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Dental remains from the Grotte du Renne at Arcy-sur-Cure (Yonne)

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Abstract

Human remains associated with the earliest Upper Paleolithic industries are sparse. What is preserved is often fragmentary, making it difficult to accurately assign them to a particular species. For some time it has been generally accepted that Neandertals were responsible for the Châtelperronian and anatomically modern humans for the early Aurignacian industries. However, the recent re-dating of several of the more-complete modern human fossils associated with the early Aurignacian (e.g., Vogelherd) has led some to question the identity of the makers and the context of these early Upper Paleolithic industries. The Grotte du Renne at Arcy-sur-Cure, France has yielded many hominin remains, from Mousterian, Châtelperronian, Aurignacian, and Gravettian layers. Previously, a child's temporal bone from the Châtelperronian Layer Xb was recognized as belonging to a Neandertal; however, most of the teeth from Châtelperronian layers VIII-X remain unpublished. We describe the dental remains from the Châtelperronian layers, place them in a comparative (Mousterian Neandertal and Upper Paleolithic modern human) context, and evaluate their taxonomic status. The teeth ($n = 29$) represent a minimum of six individuals aged from birth to adult. The permanent dental sample ($n = 15$) from the Châtelperronian layers of Arcy-sur-Cure exhibits traits (e.g., lower molar mid-trigonid crest) that occur more frequently in Neandertals than in Upper Paleolithic modern humans. Furthermore, several teeth show trait combinations, including Cusp 6/mid-trigonid crest/anterior fovea in the lower second molar, that are rare or absent in Upper Paleolithic modern humans. The deciduous teeth ($n = 14$) significantly increase the sample of known deciduous hominin teeth and are more similar to Mousterian Neandertals from Europe and Asia than to Upper Paleolithic modern humans. Thus, the preponderance of dental evidence from the Grotte du Renne strongly supports that Neandertals were responsible for the Châtelperronian industry at Arcy-sur-Cure.

Keywords: Neandertal; Châtelperronian; Upper Paleolithic; Teeth; Dental morphology; Dental metrics

Introduction

The processes responsible for the emergence of anatomically and behaviorally modern humans in Eurasia around 40,000 years ago have been the focus of much debate. The so-called "Out of Africa" model has gradually become the dominant paradigm (Klein, 1999). This model primarily promotes a replacement of local Eurasian Upper Pleistocene populations by modern immigrants originating in Africa. However, the exact mechanism of the spread of modern populations is still debated. Is some level of hybridization/gene flow with local populations detectable? If so, do we find evidence of genetic "swamping" rather than physical replacement? Were there cultural or behavioral influences of one population over the other? While genetic studies can shed some light on important questions related to these issues, the paleoanthropological record is generally too scarce to allow detailed scenarios of replacement to be demonstrated in most geographical areas. In fact, only Europe has yielded sufficient archaeological and paleontological evidence to allow attempts to reconstruct these mechanisms.

Research on the Middle to Upper Paleolithic transition in western Eurasia has tended to focus on three key issues. The first involves the possible chronological overlap between Mousterian or other industries assigned to Neandertals on the one hand, and genuine early Upper Paleolithic assemblages

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assigned to modern humans on the other. Although the chronology of many sites is disputed, as is the calibration of the ^{14}C dates beyond 30,000 BP, there is evidence from the northern Caucasus, the Crimea, Croatia, and part of the Iberian Peninsula that Neandertals continued to exist even as the first modern humans arrived into Europe (Hublin et al., 1995; Marks and Chabai, 1998; Pettitt, 1998; Smith et al., 1999; Golovanova and Doronichev, 2003; Chabai et al., 2004). This clearly opens the possibility for long or short distance interactions between Neandertals and modern humans.

A second question concerns the significance of "transitional industries" in the context of a biological replacement. According to some authors, "transitional industries" are thought to display features of both Middle and Upper Paleolithic assemblages (Harrold, 1989; Valoch, 1990). This pattern has been interpreted by some as resulting from an acculturation effect (Demars and Hublin, 1989; Harrold, 1989; Hublin et al., 1996; Mellars, 2004) and by others as resulting from independent local evolution (Cabrera Valdés et al., 2000; d'Errico, 2003). At the center of this discussion is the Châtelperronian, an industry initially considered fully Upper Paleolithic, and later claimed to display Middle Paleolithic features (Leroi-Gourhan, 1968; Guilbaud, 1993).

Finally, a third question concerns the identity of the makers of the lithic assemblages found in Europe between 45,000 and 30,000 BP. In the early Upper Paleolithic of Western Europe, these assemblages include so-called 'proto-Aurignacian', 'genuine' early Aurignacian, and Châtelperronian industries. The first of these, the 'proto-Aurignacian,' is mostly represented in the Mediterranean region. It should be underlined that the increasingly popular distinction between the 'proto-Aurignacian' and the genuine early Aurignacian is based on the idea that they represent distinct techno-complexes at least partly contemporary in different geographical areas (Bon, 2002). To date, significant human remains are yet to be associated with this industry. The sample of human remains associated with the second group—'genuine' early Aurignacian—has dwindled significantly in the past decade; the development of direct dating by ^{14}C Accelerator Mass Spectrometry (AMS) has resulted in the reassignment of some specimens previously considered early Upper Paleolithic to later periods (Smith et al., 1999; Trinkaus and Pettitt, 2000; Terberger et al., 2001; Svoboda et al., 2002; Conard et al., 2004). The remaining securely-associated and well-dated fossils are generally agreed to represent anatomically modern humans. The oldest modern humans found in Europe (i.e., in Peştera cu Oase) are unfortunately out of archaeological context (Trinkaus et al., 2003). However, they are quite close in age to the earliest development of the Aurignacian. More or less fragmentary specimens have been discovered in various Aurignacian contexts at Fontechevade and Les Rois (Charente, France), La Crouzade (Aude, France), and El Castillo (Spain). When described, they are argued to be undistinguishable from recent humans (Gambier, 1989). At Brassempouy (Landes, France), a series of teeth well dated between 30,000 and 34,000 BP have been claimed to be undiagnostic (Henry-Gambier et al., 2004) but are clearly modern in our view (Bailey and Hublin, 2005). More complete are the specimens from Mladeč, dated to 31,000 BP (Wild et al., 2005). Although the Mladeč fossils are said by some to display a mosaic of features (Wolpoff et al., 2000; Frayer et al., in press), they are considered clearly anatomically modern by others (Bräuer et al., in press). Finally, the third group of assemblages in this time range, apparently overlapping with the Aurignacian, is the Châtelperronian. This assemblage has yielded human remains only in two sites: Arcy-sur-Cure (Leroi-Gourhan, 1958) and St. Césaire (Lévêque and Vandermeersch, 1980). Although Neandertal remains have been identified at both sites (Leroi-Gourhan, 1958; Lévêque and Vandermeersch, 1980), some have challenged the integrity of the association between the Châtelperronian assemblage and the Neandertal remains, claiming that complex site formation processes could account for their association (Rigaud, 2000; Connet, 2002).

A large proportion of the fossils excavated from the Grotte du Renne (Arcy-sur-Cure) remain unpublished until now. The goal of this paper is to provide a description of these important fossils and assess their taxonomic position by placing them in a larger late Pleistocene context. This will directly address the third question regarding the biological identity of the makers of one of the early Upper Paleolithic industries (Châtelperronian). Whether they were Neandertals or early modern humans will indirectly shed new light on the second issue concerning the significance of the "transitional" industries.

The Grotte du Renne at Arcy-sur-Cure

The Grotte du Renne at Arcy-sur-Cure is one of several caves in the karstic network of the Jurassic calcareous solid mass which opens out of the left bank of the Arcy-sur-Cure. The site, located 200 km south-east of Paris in the Yonne department of France, was excavated between 1949 and 1963 under the direction of Andre Leroi-Gourhan (1961) (Fig. 1). At the entrance of the cave, fifteen stratigraphic units covering a thickness of four meters were identified and numbered I to XV, and subdivided into alphabetically identified subunits beginning with 'a' at the top of the Layer (Fig. 2). Gravettian cultural remains have been found in Layers IV, V, and VI; Aurignacian in Layer VII; Châtelperronian in Layers VIII, IX, and X; and Mousterian in Layers XI, XII, XIII, and XIV. The reliability of the excavation by Leroi-Gourhan, as well as the integrity of the archaeological layers, has been questioned (White, 2001; Bar-Yosef, in preparation). However, a recent excavation of a preserved section located virtually in the center of the cave, as well as the re-evaluation of the lithic assemblages (David et al., 2001; Connent, 2002) and bone tools (d'Errico et al., 2004) at the Grotte du Renne have confirmed that the Châtelperronian layers represent an undisturbed deposit yielding a well-characterized industry. Although questions can be raised regarding possible admixture in the section where the archaeological layers display a dramatic thinning along a well-marked slope closer to the back of the cave, the Châtelperronian layers are horizontal and display extensive vertical development (Fig. 2). It should also be noted that the Châtelperronian body ornaments do not come preferentially from the uppermost layer

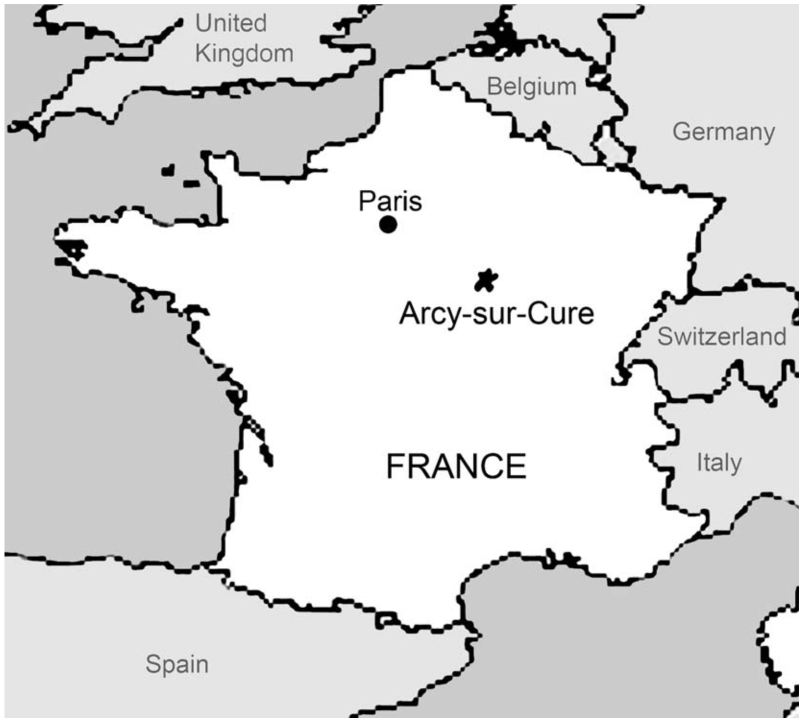

Fig. 1. Map showing the location of the Arcy-sur-Cure site, Yonne, France.

in contact with Aurignacian Layer VII, but rather from the far underlying Layer Xb (d'Errico et al., 1998). In our view, it is therefore unlikely that they could represent exclusive Aurignacian intrusions (no other clear Aurignacian elements have been recognized in these layers). The isolated human teeth analyzed in this paper come from Layers VIII, IX, and X (Xa, b, and c). Their spatial distribution in sections of the site where the Châtelperronian layers span more than 1 m of thickness leaves little doubt as to their stratigraphic assignment.

