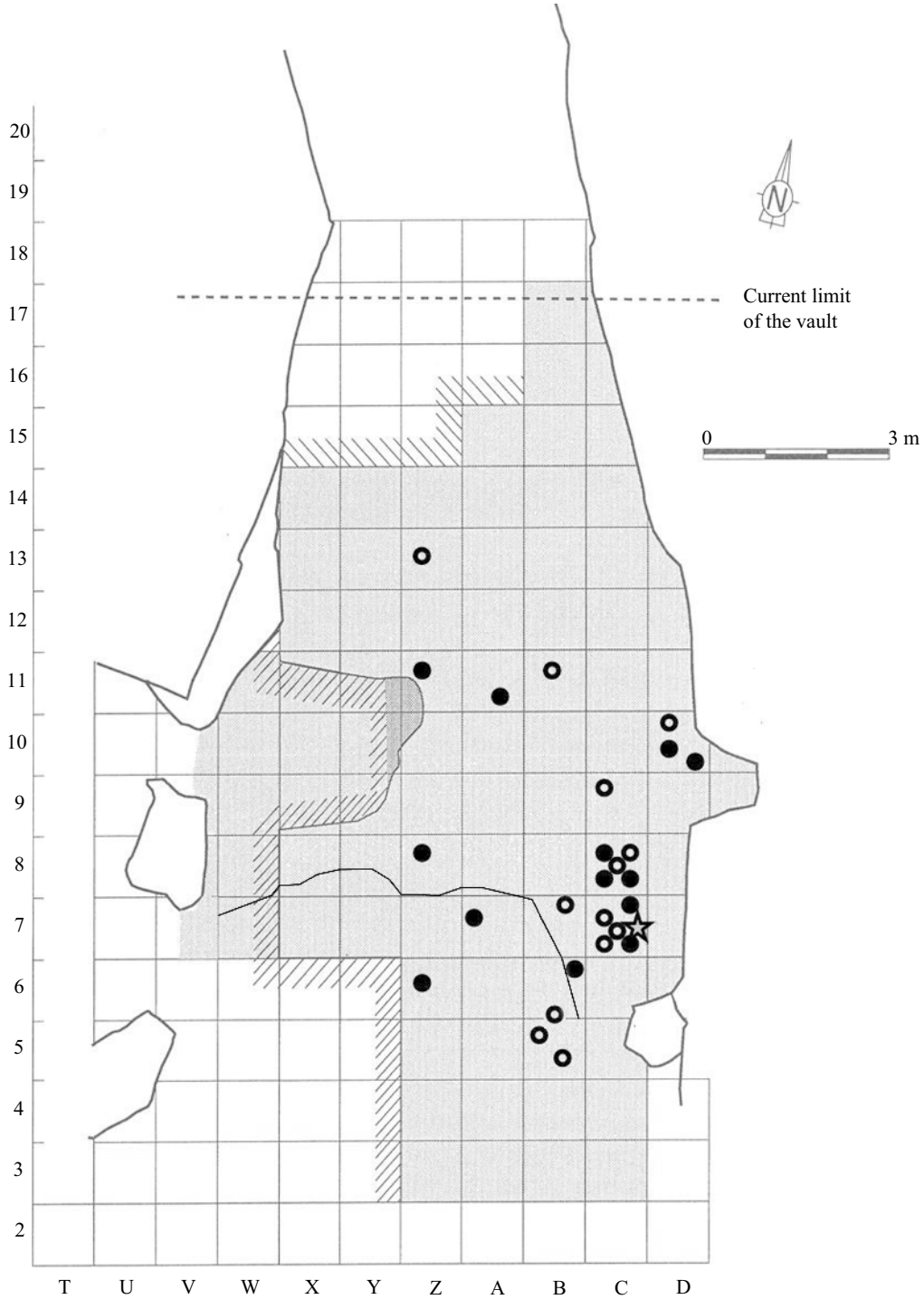

Figure 2. Distribution of the isolated teeth at the Grotte du Renne in Châtelperronian levels. Black dot: tooth with diagnostic Neanderthal features; unfilled circle: tooth consistent with (but not proving) Neanderthal morphology; grey star: child's temporal bone. Black line extending from W7 to B6 shows limit between the plateau (above) and the slope (below) in the site. All tooth positions take into account changes in the coordinate system before 1956. Four teeth (Nos. 4, 5, 6 & 7 are not plotted because of the uncertainty of their exact location (see Note 2, Table 1). Original drawn by R. Humbert, modified (with permission) from Connet, 2002.

The Dental Sample

Leroi-Gourhan (1958) originally described six human teeth recovered from the Châtelperronian levels, two of which were later identified as non-human. Subsequent excavations between 1959 and 1963 uncovered an additional 25 human teeth. The dental sample now consists of 15 permanent and 14 deciduous teeth. Most are relatively unworn and derive from young individuals. A complete description of the entire dental set can be found in Bailey and Hublin (2006).

Table 1 presents the list of Châtelperronian-associated specimens. While the 14 deciduous teeth greatly expand the fossil deciduous tooth sample, to date there has been no systematic study comparing Neanderthal and anatomically modern deciduous tooth morphology using agreed upon methods and standards. Therefore, the taxonomic assessment presented here will be based primarily on the permanent teeth.