Based on information from various sites, the Châtelperronian dates to between 38,000 and 33,000 ^{14}C years BP, although a later persistence has been proposed for Les Cottés and Quincay (Leroyer, 1990). The 25 ^{14}C dates obtained in Arcy-sur-Cure display many inconsistencies (David et al., 2001; White, 2001). For Layer X, they range from 15,350 to 33,820 BP; for Layer IX, they range from 15,700 to 45,000 BP; and for Layer VIII, they range from 32,000 to 33,860 BP. It is difficult today to assess the validity of most of these dates, acquired before the 1980s from samples of bone charcoal collected during the 1947–1963 excavations from unknown locations. When only the recently obtained AMS dates are considered, the pattern is more consistent. The AMS dates for Layer Xb, which yielded most of the Châtelperronian remains, are $33{,}820 \pm 720$ BP (OxA-3462), $34{,}450 \pm 750$ BP (OxA-8452/Ly-895), and

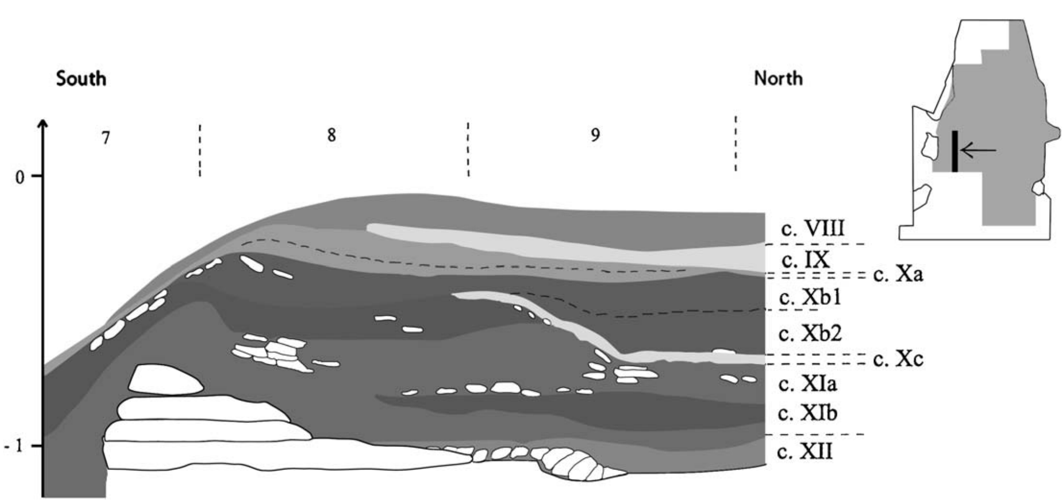

Fig. 2. Profile showing the stratigraphic layers at the Grotte du Renne, Arcy-sur-Cure. Roman numerals indicate layers referred to in the text. Smaller figure shows the site plan with an arrow pointing to the location of the profile. Original drawn by R. Humbert. Reproduced (with permission) from Connet (2002).

33,400 (OxA-9122/Ly-1055) (David et al., 2001). However, in the 1980s an older AMS date of 38,300 ± 1300 (OxA-8451/ly-894) in Xb and a younger date of 31,300 ± 600 BP (OxA-8533/Ly-896) in the underlying Layer Xc were obtained. According to David et al. (2001) and Connet (2002), some sample inversions may have occurred. Alternatively, the inconsistency in dates may result from the existence of a complex plateau in the calibration curve of the ^{14}C dates at around 35,000 BP.

As is often the case in the fossil record, the human remains from the Grotte du Renne are predominantly teeth. Most of the dental remains (29 isolated teeth) come from Châtelperronian layers (especially Layer X; Table 1), as do some immature cranial and postcranial remains (Hublin et al., 1996). A maxillary premolar preserving only the lingual portion of the crown and the lingual root comes from the Aurignacian layer and an additional six teeth come from the Mousterian layers.

Table 1
List of teeth from the Châtelperronian layers of the Grotte du Renne at Arcy-sur-Cure (arranged by level)

Spec no	Layer	Specimen label	Identification	Age	Published
2†	VIII	Z13	Not human		Leroi-Gourhan*
10	VIII	D11.533	Not human		Unpublished
11	VIII	Z11.451	I_2 (L)	Subadult > 8yrs	This study
12	VIII	D10.396	Not human		Unpublished
3†	IXa	Z13	Not human		Leroi-Gourhan*
4†	IXb	B7	P_4 (L)	12-18 yrs	Leroi-Gourhan*
13	IXc	Z13	P^4 (R)	15-18 yrs	This study
16	IX	B7.715	M_2 (R)	older adult	This study
5†	Xb	A6	M_2 (R)**	>15 yrs	Leroi-Gourhan*
6†	Xb	A6	M_3 (R)	older adult	Leroi-Gourhan*
7†	Xb	Z8	C, (L)	>12 yrs	Leroi-Gourhan*
17	Xa	C7	M_{12} (R)	>7 yrs	This study
18[1]	Xb1	D10	dm_1 (R)	4-7 yrs	This study
19[1]	Xb1	D10	I^2 (L)	4-6 yrs	This study
20[1]	Xb1	D10	P^3 (L)	5-7 yrs	This study
21	Xb1c	A11.1916	M_2 (R)	7-9 yrs	This study
22[2]	Xb2	B5	di^2 (R)	4-6 yrs	This study
23[2]	Xb2	B6.1506	I^2 (L)	6-8 yrs	This study
24[2]	Xb2	B6 or B5	P^3 (L)	5-7 yrs	This study
25	Xb2	B11.3191	dm_1 (R)	5-7 yrs	This study
26[3]	Xb2	C7	dm^2 (R)	9-12 mo	This study
27[3]	Xb2	C7	di^1 (R)	<18 mo	This study
28[3]	Xb2	C7	di^2 (R)	7-12 mo	This study
34[3]	Xb2	C7	dm^1 (L)	7-11 mo	This study
29[4]	Xb2	C8	dm_2 (R)	7-15 mo	This study
30[4]	Xb2	C8	M_1 (R)	9-18 mo	This study
31[4]	Xb2	C8	dc_1 (R)	7-15 mo	This study
32	Xb2	C8	di^1 (L)?	>5 yrs	This study
33[4]	Xb2	C8	dm_1 (R)	6-11 mo	This study
35	Xc	A7.806	M_1 (R)	6-9 yrs	This study
36	Xc	A7 or RXb2 B5	di^1 (L)	birth	This study
37	Xc	Z6.2085	dc^1 (R)	3-7 yrs	This study
38	Xc	C9	dc^1 (L)	4-8 mo	This study

[1,2,3,4] Designates that these teeth may come from the same individual (individuals 1,2,3 or 4).
* Leroi-Gourhan, 1958.
** Leroi-Gourhan, 1958 identified as *either* M_1 or M_2.
† These teeth are of uncertain location because of changes in the coordinate system before 1956. The locations of all other teeth have been verified according to the post-1956 grid.

It is important to note that within the Châtelperronian time frame, both anatomically modern humans and Neandertals are documented in Europe (Trinkaus et al., 2003). Leroi-Gourhan's (1958) initial analysis of the teeth from Châtelperronian Layers VIII-X at the Grotte du Renne suggested affinity with Neandertals based on the presence of "primitive" tooth morphology. This was viewed as problematic since the remains were found with Upper Paleolithic tools. Since that time, an analysis of the inner ear morphology of an infant temporal bone has shown clear Neandertal affinities (Hublin et al., 1996), supporting Leroi-Gourhan's earlier assessment. Four of the nine teeth from the Châtelperronian layers identified by Leroi-Gourhan (1958) were never published. In addition, many more teeth have been discovered from the Châtelperronian layers since the initial publication. The description and comparative analysis of these teeth can potentially support or refute a Neandertal affiliation of the remains and thus provide a clearer picture of the makers of the industry.

Because of the temporal overlap of modern humans and Neandertals in Upper Paleolithic Europe, the analysis of the Châtelperronian-associated dental remains at the Grotte du Renne is important for understanding the nature of the Neandertal/modern human transition in Western Europe. If the affinities with Neandertals are substantiated by description and comparison of this sample to the more substantial comparative dental sample of late Pleistocene humans now available, we may also gain important insight into the evolution of the Neandertal lineage. If these remains can be confidently identified as Neandertals, then we can also address whether Neandertals remained essentially unchanged over time or showed morphological evidence suggesting gene flow with the anatomically modern humans.

Materials

Table 1 presents the teeth recovered from the Châtelperronian layers of the Grotte du Renne, and Figure 3 provides a map of their distribution. Teeth are identified by their provenience (layer and square number), as well as by a specimen number, which was assigned by JJH.[1] Four of these—only two of which were published by Leroi-Gourhan (1958)—were originally identified as human but have since been determined by the authors to be non-human. The remaining human teeth are nearly equally distributed between permanent (n = 15) and deciduous (n = 14). Infants, subadults, and adults are represented; however, the majority of the specimens belong to subadults. The preservation of the teeth is generally quite good and most tooth crowns present little to no wear. The relatively large collection of deciduous teeth greatly expands the deciduous tooth sample for fossil hominins.

For our comparative analysis, we included samples to which the teeth would most likely belong: Neandertals and Upper Paleolithic modern humans. Table 2 provides the

[1] Because in many cases the teeth were marked only with their square and layer numbers, the entire set was given a series of arbitrary numbers from 1 to 38 (see Table 1).

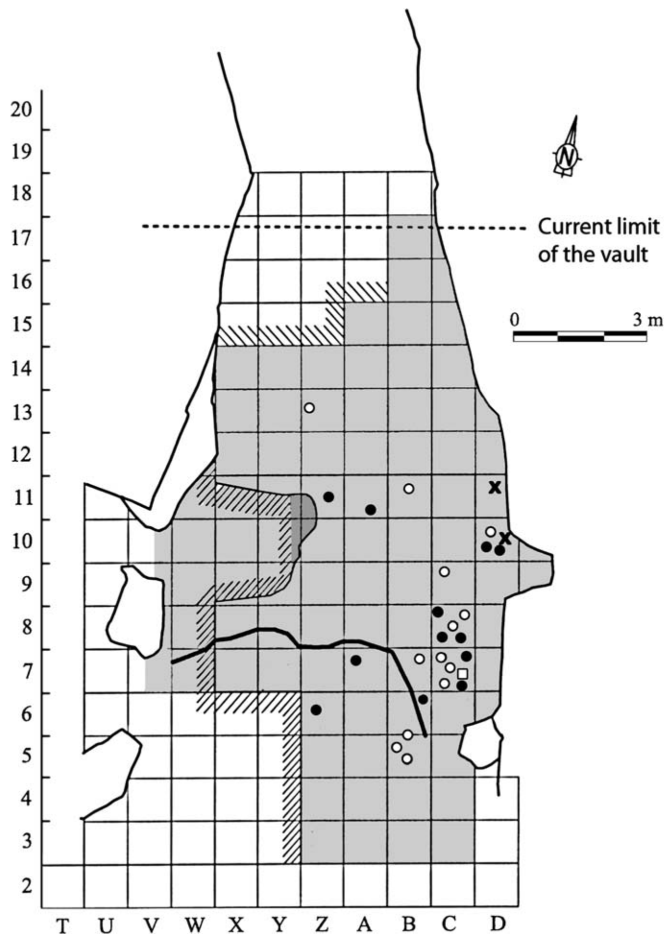

Fig. 3. Site plan with the distribution of the teeth and the temporal bone recovered from the Grotte due Renne, Arcy-sur-Cure. White box: Neandertal child's temporal bone; black circles: teeth that are diagnostically Neandertal; white circles: teeth consistent with (but not proving) Neandertal affiliation; Xs: non-human teeth. Black line extending from W7 to B6 indicates the 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 of the human teeth (Nos. 4, 5, 6 & 7) are not plotted because of the uncertainty of their exact location (see note Table 1). Original drawn by R. Humbert and modified (with permission) from Connet (2002).

composition of the comparative sample of permanent teeth and Table 3 provides the composition of the comparative sample of deciduous teeth.

Methods

Both metric and non-metric data were collected for each specimen. Terminology used for cusp identification follows that of Cope (1888) and Osborn (1888) (see Scott and Turner, 1997:18 for analogous numbering system). Crest and furrow system terminology follows that of Carlsen (1987). Non-metric data were collected using the Arizona State University dental anthropology system (ASUDAS), which currently consists of more than 36 tooth crown and root traits (Turner et al., 1991). Supplemental characters, as outlined in Bailey (2002b: Appendices A and B), were also scored. Where appropriate, we provide a 'score' for the trait's morphological expression based on one of these systems. In the ASUDAS, characters are scored according to discrete criteria based on detailed morphological descriptions and the aid of 23 reference plaques to ensure accurate assessment of variation. Descriptions of the non-metric traits can be found in Scott and Turner (1997), Turner et al. (1991), and Bailey (2002b). The larger permanent tooth samples permit trait frequencies to be calculated for Mousterian Neandertals and Upper Paleolithic modern humans for comparison with the Grotte du Renne sample. Trait frequencies are based on breaking quasi-continuous data into presence/absence states. In our trait-frequency analysis, we use standard breakpoints for ASUDAS traits (Turner, 1987; Irish and Turner, 1990), except when none is given. In those cases, the breakpoint is set at the presumed threshold for the particular trait (e.g., P_4 transverse crest; see Bailey, 2002b). The much smaller deciduous tooth samples of Mousterian Neandertals and Upper Paleolithic modern humans permit only broader morphological comparisons and, therefore, no frequency data are provided. Standard dental measurements, including buccolingual and mesiodistal breadths and root length, were taken with digital calipers. Throughout the text, all measurements are presented in millimeters.

Dental developmental age determinations were based on Schour and Massler (1941). However, we note that the use of modern human age standards may overestimate actual age at death, as earlier hominins, especially Neandertals, may have experienced a faster growth rate than recent modern humans (Dean et al., 2001; Ramirez Rozzi and Bermúdez de Castro, 2004).

Tooth wear was assessed through visual examination with a 10x hand lens. There are several methods available for recording tooth wear in archaeologically derived human populations (Murphy, 1959; Molnar, 1971; Brothwell, 1981). Since our goal was not to extract age estimates from wear status or to compare individuals and/or samples, use of such complex scoring systems did not seem warranted. Therefore, we limited our assessments of wear status to the method outlined by Turner et al. (1991), where scores range from 0 (unworn) to 4 (functional root stump with most of the crown worn away: see also Table 4).

All teeth were examined for pathological conditions, including carious lesions, enamel hypoplasia, and the formation of secondary cementum on the roots. A 10× hand lens was used to identify defects. Enamel hypoplasia was recorded as furrow type, pit type, or plane type (see Hillson, 1996). The furrow type has also been referred to as Linear Enamel Hypoplasia or LEH (Goodman and Rose, 1990).

Descriptions of the permanent teeth (Figs. 4–6)

The dimensions of the Grotte du Renne teeth and their wear status/preservation are listed in Table 4. Comparative dental metrics for the permanent teeth are provided in Table 5, for the deciduous teeth in Table 6, and for the permanent tooth roots in Table 7.

Table 2
Comparative permanent dental samples used in this analysis. Sites and teeth available for morphological and/or metric assessment

Site	Teeth[1,2]	Site	Teeth[1,2]
Neandertals		**Upper Paleolitic modern humans**	
Amud	I^2, C′, P_4	Abeilles	M_1, M_2
Arcy-sur-Cure (Mousterian)	P^4, P_4	Abri Blanchard	M_3
Chateauneuf	I^2	Abri Labatut	M_3
Ciota Ciara (Monte Fenera)	P^3, M_2	Abri Pataud	P^3, P^4, M_1, M_2, M_3
Combe Grenal	I^2	Arcy-sur-Cure UP level	P_4
Eringsdorf	I^2, M_1, M_2	Aurignac	I^2, P^3, P_4, M_1, M_2
Devil's Tower, Gibraltar	M_1, M_2	Castanet	M_2
Grotte Taddeo	C′, P^4, M	Dolní V?stonice	I^2, C′, P_4, M_1, M_2, M_3
Guattari	M_1, M_2, M_3	Farincourt	P_4, M_1, M_2, M_3
Hortus	I^2, P^3, P^4, P_4, M_1, M_2, M_3	Fourneau du Diable	P_4
Kebara	P_4, M_1, M_2, M_3	Fontechevade	M_1
Krapina	I^2, C′, P^3, P^4, P_4, M_1, M_2, M_3	Grotte des Rois	C′, P^3, P^4, P_4, M_1, M_2, M_3
Kůlna	C′, P^3, P^4	Gough's Cave	I^2, C′, P^3, P_4, M_1, M_2
La Fate	M_1, M_2	Grotte des Abeilles	M_1, M_2
La Ferrassie	M_1	Isturitz	M_1, M_2, M_3
La Quina	I^2, P^3, P^4, P_4, M_1, M_2, M_3	La Chaud	P_4, M_1, M_2, M_3
Malarnaud	M_1	La Ferrassie	M_2, M_3
Monsempron	I^2, C′, P^3, P^4, P_4	La Gravette	M_1
Montgaudier	M_1	La Greze	M_2
Montmaurin	M_1, M_2, M_3	La Linde	M_1, M_2
Ochoz	P_4, M_1, M_2, M_3	La Madeleine	M_1
Petit-puymoyen	P_4, M_1, M_2,M_3	Laugerie Basse	I^2, P^3, M_1, M_2, M_3
Pontnewyedd	P^4, P_4, M_1, M_2	Les Vachons	M_2
Regourdou	P_4, M_1, M_2, M_3	Miesslingtal	M_1
Saccopastore	C′, P^3, P^4	Mladeč	P^3
Shanidar	P_4, M_1, M_2, M_3	Oase	M_2, M_3
Spy	P_4, M_1, M_2, M_3	Oberkassel	I^2, C′, P_4, M_1, M_2, M_3
Tabun	I^2, P^3, P^4, P_4, M_1, M_2, M_3	Pavlov	M_3
Taubach	M_1	Peche de la Boissiere	M_2
Vindija	I^2, C′, M_1, M_2, M_3	Roc de Combe	I^2
		Solutre	M_1
		St Germain la Rivière	I^2, C′, P^3, P^4, P_4, M_1, M_2, M_3

[1] Not all teeth were used in all analyses. Worn teeth on which morphology could not be scored were used for metric comparison only.
[2] Some sites contain teeth from more than one individual and more than one of the teeth listed.

Maxillary incisors

Tooth No. 19: Left I^2. Sq. Xb1.D10 (unpublished). This is a well-preserved, unworn crown with only 2.9 mm of root development on the distal surface. The lack of wear and degree of root development suggest the tooth was unerupted and indicate a developmental age of 4–6 years. No pathological conditions are noted.

The lingual surface is strongly shovel shaped (ASUDAS grade 5), possessing thick mesial and distal marginal ridges. These ridges circumscribe a deep sulcus and converge at a moderately developed cingulum. The cingulum forms a lingual tubercle lacking a free apex (ASUDAS *tuberculum dentale*: grade 5-). Two distinct ridges extend from the lingual tubercle mid-way to the incisal edge. Of these, the distal ridge is more strongly developed. An interruption groove is present between the lingual tubercle and the distal marginal ridge. The labial surface is mesiodistally and superiorinferiorly convex but is otherwise featureless.