It has sometimes been assumed that the teeth of Neanderthals and anatomically modern humans are very much alike. However, recent comprehensive analyses of the Neanderthal dentition have shown this assumption to be misconceived. While simple measurements of the postcanine teeth show complete overlap between Neanderthals and anatomically modern humans, the anterior

Table 1. List of human teeth from the Châtelperronian levels of the Grotte du Renne, Arcy-sur-Cure

Spec no	*Level*	*Specimen label*	*Tooth (side)*	*Age*	*Publication*
11	VIII	Z11 451	I_2 (L)	Subadult >8 yrs	Bailey and Hublin, 2006
4[2]	IX	IXb B7	P_4 (L)	12–18 yrs	Leroi-Gourhan, 1958
13	IX	IXc Z13	P^4 (R)	15–18 yrs	Bailey and Hublin, 2006
16[1]	IX	RIX B7	M_2 (R)	adult	Bailey and Hublin, 2006
5[2]	X	RXb A6	M_2 (R)	>15 yrs	Leroi-Gourhan, 1958
6[2]	X	RXb A6	M_3 (R)	adult	Leroi-Gourhan, 1958
7[2]	X	RXb Z8	C, (L)	12+ yrs	Leroi-Gourhan, 1958
17[1]	X	RXa C7	M_{1-2} (R)	>15 yrs	Bailey and Hublin, 2006
18	X	RXb1 D10	dm_1 (R)	4–7 yrs	Bailey and Hublin, 2006
19	X	RXb1 D10	I^2 (L)	4–6 yrs	Bailey and Hublin, 2006
20	X	RXb1 D10	P^3 (L)	5–7 yrs	Bailey and Hublin, 2006
21	X	RXb1c A11	M_2 (R)	7–9 yrs	Bailey and Hublin, 2006
22	X	RXb2 B5 1916	di^2 (R)	4–6 yrs	Bailey and Hublin, 2006
23	X	RXb2 B6 1506	I^2 (L)	6–8 yrs	Bailey and Hublin, 2006
24	X	RXb2 B6	P^3 (L)	5–7 yrs	Bailey and Hublin, 2006
25	X	RXb2 B11 3191	dm_1 (R)	5–7 yrs	Bailey and Hublin, 2006
26	X	RXb2 C7	dm^2 (R)	9–12 mo	Bailey and Hublin, 2006
27	X	RXb2 C7	di^1 (R)	<18 mo	Bailey and Hublin, 2006
28	X	RXb2 C7	di^2 (R)	7–12 mo	Bailey and Hublin, 2006
29	X	RXb2 C8	dm_2 (R)	7–15 mo	Bailey and Hublin, 2006
30	X	RXb2 C8	M_1 (R)	9–18 mo	Bailey and Hublin, 2006
31	X	RXb2 C8	dc, (R)	7–15 mo	Bailey and Hublin, 2006
32	X	RXb2 C8	di^1 (L)?	>5–6 yrs	Bailey and Hublin, 2006
33	X	RXb2 C8	dm_1 (R)	6–11 mo	Bailey and Hublin, 2006
34	X	RX C7	dm^1 (L)[1']	7–11 mo	Bailey and Hublin, 2006
35	X	RXc A7	M_1 (R)	6–9 yrs	Bailey and Hublin, 2006
36	X	RXb2 B5	di^1 (L)	birth	Bailey and Hublin, 2006
37	X	RXc Z6	dc' (R)	3–7 yrs	Bailey and Hublin, 2006
38	X	RXc C9	dc' (L)	4–8 mo	Bailey and Hublin, 2006

[1] Not used in the analysis because worn or damaged.
[2] These teeth are of uncertain location because of changes in the coordinate system before 1956. The locations of all other teeth have been checked according to the post-1956 grid.

Table 2. A list of trait frequencies that distinguish Neanderthals from Upper Paleolithic moderns and their presence or absence in the Arcy-sur-Cure sample

Tooth	*Trait*	*Trait presence (based on ASUDAS[1] and Bailey, 2002b)*	*Arcy-sur-Cure*	*Mousterian Neanderthal % present (n)*	*Upper Paleolithic Modern % present (n)*
I^2 ($n = 2$)					
	Shoveling	Grade 3+	present	93 (27)	43 (7)
	Lingual tubercles (*Tuberculum dentale*)	Grade 1+	present	100 (25)	0 (7)
	Two of the above		**present**	**100 (24)**	**0 (7)**
P^3 ($n = 2$)					
	Essential crest	Grade 1+	present	100 (19)	43 (7)
	Maxillary Premolar Accessory Ridges (MxPAR)	Grade 1+	present (1/2)	69 (16)	25 (4)
	Two of the above		**present (1/2)**	**88 (16)**	**0 (5)**
P^4 ($n = 1$)					
	Essential crest	Grade 1+	present	100 (18)	67 (6)
	Maxillary Premolar Accessory Ridges (MxPAR)	Grade 1+	present	77 (22)	50 (2)
	Two of the above		**present**	**78 (18)**	**50 (2)**
C, ($n = 1$)					
	Distal accessory ridge	Grade 2+	present	67 (12)	29 (7)
P_4 (n = 1)					
	Distolingual cusp	Grade 2+	present	90 (30)	39 (13)
	Transverse crest	Grade 2+	absent	77 (27)	7 (14)
	Asymmetry	Grade 1+	present	92 (25)	33 (9)
	Two of the above (distolingual cusp + asymmetry)		**present**	**91 (22)**	**9 (11)**
M_1 ($n = 2$)					
	Mid-trigonid crest	Grade 1+	present	94 (28)	0 (23)
	Cusp 6	Grade 1+	present	26 (19)	19 (21)
	Two of the above		**present (1/2)**	**57 (7)**	**0 (15)**
M_2 ($n = 2$)					
	Y-pattern	Y	present (1/2)	79 (34)	44 (25)
	Cusp 6	Grade 1+	present	55 (20)	24 (17)
	Mid-trigonid crest	Grade 1+	present	91 (24)	9 (23)
	Anterior fovea	Grade 2+	present	88 (24)	53 (19)
	Three of the above (Cusp 6+ mid-trigonid crest +anterior fovea)		**present**	**63 (20)**	**0 (13)**
M_3 ($n = 1$)					
	Four cusps		absent	0 (23)	32 (19)

[1] ASUDAS: Arizona State University dental anthropology system (Turner et al., 1991).

dentition of Neanderthals is relatively larger than that of anatomically modern humans (Bytnar et al., 1994). A recent study of tooth root lengths also indicates that the roots of several teeth are significantly longer in Neanderthals than in Upper Paleolithic modern humans (e.g., I^1, I^2, C′, I_1, I_2, C, P_3, P_4 and M_2); and, for some teeth (e.g., I^1, C′ and I_1) there is little or no overlap in their ranges (Bailey, 2005).