Tooth No. 23: Left I^2. Sq. Xb2. B6.1506 (unpublished). This completely formed crown and incompletely formed root are cracked labiolingually but are otherwise well preserved. The root is one-half to two-thirds formed (approximately 8 mm), suggesting a developmental age of 6–8 years. Two bands of hypoplastic pitting can be observed on both lingual and labial surfaces. The first band occurs ~2.8 mm from the crown tip (total crown height–11.9 mm) and is ~1.0 mm wide. The second, smaller band of pits occurs ~4.9 mm from cusp tip. A shallow labial furrow occurs just below and mesial to the second hypoplastic band.

Three mammelons are present along the incisal edge, and their associated furrows are visible on the lingual surface. Lingually, the crown exhibits strong shoveling (ASUDAS grade 5) with well-developed marginal ridges that meet at the cingulum and form a deep lingual sulcus. The cingulum comprises a moderately-sized lingual tubercle lacking a free apex (ASUDAS *tuberculum dentale*: grade 5-). At the base of the distal marginal ridge there is a marked interruption groove dividing it from the cingulum. The crown is both mesiodistally and superioinferiorly convex.

Maxillary premolars

Tooth No. 20: Left P^3. Sq. Xb1.D10 (unpublished). This is a well-preserved, fully formed crown with less than 1.0 mm of root development. The lack of wear and extent of root

Table 3
Comparative deciduous dental samples used in this analysis. Sites and teeth available for morphological and/or metric assessment

Site	Teeth[1,2]
Neandertals	
Dederiyeh	di^1, dc', dm^1, dm^2, dm_1, dm_2
Pech de l'Azé	di^1, dm^1, dm^2
Roc de Marsal	di^1, di^2, dc', di_1, di_2, dc, dm^1, dm^2, dm_1, dm_2
Archi	dm_1, dm_2
La Quina	dm^1, dm^2
Upper Paleolithic modern humans	
Isturitz III	dm_1, dm_2
St Germain la Rivière	dc', dm^1, dm^2, di_2, dm_1, dm_2
Solutre	dm_1, dm_2
Miesslingtal	dm_2
Bruniquel	di^1, di^2, dm_1, dm_2
La Madeleine	di^1, di^2, dc', dm^1, dm^2, di_1, di_2, dc, dm_1, dm_2
Fontechevade	dm_2
Rebenley Oberkassel	dc, dm^2
Aveline	dm_2
Capelle	dm_2, dm^1, dm^2

[1] Not all teeth were used in all analyses. Worn teeth on which morphology could not be scored were used for metric comparison only.
[2] Some sites contain teeth from more than one individual and more than one of the teeth listed.

Table 4
Dimensions, wear status and preservation of the tooth crowns from the Grotte du Renne at Arcy-sur-Cure (arranged by tooth type)

Tooth	Spec no	BL (in mm)	MD (in mm)	Wear status, preservation
I^2 (L)	19	8.8	8.7	0
I^2 (L)	23	8.2	8.1	0
P^3 (L)	20	11.3	8.3	0
P^3 (L)	24	–	–	0, only half crown present
P^4 (R)	13	10.5	7.3	0-1
I_2 (L)	11	7.8	6.7	1
$C_,$ (L)	7	9.8	7.5	0
P_4 (L)	4	10.2	8.5	0-1
M_1 (R)	30	7.6	9.4	0, incompletely formed crown
M_1 (R)	35	11.1	12.0	0-1
M_{12} (R)	17	–	–	1, only half crown present
M_2 (R)	5	11.6	12.2	1
M_2 (R)	21	11.6	12.6	0
M_2 (R)	16	8.8	9.3	2, damaged protoconid
M_3 (R)	6	10.8	11.3	2, damaged metaconid
di^1 (L)?	32	5.7	7.3	2
di^1 (L)	36	4.7	7.2	0, incompletely formed crown
di^1 (R)	27	5.6	7.3	0
di^2 (R)	22	5.3	6.1	1, crown chipped mesially
di^2 (R)	28	5.1	6.3	0
dc' (L)	37	7.5	8.0	1
dc' (L)	38	7.0	7.4	0
dm^1 (L)	34	8.9	9.0	0
dm^2 (R)	26	9.8	9.9	0
$dc_,$ (R)	31	5.7	6.5	0
dm_1 (R)	18	7.6	9.6	0-1, crown chipped distally
dm_1 (R)	25	7.5	8.4	2
dm_1 (R)	33	7.3	8.3	0
dm_2 (R)	29	8.9	10.0	0

Unless indicated, tooth is well preserved (not chipped, broken, or severely fractured).
Tooth status (from Turner et al., 1991):
0: unworn, as in unerupted or erupting teeth
0-1: Wear facets can be seen with a 10x hand lens on one or more cusp occlusal planes
1: Dentin is exposed on one or more cusps
2: Cusps worn off
3: Exposed pulp
4: Root stump is functional. All or most of the enamel is worn off.

formation indicate a developmental age of 5–7 years. There are tiny hypoplastic pits on the buccal surface that appear to be randomly distributed.

A deep and uninterrupted sagittal sulcus runs the length of the tooth, bisects the mesial margin, and continues onto the mesial interproximal surface. The paracone is larger than the protocone, the bulk of which is oriented mesially. In addition to the two major cusps, the crown possesses a medium-sized distal accessory cusp (Bailey, 2002b grade 2). The essential crests of the major cusps are well developed. The crest on the protocone is bifurcated. The mesial marginal ridge is well developed. Buccally, there is a slight swelling of the paracone essential lobe but the surface is otherwise featureless. The cervical enamel line is straight with no enamel extension.

Tooth No. 24: Left P^3. Sq. Xb2.B5 or B6 (unpublished). This tooth consists of a completely-formed, but only partially-preserved crown with approximately 1.0–1.5 mm of root development. The buccal half of the paracone has been broken at the occlusal crest, and there are multiple microfractures on the protocone. Otherwise, the tooth is well preserved. The absence of wear and degree of root development suggest the tooth was unerupted and indicate a developmental age of 5–7 years. No pathological conditions are noted.

The occlusal surface possesses multiple ridges and accessory fissures. The bulk of the protocone is mesially placed relative to the paracone. The moderately developed essential crest of the paracone bifurcates near the sagittal sulcus. The essential crest of the protocone is trifurcated, comprising one large medial and two smaller mesial and distal crests. In addition, accessory ridges are present on both the paracone (distal accessory ridge) and protocone (mesial and distal accessory ridges). The mesial marginal ridge is well developed and the distal marginal ridge comprises a large distal accessory cusp (Bailey, 2002b grade 3). The cervical enamel line is straight with no enamel extension.

Tooth No. 13: Right P^4. Sq. IXc.Z13 (unpublished). This well-preserved crown and root exhibits vertically oriented microfractures on all surfaces. The crown is minimally worn (stage 0–1), with only a small occlusal facet (~1.8 mm × 2.0 mm) on the protocone. The root is completely formed and the tooth would have been in full occlusion when the individual died. Considering the minimal wear on this tooth and completely developed root, it likely belonged to a subadult or young adult (15–18 years). There is a small amount of calculus adhering to the buccal surface of the crown, and there is some cementum present on the apical third of the root. No pathological conditions are noted.

The mesial interproximal facet measures 4.2 mm × 2.3 mm, while the distal interproximal facet measures 5.9 mm × 2.6 mm. Neither the mesial nor distal interproximal facets

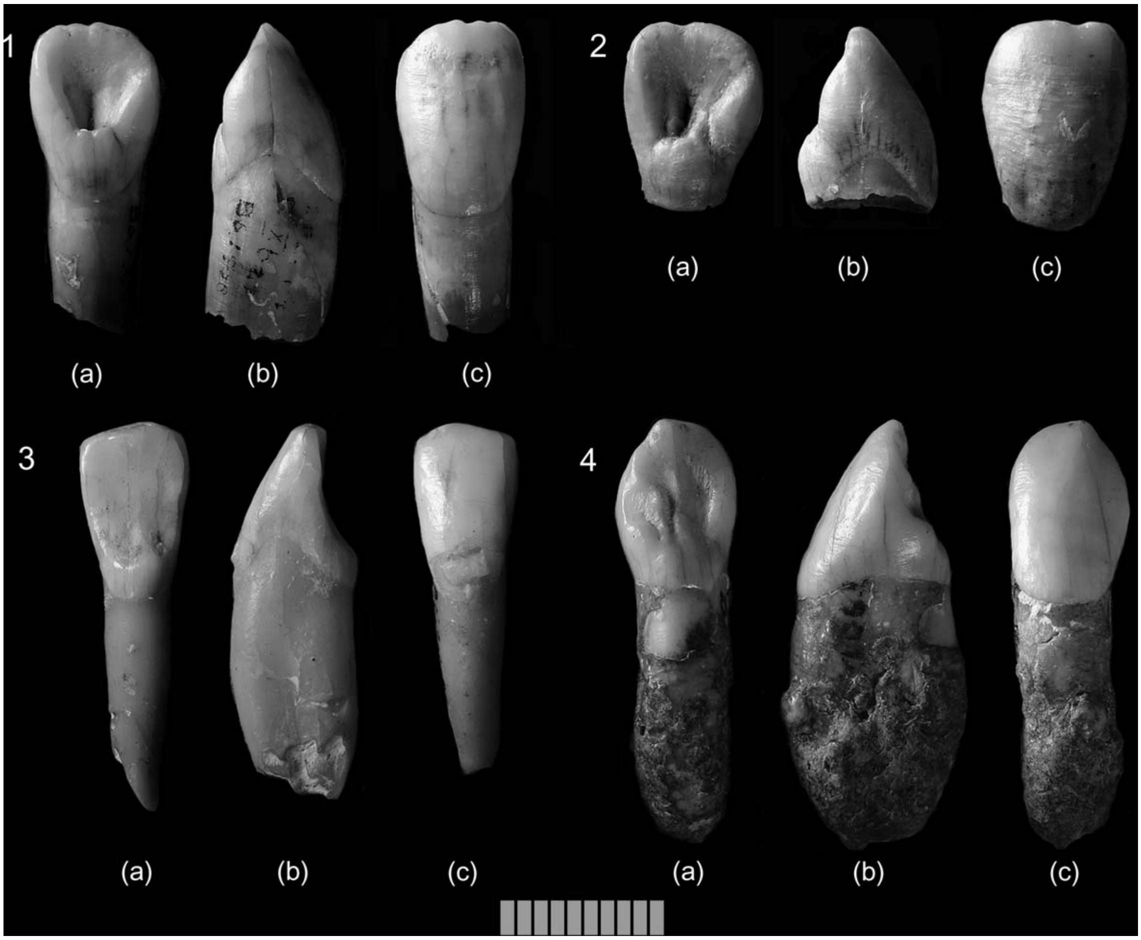

Fig. 4. The Grotte du Renne, Arcy-sur-Cure permanent incisors and canine. 1: Tooth No. 19, left I^2 (a) lingual (b) distal (c) labial; 2: Tooth No. 23, left I^2 (a) lingual (b) distal (c) labial; 3: Tooth No. 11, left I_2 (a) lingual (b) distal (c) labial; 4: Tooth No. 7, left C_1 (a) lingual (b) distal (c) labial. Scale bar in mm.

exhibit the subvertical grooves that are often observed in Middle-Pleistocene postcanine teeth (Villa and Giacobini, 1995).