Morphologically, while no single dental morphological character is uniquely present in Neanderthals, the frequencies with which certain traits occur and, perhaps more importantly, the combination of traits in a single individual or in individual teeth has proven to be an important set of diagnostic tools (Bailey, 2002a, b, 2004; Bailey and Lynch, 2005). Table 2 provides a list of tooth traits in which frequencies distinguish Neanderthals from Upper Paleolithic modern humans and their presence or absence in the Grotte du Renne sample.

For example upper incisors show marked differences between Neanderthals and anatomically modern humans. Not only do they tend to be relatively larger in Neanderthals (especially buccolingually), but they show a distinctive combination of morphological features as well (Mizoguchi, 1985; Crummett, 1995; Bailey, 2000). Mizoguchi described Neanderthal incisors as having "extremely developed marginal ridges which run parallel to each other, a very deep lingual fossa and a

Table 3. Comparative buccolingual measurements for the Arcy-sur-Cure sample, Mousterian Neanderthals and Upper Paleolithic modern humans

	The Grotte du Renne, Arcy-sur-Cure	*Mousterian Neanderthal mean (n) range*[1]	*Upper Paleolithic modern mean (n) range*[1]
I^2	8.2, 8.8	8.2 (n = 8) 7.4–8.8	6.7 (n = 11) 5.8–8.3
P^3	11.3	10.1 (n = 17) 8.1–11.3	9.7 (n = 12) 8.7–10.6
P^4	10.5	10.2 (n = 11) 8.2–11.3	9.7 (n = 12) 8.8–10.9
I_2	7.8	7.5 (n = 7) 6.0–8.0	6.8 (n = 21) 6.0–7.5
C,	9.8	8.5 (n = 10) 5.6–9.8	8.4 (n = 16) 7.2–9.7
P_4	10.2	8.8 (n = 11) 7.6–10.5	8.4 (n = 14) 7.1–9.2
M_1	11.1	10.8 (n = 18) 9.7–11.8	10.9 (n = 28) 9.8–11.9
M_2	11.6, 11.6	10.9 (n = 16) 9.9–12.1	10.7 (n = 30) 8.6–12.3
M_3	10.8	10.8 (n = 13) 7.8–13.1	10.6 (n = 12) 7.7–12.5

[1] Bailey, unpublished data: Comparative samples include the following sites:
Mousterian Neanderthals: Arcy-sur-Cure (levels XI and XII), Ciota Ciara, Grotte Guattari, Hortus, Krapina, Kůlna, La Fate, La Quina, Melpignano, Montmaurin, Ochoz, Pontnewydd, Petit Puymoyen, Régourdou and Spy.
Upper Paleolithic moderns: Abeilles, Abri Blanchard, Abri Castanet, Abri Pataud, Aurignac, Bruniquel, Gough's Cave, Dolní Věstonice, Farincourt, Fourneau-du-Diable, Grottes d'Isturitz, La Chaud, La Ferrassie, La Gravette, La Grèze, La Linde, La Madeleine, Les Vachons, Laugerie Basse, Les Rois, Mieslingtal, St. Germain-la-Rivière and Vindija.

large lingual tubercle" ("Type 2" shoveling: Mizoguchi, 1985: 47). He clearly distinguished this form from that of modern humans and also noted that the presence of this morphology in the lateral incisors further distinguished Neanderthals from *Homo erectus*. Crummett (1995) noted that, in addition to the aforementioned characters, Neanderthal incisors are typified by marked labial convexity. Shoveling and lingual tubercles on the upper central incisor are primitive characters found in other fossil hominins as well (Mizoguchi, 1985). The degree of expression and the combination of these three characters in a single tooth, however, is distinctive of Neanderthals.

The two upper lateral incisors in the Châtelperronian sample are large. The buccolingual dimension of one falls at the upper end of the Upper Paleolithic variation, and that of the other falls above its range (Table 3). Morphologically, they show strong shoveling, marked lingual tubercles and labial convexity (Figure 3). The combination of shoveling and *lingual tubercles* in the I^2 occurs in 92% of Neanderthals and only 13% of Upper Paleolithic moderns (Table 2). In their combination and expression of these three features they clearly show affiliation to Neanderthals.

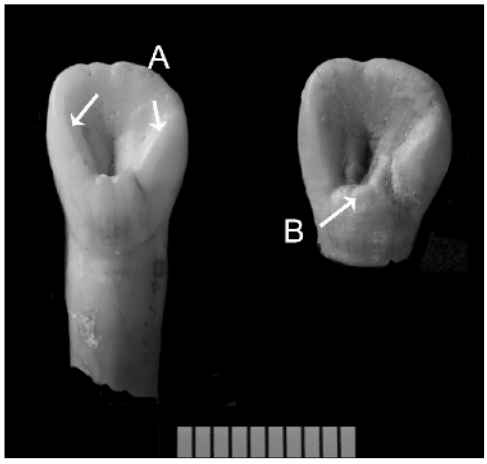

Figure 3. Two left I^2s from Level X, Grotte du Renne. Both show strong shovel shape (A), lingual tubercles (B) and labial convexity (not shown).

Upper premolars of Neanderthals are quite similar to those of other archaic humans. The three upper premolars recovered from the Grotte du Renne are, as Leroi-Gourhan first described them, "paleoanthropic". They

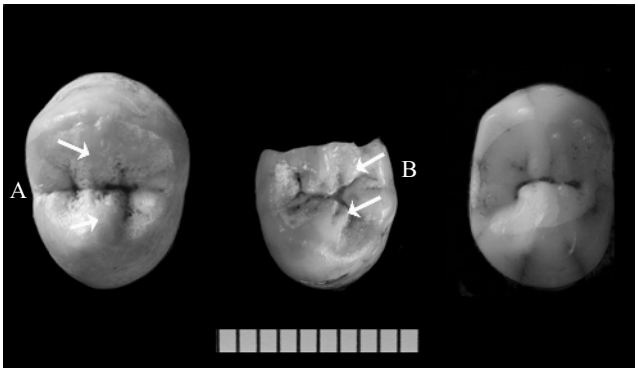

Figure 4. Upper premolars from the Grotte du Renne. Left: left P^3 (Level X). Middle: left P^3 (Level X). Right: right P^4 (Level IX). A: essential crest, B: MxPAR (maxillary premolar accessory ridges).

present strong essential (median) crests on the buccal and lingual cusps and two of the three present accessory ridges (MxPAR: Burnett, 1998) (Figure 4). The frequencies of these features are lower in Upper Paleolithic modern specimens than in Neanderthals. Separately they are not particularly useful traits for taxonomic affiliation; however, in combination they are more informative. One of the five scorable Upper Paleolithic modern P^3s presents accessory ridges (Table 2), but it does not exhibit a definite essential crest. However, a majority (88%) of the Neanderthal specimens present these traits in combination. For the P^4, again, 78% of Neanderthals show these traits in combination while only one of the two scorable Upper Paleolithic moderns shows this combination.

Metrically, the buccolingual dimension of the P^3 falls outside the range of Upper Paleolithic modern specimens and within the range of Neanderthals (Table 3), while that of the P^4 falls within the range of both Upper Paleolithic moderns and Neanderthals. The root of the P^4, however, is quite long. It falls within the range of Neanderthals and is much longer than the two Upper Paleolithic modern P^4s with measurable roots (Table 4).

The single lower incisor (an I_2) possesses archaic features, including moderate shoveling, median ridge development and a cingulum shelf (Figure 5). Its buccolingual breadth falls outside the range of Upper Paleolithic moderns and within the range of Neanderthals (Table 3). Bytnar et al. (1994) have shown that late archaic humans (Neanderthals) and early modern humans in the Near East differ significantly in I_2 buccolingual dimensions. SEB has found that European Neanderthals also have I_2s with significantly larger buccolingual dimensions than those of Upper Paleolithic moderns (see Table 3, $t = 4.34$, $p < .0001$, df = 34, Bailey unpublished data). The buccolingual dimensions of this tooth, together with its archaic morphology, suggest Neanderthal affiliation.

Like the I_2, the lower canine is archaic in its size and morphology. Leroi-Gourhan (1958) noted that its robust crown dimensions and

Table 4. Root lengths in the Arcy-sur-Cure sample compared to that of Mousterian Neanderthals and Upper Paleolithic modern humans

	The Grotte du Renne, Arcy-sur-Cure	*Mousterian Neanderthal mean (n) range*[1]	*Upper Paleolithic modern mean (n) range*[1]
P^4	16.6	17.6 ($n = 10$) 16.2–19.0	11.9 ($n = 2$) 10.5, 13.3
C,	18.0	19.7 ($n = 7$) 17.3–23.2	15.9 ($n = 4$) 13.2–19.0
P_4	17.4	18.7 ($n = 7$) 14.5–21.0	14.5 ($n = 6$) 13.0–17.1
M_1	13.6	14.3 ($n = 9$) 12.2–16.8	13.2 ($n = 3$) 11.6–14.0
M_2	14.4	15.3 ($n = 6$) 14.3–16.3	13.7 ($n = 7$) 12.6–16.8
M_3	15.0	14.3 ($n = 5$) 11.8–14.1	no data

[1] Bailey, unpublished data: Comparative samples include the following sites:
Mousterian Neanderthals: Krapina, Hortus, Ciota Ciara, Petit Puymoyen, Régourdou, La Quina and Spy.

Upper Paleolithic moderns: Fourneau-du-Diable, Gough's Cave, Grottes d'Isturitz, La Chaud, La Ferrassie, La Gravette, La Grèze, Les Vachons, Les Rois and St. Germain-la- Rivière.

Figure 5. Left I_2 from Level VIII, Grotte du Renne with cingulum (A) and median ridge (B) development. Left: lingual view, Right: distal view.

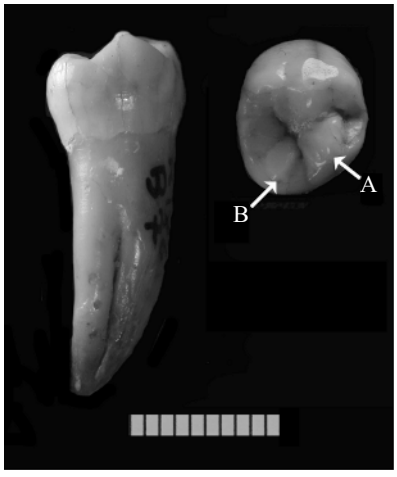

Figure 7. Left P_4 from Level IX, Grotte du Renne possessing a large mesially placed metaconid (A) and an second lingual cusp (B). Occlusal outline is markedly asymmetrical. Left: buccal view, right: occlusal view.