The protocone and paracone are subequal in size and are separated by a well-defined, uninterrupted sagittal sulcus. This sulcus is confined to the central portion of the tooth and does not extend to either the mesial or distal margins. The distal marginal ridge is thicker than the mesial marginal ridge and presents a small accessory cusp (Bailey, 2002b grade 1). The essential crests of both paracone and protocone are well developed and bifurcate near the sagittal sulcus. The paracone also possesses a distal accessory ridge. The root deflects distally and presents a shallow but wide developmental groove both mesially and distally.

Mandibular incisor

Tooth No. 11: Left I_2. Sq. VIII.Z11.451 (unpublished). The crown and root of this left I_2 are completely formed. The root apex was broken post-mortem but otherwise the tooth is well preserved. The incisal edge of the crown is slightly worn on the distal aspect, presenting a small area of exposed dentine (stage 1). The completely developed root and presence of incisal wear indicate that the tooth was in functional occlusion. Considering the rapidity with which Late Paleolithic hominins wore their incisors, the degree of wear on this tooth suggests that it belonged to a subadult (>8 years). No pathological conditions are noted.

No mammelons are present. The lingual surface presents trace shoveling (ASUDAS grade 1) with only the slightest development of the mesial and distal marginal ridges. The moderately expressed cingulum blends into a slightly expressed median ridge (no scoring standards apply). The labial surface is featureless.

The root presents moderately expressed mesial and distal developmental grooves that become wider towards the root apex. Both tooth crown and root are superioinferiorly convex.

Mandibular canine

Tooth No. 7: Left C_1. Sq. Xb.Z8 (Leroi-Gourhan, 1958). This tooth has a completely formed crown and root. The crown presents long thin microfractures running lengthwise but is otherwise well preserved. The crown is completely unworn, with neither interproximal nor occlusal facets. In modern humans

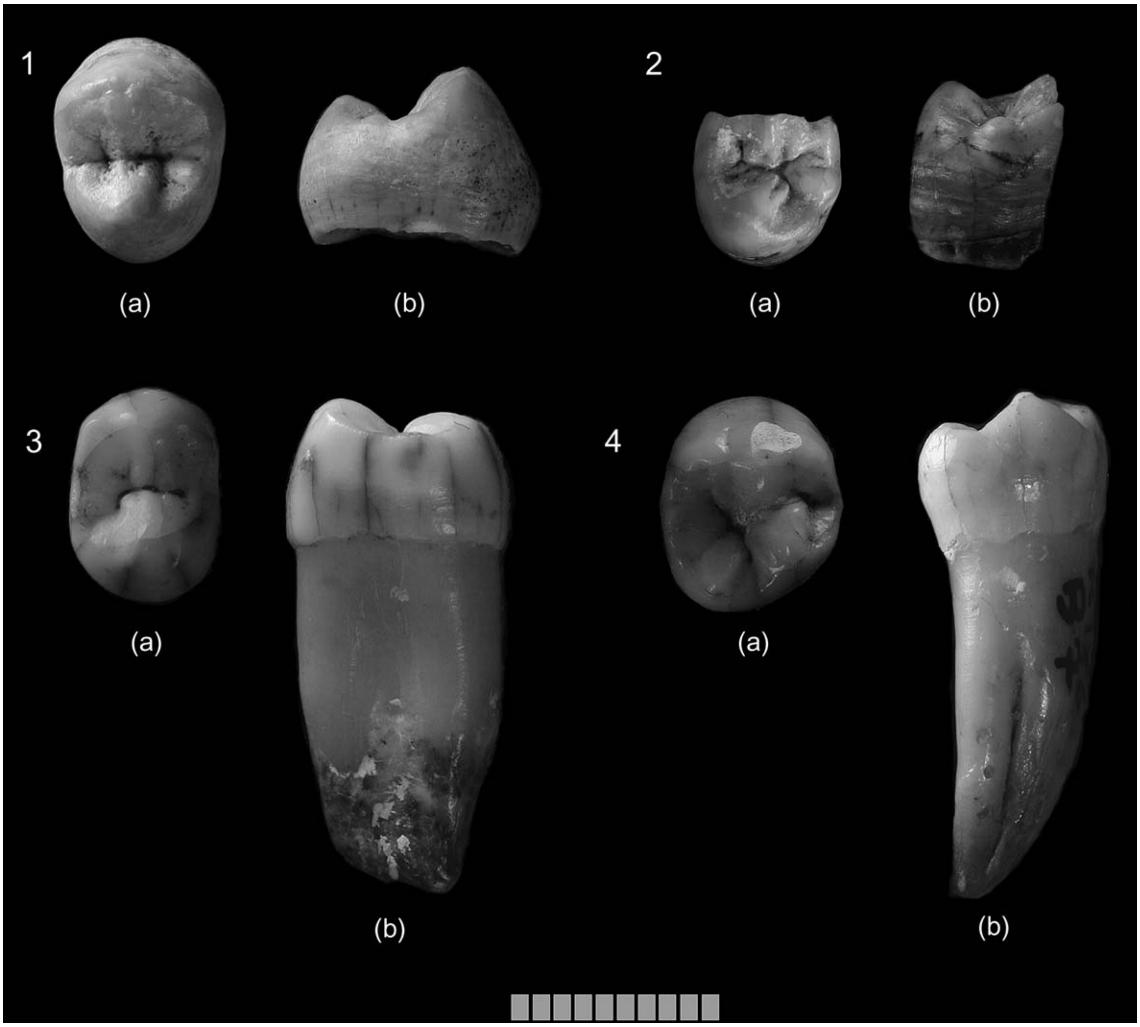

Fig. 5. The Grotte du Renne, Arcy-sur-Cure permanent premolars. 1: Tooth No. 20, left P^3 (a) occlusal (b) distal; 2: Tooth No. 24, left P^3 (a) occlusal (b) distal; 3: Tooth No. 13, right P^4 (a) occlusal (b) distal; 4: Tooth No. 4, left P_4 (a) occlusal (b) lingual. Scale bar in mm.

the root of the mandibular canine is formed by 12 years of age, at which point the tooth is also in functional occlusion. The complete lack of occlusal and interproximal wear is unusual and suggests that the tooth was malpositioned (not in occlusion), impacted, and/or that the adjacent teeth (I_2 and P_3) were missing.

A buccally displaced pit at the crown apex is most likely a developmental defect. In addition, the crown shows evidence of furrow-type linear hypoplasia (LEH) roughly one-half (7.7 mm) and two-thirds (9.8 mm) the distance from the apex. The entire root is covered in cementum, and the lower half exhibits marked hypercementosis, resulting in an irregular shape.

The crown and root are convex when viewed from the side. The crown apex is distinct, being set off from the rest of the incisal margin. The distal crown margin is steeply angled. The lingual surface is somewhat shovel shaped (ASUDAS grade 2) with moderately developed mesial and distal marginal ridges. The medial ridge blends into a distinct lingual cingulum, and there is a thin but well-developed distal accessory ridge (ASUDAS grade 5). The root presents two radicals.

Mandibular premolar

Tooth No. 4: Left P_4. Sq. IXb.B7 (Leroi-Gourhan, 1958). The crown and root of this tooth are completely formed and well preserved. The crown exhibits minor occlusal wear, which is limited to small facets on the mesiobuccal face, the distolingual cusplet and the distal cusplet (stage 0–1). The mesial and distal interproximal facets are small (1.5 mm × 1.8 mm and 2 mm × 2.1 mm, respectively) and lack subvertical grooves. The completely formed root and minor wear suggest that this tooth belonged to a subadult or young adult between 12 and 18 years of age. There is a vertical line of hypoplastic pitting on the distobuccal aspect of the protoconid.

The tooth is asymmetrical in occlusal view with a marked inclination of the mesiolingual border (Bailey, 2002b grade 2). The tooth possesses three lingual cusps. Of these, the