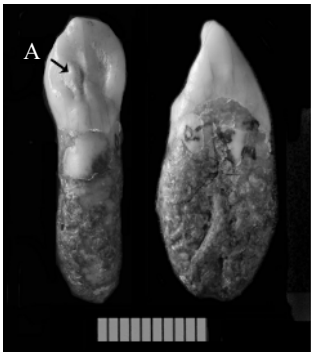

Figure 6. Left C, from Level X, Grotte du Renne showing marked distal accessory ridge (A). Left lingual view, right: mesial view.

double channeled root were similar to canines from earlier Mousterian levels. Indeed, its buccolingual dimensions are outside the range of Upper Paleolithic moderns and at the high end of the range for Neanderthals. The presence of a strong distal accessory ridge is also more common in Neanderthals than in Upper Paleolithic moderns (Table 2). Compared to other Neanderthal lower canines, the fully formed root is somewhat diminutive in length. However, the marked hypercementosis and absence of crown wear strongly suggest that the tooth was impacted (Figure 6). Therefore, we caution against using root length in the interpretation. In all other attributes the tooth is most closely affiliated with Neanderthals.

The single P_4 presents a markedly asymmetrical occlusal crown outline and multiple lingual cusps. It also possesses a large and mesially placed metaconid (Figure 7). The combination of asymmetry and multiple lingual cusps can be found in 91% of Neanderthals, but it is rare (~8%) in Upper Paleolithic moderns (Table 2). About 60% of Neanderthals also present a prominent continuous transverse crest connecting the metaconid and protoconid. However, while the essential crests of the buccal and lingual cusps of this tooth are markedly developed, they do not join to form a transverse crest. The buccolingual breadth of the P_4 is at the high end of the Neanderthal range of variation and two standard deviations above the range for Upper Paleolithic moderns (Table 3). Its root length is also above the Upper Paleolithic modern range. In morphology and size the affinity of this tooth is much closer to Neanderthals than to Upper Paleolithic moderns.

Seven lower molars have been recovered from the Châtelperronian levels of the Grotte du Renne. Three of these provide little or no morphological information due to their marked wear or partial preservation. Because molar length and breadth dimensions of Neanderthals and anatomically modern humans overlap extensively, there is little we can reliably infer about the taxonomic affiliation of these three worn teeth. However, the remaining teeth are less worn and more informative (Figure 8). Each of the two M_1 present a mid-trigonid crest (or epicristid: Zubov, 1992), which has a much higher frequency in Neanderthals than in Upper Paleolithic moderns (Table 2). Of the two M_2s, one presents a continuous mid-trigonid crest, while the other presents a mid-trigonid crest that is divided by a shallow groove. Both M_2s possess large hypoconulids (Cusp 5). In addition, at least one clearly possesses a *tuberculum sextum* (Cusp 6). The distal portion of the other M_2 is obscured by wear. The trait combination – mid-trigonid crest + anterior fovea + cusp 6 – is observed in 63% of Neanderthals but not in Upper Paleolithic moderns (Table 2). Thus, the combination of traits observed in the M_2 clearly suggests Neanderthal affinity. Although quite worn, the single M_3 certainly possessed more than four cusps – a characteristic found in 100% of Neanderthals and 68% of Upper Paleolithic moderns.

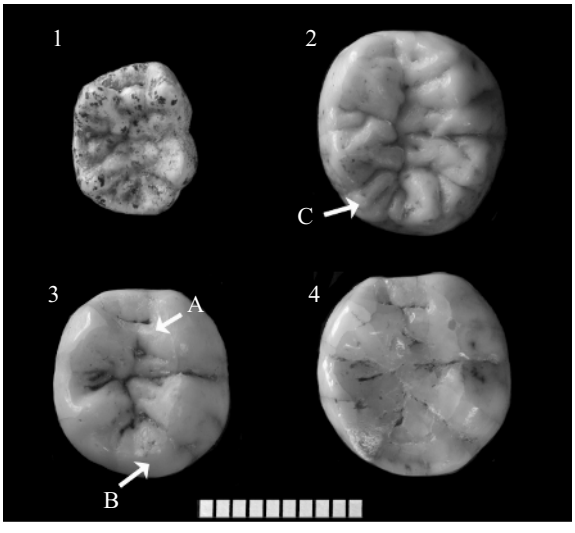

Figure 8. Unworn or slightly worn lower molars, Level X, Grotte du Renne. 1: right M1, 2: right M2, 3: right M1, 4: right M2. Traits referred to in the text: mid-trigonid crest (A), hypoconulid (B) and tuberculum sextum (C).

To summarize, in size and morphology all of the teeth from the Châtelperronian levels at the Grotte du Renne are consistent with Neanderthal affinity. Certain teeth in this sample present traits and/or trait combinations that are rare or absent in Upper Paleolithic modern humans, but occur with high frequency in Neanderthals. When we consider each of the traits for which Upper Paleolithic and Neanderthals have substantial differences in frequency (Table 2), and combine that with the available metric data, it is clear that the likelihood that these teeth come from anatomically modern humans is quite low. In fact, if we assume that the Châtelperronian assemblage represents a single population, and compare it to the combination of trait frequencies observed in Neanderthals and Upper Paleolithic moderns, we find the posterior probability that the population can be assigned to Upper Paleolithic moderns to be 0^1.

SPATIAL DISTRIBUTION

Three teeth likely belonging to a single individual between the ages of 4 and 6 years were recovered from level Xb1, Square D10 located towards the back of the shelter (Figure 9). In addition to developmental age, the color and the state of preservation all suggest the teeth derive from the same individual. The I^2 possesses the distinctive Neanderthal combination of strong shovel shape, labial convexity and a well-developed lingual tubercle. The dm_1 presents a strong crest connecting buccal and

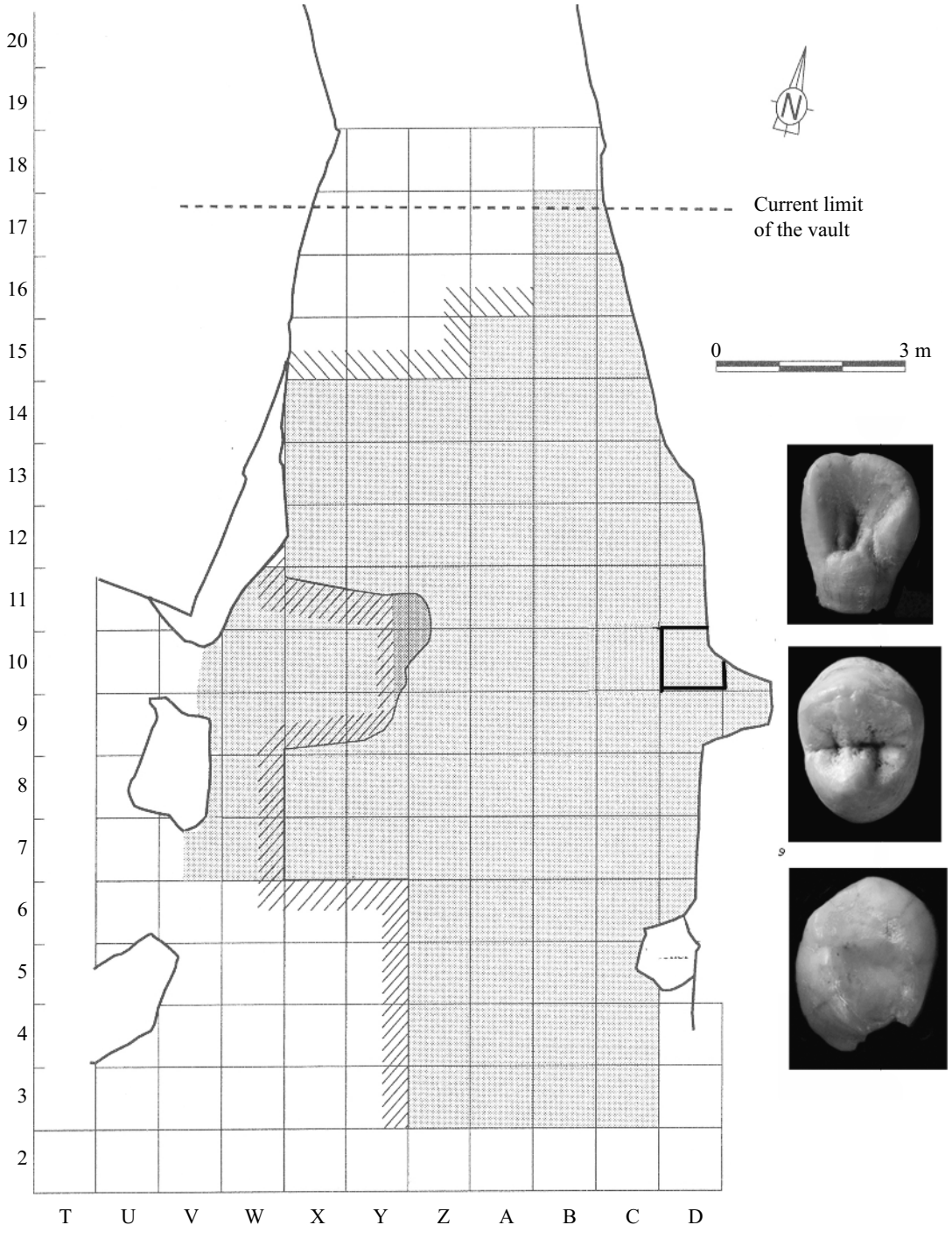

Figure 9. Location of square D10 and associated teeth (see Table 1) Original drawn by R. Humbert, modified (with permission) from Connet, 2002.

lingual cusps, which is similar to that found in the permanent P_4 of Neanderthals. The P^3 presents a strong and bifurcated essential crest, consistent with (but not proving) Neanderthal affinity. The fragmentary nature and incompleteness of this set suggest possible disturbance. However, it remains that three teeth likely belong to the same individual and come from a square that is in the back of the shelter, away from the sloping part of the deposits. This suggests some level of integrity of the layer in this particular square.

Similarly, four of the five teeth recovered from Xb2, Square C8 (Figure 10) have a high probability of belonging to the same individual with a developmental age of 9 to 18 months (dc_1, dm_1, dm_2, M_1 but not the di^1). The permanent M_1 has a high probability of belonging to a Neanderthal, with its marked mid-trigonid crest, low mesial marginal ridge and six cusps. The dm_2 presents compressed and internally placed cusps typical of Neanderthals, and the morphology of its mid-trigonid crest is nearly identical to that of the M_1. The dm_1 shows morphology similar to that seen in Neanderthal P_4s, including a prominent, continuous crest between the buccal and lingual cusps. The color, preservation and developmental age of these four specimens, together with the morphological similarity between the dm_2 and the permanent M_1, strongly suggest that they belong to the same infant. This again suggests that disturbance in this part of the cave, and this square in particular, was limited and likely not to account for the association between these Neanderthal teeth and the Châtelperronian assemblage.

Finally, an M_2 from Xb1c, Square A11 (Figure 11) presents a combination of traits found in 63% of Neanderthals, but not found in any Upper Paleolithic modern humans sampled. The occlusal complexity of the tooth, together with the morphology of the mid-trigonid crest strongly suggests it belonged to a Neanderthal. Square A11, is located in the back of the shelter where the likelihood is low that vertical displacement would explain the presence of a Neanderthal tooth in this level.