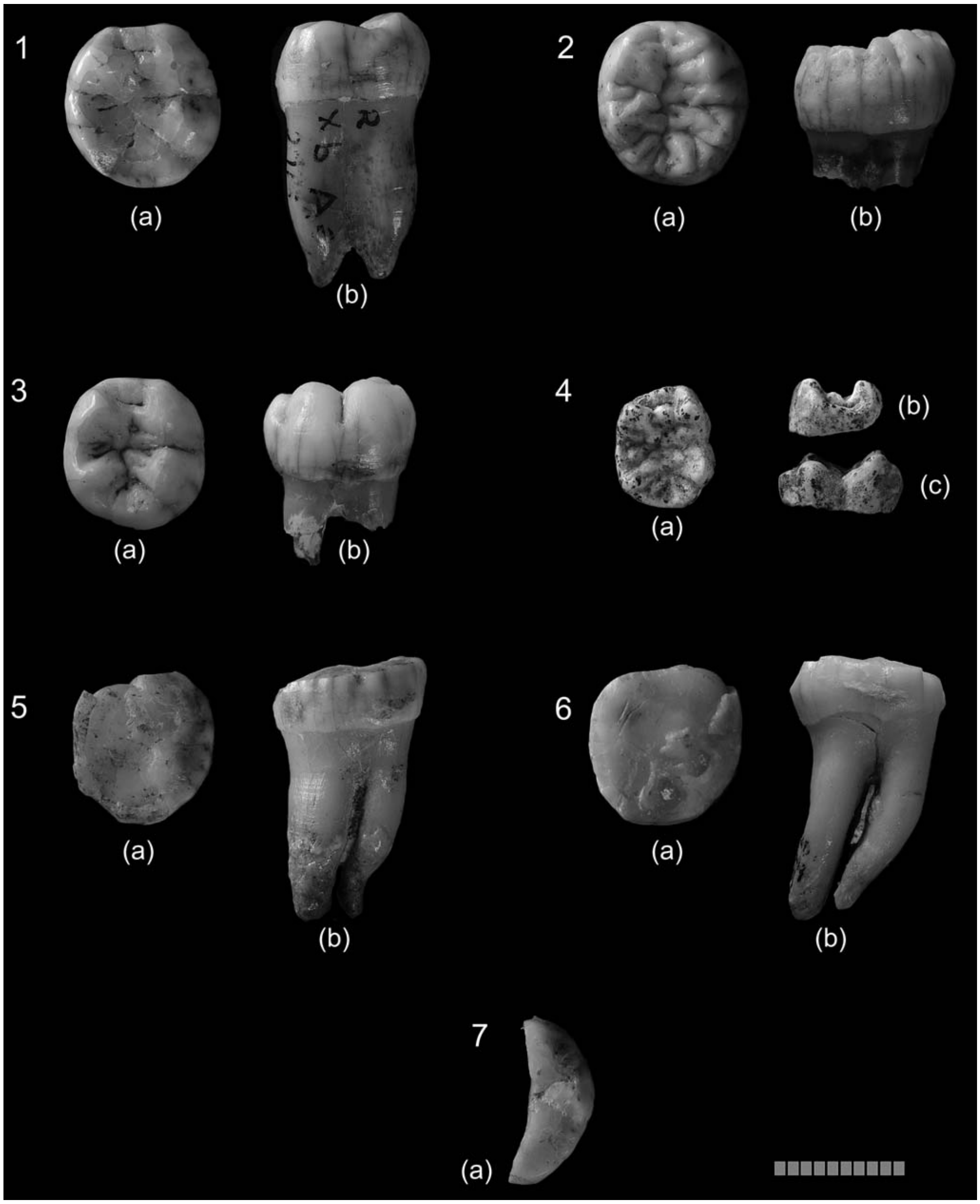

Fig. 6. The Grotte du Renne, Arcy-sur-Cure permanent molars. 1: Tooth No. 5, right M_2 (a) occlusal (b) mesial; 2: Tooth No. 21, right M_2 (a) occlusal (b) distal; 3: Tooth No. 35, right M_1 (a) occlusal (b) buccal; 4: Tooth No. 30, right M_1 (a) occlusal (b) mesial (c) lingual; 5: Tooth No. 6, right M_3 (a) occlusal (b) buccal; 6: Tooth No. 16, right M_2 (a) occlusal (b) buccal; 7: Tooth No. 17, right M_1 or M_2 (a) occlusal. Scale bar in mm.

metaconid (mesio-lingual cusp) is the largest, followed by the distolingual and distal cusps (ASUDAS grade 8). Both the protoconid and metaconid have well-developed essential crests that are separated by a weak fissure and so do not form a transverse crest. The essential crests define the distal border of a large anterior fovea (Bailey, 2002b grade 3). There is a well-developed distal accessory ridge on the protoconid (Bailey, 2002b grade 3). The buccal aspect of the crown is superioinferiorly convex.

The root is convex when viewed from the side, and the root apex deflects distally. A deep mesio-lingual groove nearly separates the root in two (ASUDAS Tomes root: grade 4). The distal component of the root consists of lingual and buccal components separated by a wide, shallow developmental groove.

Mandibular molars

Tooth No. 30: Right M_1. Sq. Xb2.C8 (unpublished). This incompletely formed tooth cap is well preserved. Approximately one-half the crown is formed, suggesting a developmental age of 9–18 months. No pathological conditions are noted.

The occlusal surface presents six cusps, although the fissure between the hypoconulid and Cusp 6 is weakly defined. The hypoconulid is large (ASUDAS Cusp 5: grade 4), and the Cusp 6 is nearly equal in size (ASUDAS grade 3). The cusp tips are high, and the essential crests of the four major cusps are moderately developed. The protoconid and metaconid are joined by a marked bridge of enamel that is separated from the adjacent cusps by weak furrows. The form of this

Table 5
A comparison of the Grotte du Renne permanent tooth metrics (bucco-lingual breadth) to that of Neandertals, Upper Paleolithic, and contemporary modern humans (in mm). Comparative data from Bailey, unpublished

Group	I^2 mean (range) n	P^3 mean (range) n	P^4 mean (range) n	I_2 mean (range) n	$C_,$ mean (range) n	P_4 mean (range) n	M_1 mean (range) n	M_2 mean (range) n	M_3 mean (range) n
Grotte du Renne (Châtelperronian)	8.2, 8.8	11.3	10.5	7.8	9.8	10.2	11.1	11.6, 11.6	10.8
Neandertal (Mousterian)	8.1 (7.4-8.8) n = 5	10.3 (8.1-11.3) n = 10	10.3 (8.2-11.3) n = 9	7.5 (6.0-8.0) n = 6	8.5 (5.6-9.8) n = 8	8.9 (7.6-10.5) n = 10	10.8 (9.7-11.8) n = 16	10.8 (9.9-12.1) n = 14	10.8 (7.8-13.1) n = 11
Upper Paleolithic	6.7 (5.8-8.3) n = 11	9.6 (8.7-10.6) n = 11	9.6 (8.8-10.5) n = 10	6.7 (6.0-7.5) n = 20	8.2 (7.7-9.5) n = 19	8.3 (7.1-9.2) n = 19	10.8 (9.8-11.9) n = 32	10.6 (9.8-12.3) n = 32	10.5 (7.7-11.8) n = 16
Recent humans	6.6 (5.2-8.1) n = 69	9.3 (7.9-11.2) n = 128	9.4 (7.6-12.3) n = 127	6.2 (4.9-7.7) n = 88	7.6 (6.1-9.4) n = 84	8.3 (6.8-10.8) n = 113	10.7 (8.6-12.6) n = 146	10.2 (8.6-12.5) n = 137	10.3 (8.6-12.6) n = 91

mid-trigonid crest (Bailey, 2002b grade 2) is nearly identical to that of the dm_2 (No. 29). The moderately developed mesial marginal ridge is lower than the mid-trigonid crest. The metaconid presents a moderately developed distal accessory crest. The entoconid possesses a well-developed, bifurcated essential crest and mesial and distal accessory crests. The hypoconid essential crest rises near the occlusal basin.

Tooth No. 35: Right M_1. Sq. Xc.A7.806 (unpublished). This tooth possesses a relatively unworn crown and a broken root. Vertically oriented microfractures can be observed along the enamel, but otherwise the tooth is well preserved. Because only 4 to 8 mm of the root is preserved, the extent to which it was developed is unclear. Occlusal surface wear is limited to polishing (stage 0—1). A small mesial interproximal facet, measuring 2.9 mm × 1.9 mm, is present and contains no subvertical grooves. The small interproximal facet and the occlusal polishing suggest that the tooth had recently erupted and was probably not in full functional occlusion. The lack of a distal interproximal facet indicates that the M_2 had not yet erupted. Taken together, this indicates a likely age of 6—9 yrs, and certainly less than 12 years, for this individual. No pathological conditions are noted.

The crown presents six cusps arranged in a Y pattern. The protoconid is the largest cusp, followed by the metaconid and hypoconid (which are equal in size), the entoconid, the hypoconulid, and the Cusp 6. The hypoconulid is large (ASUDAS Cusp 5: grade 5), and the Cusp 6 is much smaller (ASUDAS grade 1). The four major cusps present well-developed essential crests. The metaconid essential crest deflects distally and comes in contact with the entoconid, forming a deflecting wrinkle (ASUDAS grade 4). The major cusps also present mesial and distal accessory crests. The mesial accessory crests of the protoconid and metaconid are joined by a bridge of enamel forming a mid-trigonid crest (Bailey, 2002b grade 2). This crest forms the distal border of a wide and deep anterior fovea (ASUDAS grade 3). Both lingual and buccal surfaces are

Table 6
A comparison of the Grotte du Renne deciduous tooth metrics (bucco-lingual breadth) to that of Neandertals, Upper Paleolithic, and contemporary modern humans (in mm). Comparative data from Bailey, unpublished, unless otherwise noted

Group	di^1 mean (range) n	di^2 mean (range) n	dc' mean (range) n	dm^1 mean (range) n	dm^2 mean (range) N	$dc_,$ mean (range) n	dm_1 mean (range) n	dm_2 mean (range) n
Grotte du Renne (Châtelperronian)	5.3 (4.7-5.7)	5.2 (5.1, 5.3)	7.25 (7.0, 7.5)	8.9	9.8	5.7	7.5 (7.3-7.6)	8.9
Neandertal (Mousterian)	6.1 (5.4-6.9) n = 6	5.7 (5.0-6.3) n = 7	6.5 (5.5-7.5) n = 6	9.1 (8.8-9.8) n = 5	10.3 (9.3-10.6) n = 5	6.0 (5.3-6.6) n = 8	7.6 (6.6-8.7) n = 13	9.4 (8.7-10.5) n = 14
Upper Paleolithic	5.1 (5.0,5.1) n = 2	4.8 (4.2-5.1) n = 3	6.3 (6.3-6.4) n = 3	9.4 (9.0-9.8) n = 3	10.5 (9.9-10.7) n = 3	5.1 (4.6,5.6) n = 2	7.0 (6.3-8.0) n = 7	9.1 (7.8-10.5) n = 11
Contemporary modern humans	5.0^	4.0^	7.0^	8.5^	10.0^	6.0 (5.6-6.3) n = 3	7.51 (7.3-7.7) n = 4	9.3 (9.0-10.0) n = 4

^ From Tillier (1979).

Table 7
A comparison of tooth root lengths from the Grotte du Renne to those of Neandertals and Upper Paleolithic modern humans*

	P^4 mean (range) n	C, mean (range) n	P_4 mean (range) n	M_1 mean (range) n	M_2 mean (range) n	M_3 mean (range) n
Arcy-sur-Cure	16.6	18	17.4	13.6	14.4	15.0
Mean Neandertal	17.6 (16.2-19.0) n = 10	19.4 (16.3-23.2) n = 8	18.7 (14.5-22.6) n = 7	14.3 (12.2-16.8) n = 9	15.3 (14.3-16.5) n = 6	13.2 (10.0-15.5) n = 8
Mean Upper Paleolithic	11.9 (10.5-13.3) n = 2	16.2 (13.1-19.0) n = 6	15.0 (12.6-17.1) n = 9	13.2 (11.6-14.0) n = 3	13.7 (11.3-16.8) n = 8	No data

* Root measurements taken from the lingual aspect of P^4, C, and P_4 and from the lingual aspect of the mesial root of M_1, M_2 and M_3.

rounded in profile. The buccal surface is also strongly angled, shifting the cusp tips of the protoconid and hypoconid towards the occlusal basin. There is a strong buccal groove separating the protoconid and hypoconid. The hypoconid and hypoconulid are also separated by a weaker buccal groove, which ends in a furrow that deflects mesially. The buccal enamel line is more or less strait, dipping slightly where the roots bifurcate, but no enamel extension is present.

Tooth No. 17: Right M_1 or M_2. Sq. Xa.C7 (unpublished). This is the buccal half of a right mandibular molar crown as judged by the deep intercuspal groove, most typical of the buccal separation between the protoconid and hypoconid, and the presence of both mesial and distal interproximal facets. The occlusal surface is somewhat worn (grade 1). The minimum age of this individual is 7 years if the tooth is an M_1 (but probably closer to 12 given the extent of wear), or 15 years if the tooth is an M_2 (but probably closer to 20 given the extent of wear). There is some pitting buccally near the cusp tip of the metaconid, and at the junction between the metaconid and entoconid. The hypoconulid presents a large defect that is obscured by matrix, making it difficult to determine if it is developmental or the result of a carious lesion. The protoconid, hypoconid, and hypoconulid are partially preserved making it impossible to determine cusp pattern. The preserved morphology shows a large hypoconulid (ASUDAS Cusp 5: grade 5). The pulp chamber is exposed by postmortem fracture and measures 6.3 mm mesiodistally.

Tooth No. 5: Right M_2. Sq. Xb.A6 (Leroi-Gourhan, 1958). The crown and root of this tooth are completely formed. Microfractures occur mesially along the midline of all cusps but are not detectable on the occlusal surface. The inferior half of the distal root is broken, but otherwise the tooth is well preserved. The occlusal surface is moderately worn with small facets on the four major cusps (stage 1). Where dentine is exposed the facets are small (pin size). This degree of tooth wear suggests the individual was an older subadult or young adult (>15 years). The mesial interproximal facet measures 4.1 mm × 2.5 mm. Within this facet, there is one shallow subvertical groove toward the lingual side. The distal interproximal facet measures 3.3 mm × 2.5 mm and contains no subvertical grooves. A small amount of calculus adheres to the crown near the crown-root junction. No pathological conditions are noted.

The crown possesses five cusps arranged in a Y pattern. The hypoconulid is large (ASUDAS Cusp 5: grade 5). Leroi-Gourhan (1958) believed there may have been a sixth cusp because of the disposition of the hypoconulid. While this seems likely, wear obscures any fissures that may have been present. The protoconid essential crest and the metaconid mesial accessory crest join to form a mid-trigonid crest that is partially interrupted by a weak fissure (Bailey, 2002b grade 1). This crest forms the distal border of a large anterior fovea (ASUDAS grade 3). The mesial and distal lobes of the metaconid are well developed. In buccal profile, the tooth is quite convex. A small buccal pit (ASUDAS protostylid: grade 1) is present, and a moderately expressed furrow appears between the hypoconid and hypoconulid on the buccal surface. The enamel line dips slightly where the mesial and distal roots divide, but no enamel extension is present.

The mesial and distal roots are well separated and deflect distally. There is a deep and wide developmental groove on the mesial root that nearly separates it into two distinct roots. Two distinct apices are present.

Tooth No. 21: Right M_2. Sq. Xb1c.A11.1916 (unpublished). This tooth consists of a completed crown with approximately 4 mm of root growth. This suggests a developmental age between 7 and 9 years. There are developmental defects (pitting) around the cusp apices and at approximately one-third of the distance to the crown base. These are especially marked distally and buccally.

The occlusal surface presents a minimum of seven cusps arranged in an X pattern with many accessory fissures and crests (ASUDAS cusp pattern: Cusps 1 (protoconid) and 4 (entoconid) in contact). The protoconid possesses a well-developed essential crest that meets the essential crest of the metaconid at the sagittal sulcus. The mesial accessory crest is also well developed and joins the mesial accessory crest of the metaconid to form a weak mid-trigonid crest that is partially interrupted by an interlobal groove (Bailey, 2002b grade 1). This crest forms the distal border of a large anterior fovea (ASUDAS grade 3). In mesial view, the crest joining the protoconid and metaconid is higher than the mesial marginal ridge. The distal accessory crest of the protoconid is very well developed and nearly forms a distinct cusp, being divided from the essential crest by a fissure that continues onto the buccal surface. This crest meets the essential crest of the entoconid. The metaconid possesses a markedly developed essential crest and a moderately developed mesial accessory crest that joins the mesial accessory crest of the protoconid. A distal accessory crest is not present. The hypoconid is rather small and compromised by the large hypoconulid. The hypoconid has an essential crest that bifurcates mid-way to the occlusal basin. The entoconid has a very well-developed essential crest that bifurcates near the occlusal basin. The distal accessory crest on the entoconid is not well defined. Between the entoconid and metaconid there is a small Cusp 7 (ASUDAS grade 2) that is delineated occlusally by mesial and distal fissures, although lingually the fissures are only weakly expressed. The large hypoconulid (ASUDAS Cusp 5: grade 5) has a well-developed essential crest and smaller mesial and distal accessory crests (the distal accessory crest is nearly a cuspule). This is unusual for the hypoconulid, which rarely has well-defined occlusal morphology (personal observation). Cusp 6 is smaller than the hypoconulid (ASUDAS grade 2) and is composed of two developed lobes, which are defined by both occlusal and lingual fissures. The presence of two lobes makes Cusp 6 appear to be composed of two cuspules. Finally, the tooth presents a small ridge that extends from the mesial marginal ridge to the mid-trigonid crest.

The lingual, buccal, and distal surfaces present furrows associated with the various cusps and cusplets. In addition, the mesial surface has a small pit lingual and inferior to the mesial marginal ridge, and the buccal surface presents a furrow on the protoconid that does not appear to be related to the main buccal groove. Therefore, it does not match the definition of a protostylid according to the ASUDAS. This morphological feature has been observed in several Middle Pleistocene hominins (Bailey, unpublished data).

Tooth No. 16: Right M_2. Sq. IX.B7.715 (unpublished). This heavily worn molar consists of a poorly preserved crown with a piece of alveolus preserved between the mesial and distal roots. The degree of occlusal wear (see below) suggests it belonged to a middle-aged adult. Side identification is based on presumed distal deflection of the roots and the presence of a dip in the enamel (<0.5 mm) near the root bifurcation, which tends to occur on the buccal surface. Wide mesial and distal interproximal facets suggest that the tooth is an M_2. A fracture between the mesial and distal roots deflects sharply distally beginning approximately 1 mm from the enamel line. There is a 3.7 mm × 2.9 mm chip missing from the mesio-buccal corner and an occlusal fracture running mesiobuccally, intersecting with the mesiolingual fracture. Some calculus adheres to the buccal crown surface.

The pattern of wear on this tooth is unusual. The occlusal enamel is completely worn off mesially and only partially preserved buccally and distally (stage 2). There is a marked mesial inclination of the occlusal wear; there is a lingually (but not occlusally) oriented facet on the distal aspect of the tooth, and there is a lingually oriented sub-facet within the distal interproximal facet that contains angled striations. Finally, in contrast with the typical wear of mandibular molars, the tooth is more worn lingually than buccally; about 4.5 mm of enamel remains on the buccal aspect, and less than 3 mm of enamel remains on the lingual aspect. Similarly, there is more than 5 mm of enamel remaining on the distal aspect but less than 2 mm on the mesial aspect. These features suggest that the tooth was likely in malocclusion. If the adjacent distal tooth had been lost antemortem, this tooth may have shifted distally resulting in uneven wear. The mesial interproximal facet is wide (5.5 mm). Within the facet subvertical grooves are present. In addition, below this facet there is a groove, likely cultural in nature, measuring 6.3 mm × 1.6 mm. The distal facet is large (5.6 mm × 2.1 mm) and lacks subvertical grooves. The extent of occlusal and interproximal wear strongly suggests that this tooth belonged to an adult. No pathological conditions are noted.

The extensive wear makes identifying cusp morphology nearly impossible. The wear pattern and shape of the tooth suggest that it possessed five cusps. In addition, distally there are buccal and lingual grooves, which most likely delineate a large Cusp 5. The roots are distinct but rather close together (also consistent with its status as an M_2). The mesial root is smaller than the distal root and possesses a shallow, wide developmental groove.

Tooth No. 6: Right M_3. Sq. Xb.A6 (Leroi-Gourhan, 1958). This worn molar has a large chip of enamel (4.3 mm × 3.3 mm) missing from the mesial aspect of the paracone, and it is also chipped distally. With nearly the entire occlusal surface worn away (stage 2), tooth side was based on the presumed distal deflection of the roots, the occlusal outline of the crown, and the presence of a buccal pit (ASUDAS protostylid: grade 1). Given the extensive tooth wear, the tooth likely belonged to a middle-aged adult. As was the case with molar No. 16, more wear occurs lingually than buccally. However, while molar No. 16 exhibits greater mesial wear, this molar exhibits greater distal wear. The occlusal wear is basin-like, especially on the area of the hypoconid and hypoconulid. The difference in the amount of enamel preserved buccally and lingually is striking; only 2.7 mm of enamel remains lingually compared to 4.0 mm buccally. The mesial interproximal facet is 2.8 mm high and contains no subvertical grooves. There is no distal interproximal facet. Secondary cementum covers the inferior third of the roots. There is a small developmental defect (pit) on the protocone, but otherwise no pathological conditions are noted.

The degree of wear obscures occlusal crown morphology; however, its overall shape suggests that five (or more) cusps were present.

Descriptions of deciduous teeth (Figs. 7 and 8)

Maxillary incisors

Tooth No. 27: Right di^1. Sq. Xb2.C7 (unpublished). This tooth consists of a complete crown and partial root. The crown exhibits microfractures along its length and near the crown root junction. The root is quite fragile and also exhibits small fractures. It is broken apically and its fragility suggests that it had not completed its development. The tooth lacks wear suggesting it was not in functional occlusion at the time of the individual's death (<18 months). No pathological conditions are noted.