Summary and Conclusions

Our goal was to use new methods (dental anthropology) to identify the makers of the Châtelperronian at the Grotte du Renne, and to investigate the likelihood that inter-level movement of objects and/or teeth could account for the association between the fossils and the cultural remains. The use of the dental sample increases the number of individuals associated with the assemblage (MNI = 6) and confirms the conclusions derived from the study of the temporal bone (Hublin et al., 1996) that Neanderthals are the only fossils associated with the Châtelperronian at Arcy-sur-Cure.

The Grotte du Renne is indeed geologically and stratigraphically complex. There is evidence of periodic roof collapse and there is the potential for mixture of once distinct archaeological units in the section of the site formed before the threshold of the bedrock located some 8 m from the back of the shelter. However, nearly half of the Neanderthal teeth derive from areas where this type of disturbance and mixture is unlikely.

After the recent excavation of a preserved section at the Grotte du Renne located virtually at the center of the cave, David et al. (2001: 218) concluded that level X is "*a key bed in the stratigraphy of sedimentary refilling of the Grotte du Renne. It is well defined by its thickness, color, nature, structure and archeological contents*". Moreover, our investigation of the association of certain fossils shows conclusively that, although some level of disturbance is possible, spatial clusters of teeth belong to particular individuals, suggesting that movement of the remains was minimal. Finally, it should be noted that level Xb, which yielded

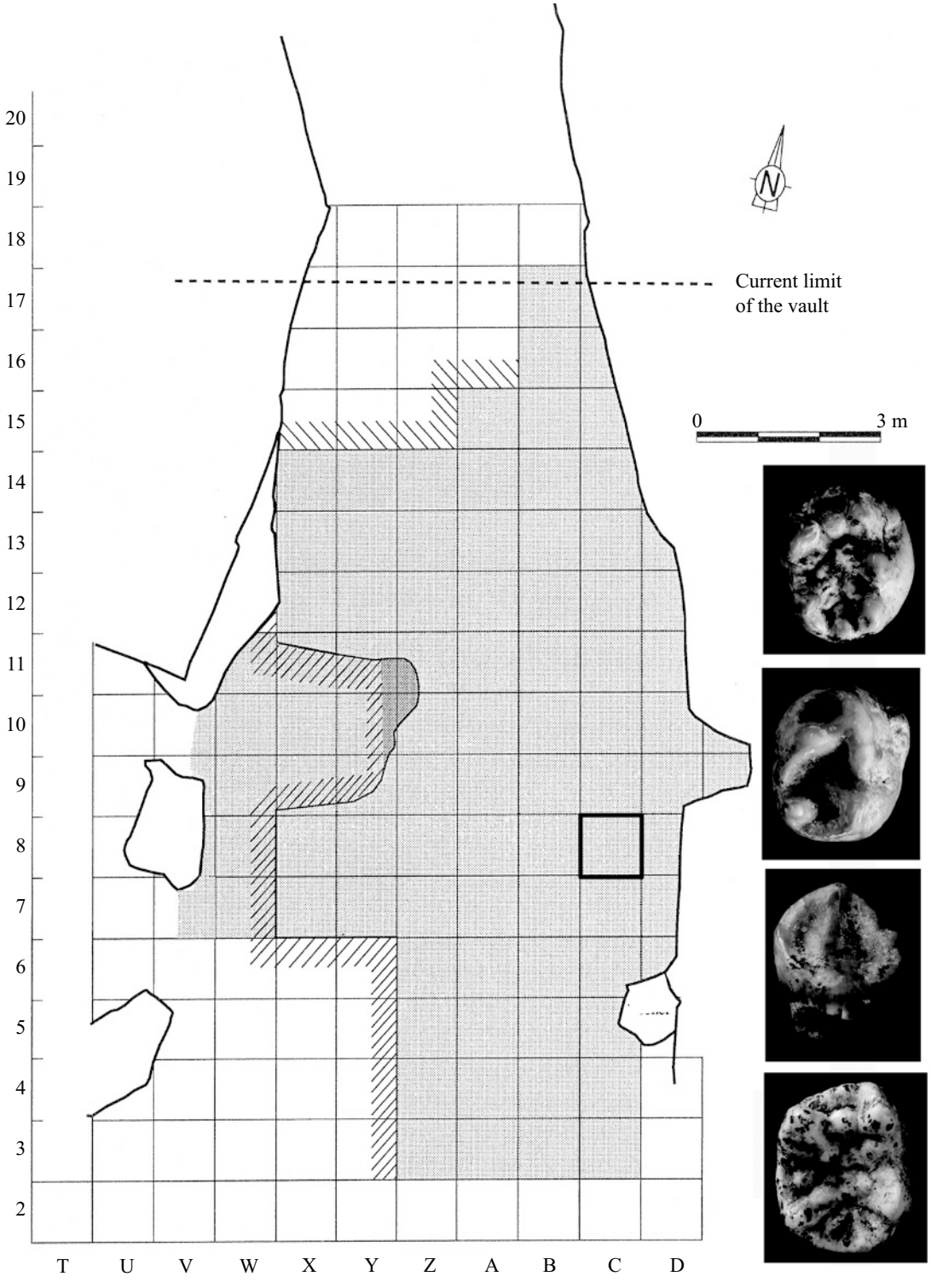

Figure 10. Location of Xb2, square C8 and associated teeth (see Table 1). Original drawn by R. Humbert, modified (with permission) from Connet, 2002.

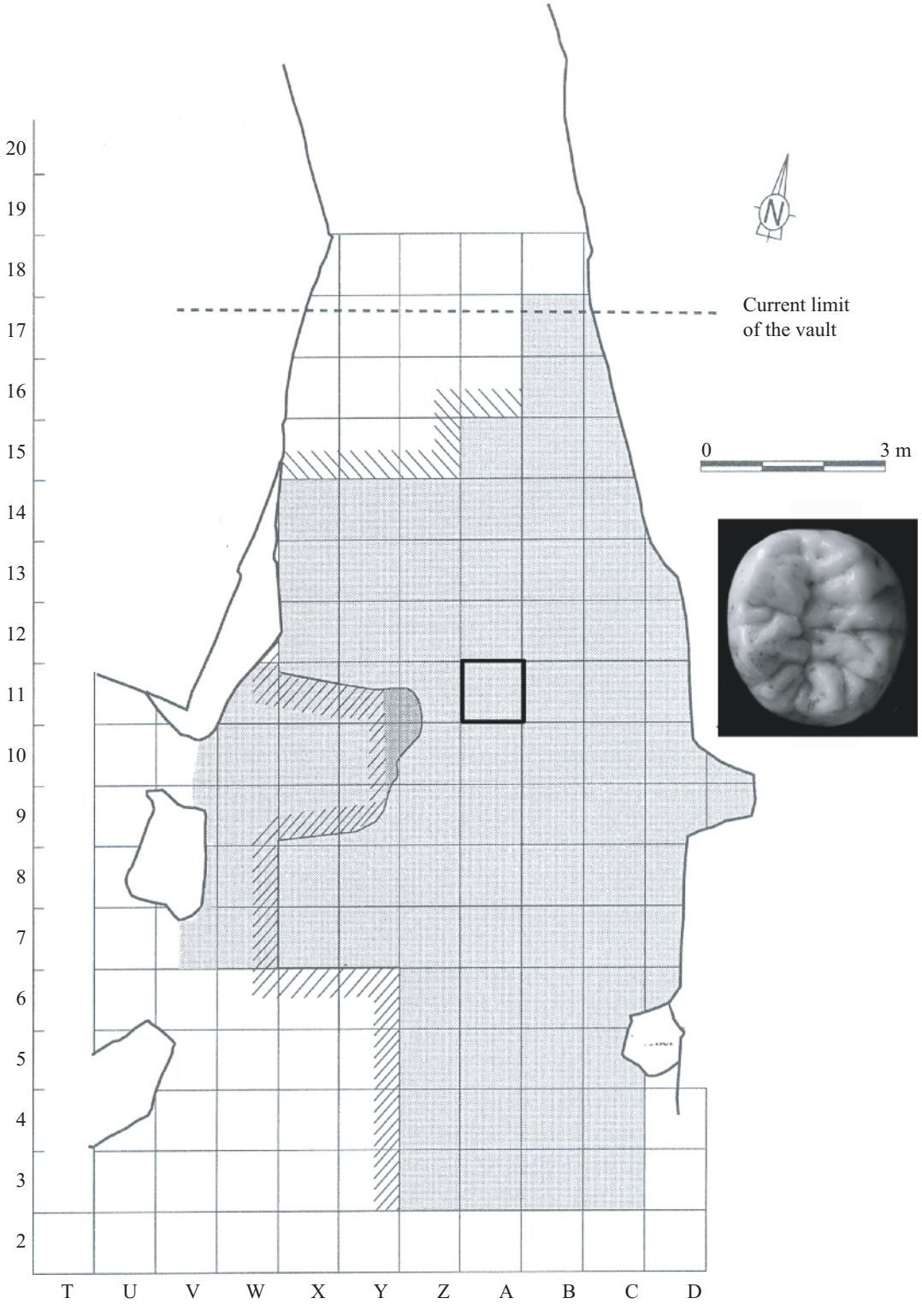

Figure 11. Location of Xb1c, Square A11 and associated tooth (see Table 1). Original drawn by R. Humbert, modified (with permission) from connet, 2002.

the majority of these remains, is not the lowermost Châtelperronian level of the site. On part of its extension it is separated from the Mousterian levels by an older Châtelperronian level (Xc). Conversely, level Xb is also separated from the overlying Aurignacian deposits by two other Châtelperronian levels (IX and VIII) reaching 50 cm and 20 cm thick in some places. The uppermost layer VIII also yielded a diagnosable Neandertal tooth, which is well above the uppermost Mousterian Layer XI. In addition, it must be noted that no Aurignacian small artifacts or modern human teeth are found in level Xb. It is, in our view, unlikely that the occurrence of body ornaments associated to the Neanderthal remains in level Xb could be explained by a selective migration of such items from level VII through levels VIII and IX (also see discussion in d'Errico et al., 1998, 2003).

Recently, the idea that there are no distinguishing characteristics of Neanderthal teeth, espoused by Boule and Vallois (1957), has been revived by Henry-Gambier et al. (2004). This idea is based on the fact that metrically there is a great deal of overlap between the groups, and morphologically there are no traits found in Neanderthals that cannot be found, at least on occasion, in anatomically modern humans. It seems to be linked to a recent trend to question the generally held assumption that the makers of the early Aurignacian were modern humans. This trend is partly the result of recent re-dating of several Aurignacian sites (e.g., Vogelherd, Cro-Magnon), which now appear to be much younger than once thought. Conard et al. (2004) have suggested that we perhaps do not know who made the Aurignacian. This suggestion has recently been echoed by Henry-Gambier et al. (2004) in their analysis of the early Aurignacian fossils from Brassempouy.

Neanderthal teeth are distinguished from those of anatomically modern humans primarily in their trait frequencies and in the combination of traits in a single tooth, not in the presence of a particular trait (the mid-trigonid crest on the M_3 may be an exception: Bailey, 2002a). However, it is misguided to conclude that taxonomic affiliation cannot be determined from isolated teeth. To date, we find no evidence to support that any hominins other than Neanderthals are associated with the Châtelperronian or that any hominins other than anatomically modern humans are associated with the early Aurignacian.

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Note

1. The combination of features found in some of the Arcy Châtelperronian teeth was never observed in the modern human series. Assuming that the Arcy series represents a homogeneous sample, a posterior probability of this series to be modern, computed from the observed frequency in our reference populations, will inevitably give a null result.

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