The distal border of the tooth crown is sharply angled, while the mesial border is straighter. The tooth is shovel shaped, possessing well-developed mesial and distal marginal ridges on the lingual surface. The mesial ridge is more developed than the distal ridge. The ridges converge at a slightly swollen cingulum from which two weak ridges extend. The labial face is markedly convex both mesiodistally and superioinferiorly.

Tooth No. 32: Left (?) di^1. Sq. Xb2.C8 (unpublished). This crown is heavily worn making it difficult to determine the side. Only about 1.5 mm of root is preserved, being either broken after deposition or resorbed (or both). If resorbed, it could indicate that this tooth was naturally shed, rather than deposited when the individual died. The crown is more worn lingually than labially. Although the pulp chamber is exposed, about one-half of the crown height still remains (stage 2). The tooth presents a mesial wear facet (2.2 mm × 2.0 mm) but lacks a distal wear facet. The extent of the wear suggests that the tooth had been in occlusion for many years, and that the individual was likely between 5 and 6 years of age when the tooth was deposited. No pathological conditions are noted.

The labial surface of the crown is moderately convex. The degree of wear precludes scoring lingual morphological characters. Labially, the tooth is featureless.

Tooth No. 36: Left di^1. Sq. Xc.A7 or Xb2.B5 (unpublished). This crown is almost completely formed, indicating an age of death at or around the time of birth. No pathological conditions are noted. The labial surface is convex both mesiodistally and superioinferiorly. Lingually, it exhibits trace shoveling with the mesial marginal ridge better developed than the distal marginal ridge. Although not completely preserved, it is evident that a slight lingual tubercle would have been present had the tooth completed its growth. Labially, the tooth is featureless.

Tooth No. 28: Right di^2. Sq. Xb2.C7 (unpublished). This crown is completely formed, but only 2.5 mm of the root is preserved; it is unclear whether root development was complete. The lack of occlusal and interproximal wear facets indicates that the crown was not in functional occlusion at the time of the individual's death. Taken together, a developmental age of about 7–12 months is suggested. No pathological conditions are noted.

The distal crown is obliquely angled. The lingual surface is slightly shovel shaped with moderately developed marginal ridges. The marginal ridges converge and then blend into a slight cingulum swelling with no distinct tubercle. The labial surface exhibits marked mesiodistal and superioinferior convexity.

Tooth No. 22: Right di^2. Sq. Xb2.B5 (unpublished). The crown and root of this tooth had completed their development and root resorption had begun. The crown is chipped on the mesiolingual and distolabial surfaces and on the labial surface near the incisal edge. In addition, microfractures run along the labial surface of the crown. About one-quarter of the crown is abraded (stage 1), with more wear distally than mesially. The extent of wear and the degree of root resorption point to an age of 4–6 years. No pathological conditions are noted.

Lingually, the tooth exhibits slight marginal ridge development, although only the distal marginal ridge is completely preserved. The crown base is bulbous and the cingulum is somewhat swollen but does not take the form of a lingual tubercle.

Maxillary canines

Tooth No. 37: Right dc^1. Sq. Xc.Z6.2085 (unpublished). This tooth possesses a completely formed crown and root. The crown is cracked along its mesiodistal length, and a small chip of enamel (1.6 mm × 3.4 mm) is missing from the distobuccal surface. Distally, the root is broken in a superior-inferior direction. There is a small patch of exposed dentin on the cusp tip indicating that the tooth was in functional occlusion. The lingual marginal ridges also show evidence of wear, but no dentin is exposed (stage 1). The tooth development and wear status suggest an age between 3 and 7 years. No pathological conditions are noted.

Lingually, the tooth presents moderately developed mesial and distal marginal ridges, which blend into a well-developed shelf-like cingulum. This cingulum is divided into three lingual tubercles, of which the medial tubercle is the largest. In addition, trace expression of the medial ridge is present. Labially, the mesial and distal lobes of the crown are apparent. When viewed from the side, the crown is strongly angled, while the root is straight.

Tooth No. 38: Left dc^1. Sq. Xc.C9 (unpublished). This is a fully formed unworn crown with only 0.7 mm of root development, indicating a developmental age of 4–8 months. No pathological conditions are noted.

The crown is remarkably symmetrical in shape. The lingual crown surface is rather complex, presenting a well-developed mesial marginal ridge and a much smaller distal marginal ridge. The mesial marginal ridge blends into the cingulum, which takes the form of a small lingual tubercle lacking a free apex. The median ridge is moderately developed, and a small distal accessory ridge extends to the cingulum.

Maxillary molars

Tooth No. 34: Left dm^1. Sq. X.C7.3820 (unpublished). This tooth consists of a complete crown with less than 1.0 mm of root development, indicating a developmental age of 7–11 months. The enamel is cracked along the buccal surface but otherwise well preserved. No pathological conditions are noted.

The tooth presents four cusps in the following configuration: paracone > protocone > metacone = hypocone. The essential crests are not developed except where the protocone and metacone are joined by a bridge of enamel (*crista obliqua*). The cusp tips are compressed internally and are joined by a ridge that is

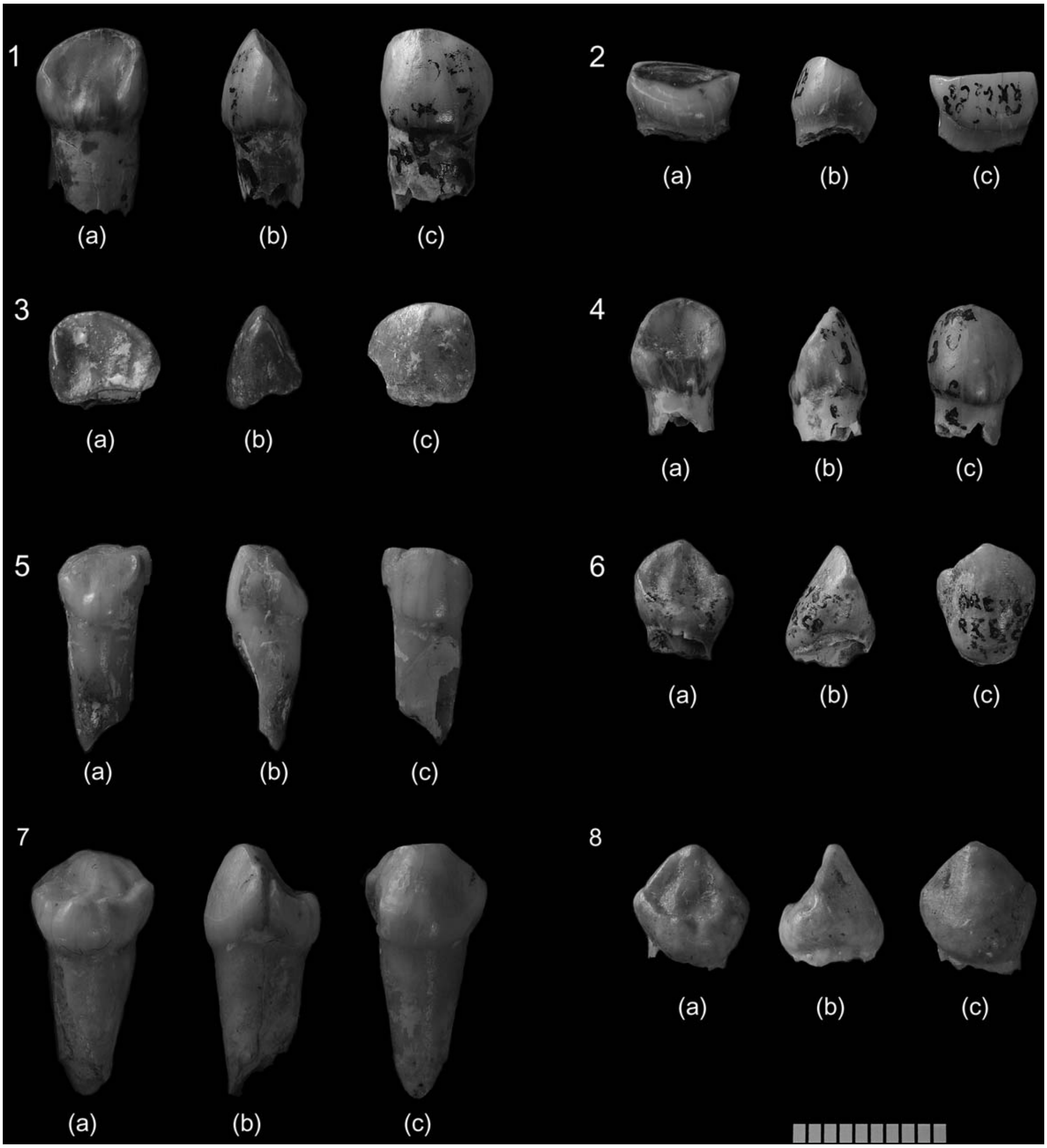

Fig. 7. Grotte du Renne, Arcy-sur-Cure deciduous incisors and canines. 1: Tooth No. 27, right di^1 (a) lingual (b) distal (c) labial; 2: Tooth No. 32, left(?) di^1 (a) lingual (b) mesial or distal (c) labial; 3: Tooth No. 36, left di^1 (a) lingual (b) mesial (c) labial; 4: Tooth No. 28, right di^2 (a) lingual (b) mesial (c) labial; 5: Tooth No. 22, right di^2 (a) lingual (b) distal (c) labial; 6: Tooth No. 31, right dc_1 (a) lingual (b) mesial (c) labial; 7: Tooth No. 37, right dc^1 (a) lingual (b) distal (c) labial; 8: Tooth No. 38, left dc^1 (a) lingual (b) distal (c) labial. Scale bar in mm.

continuous with the mesial marginal ridge. The metacone is oriented mesially and lingually. The tooth exhibits a strong cingulum bulge near the crown base and a pronounced mesiobuccal projection at the base of the paracone (*tuberculum molare*). The buccal cusps are higher than the lingual cusps, and the buccal and lingual faces are strongly angled. A weak Carabelli's structure (small, Y-shaped depression) is observable on the lingual surface of the protocone.

Tooth No. 26: Right dm^2. Sq. Xb2.C7 (unpublished). This tooth consists of a complete crown with less than 1 mm of mesial root development. The crown is well preserved and unworn. The extent of root development suggests a developmental age between 9 and 12 months. No pathological conditions are noted.

The occlusal outline is rhomboidal, with the distal cusps placed lingually relative to the mesial cusps. All four main cusps are large. The tooth presents the following cusp configuration: protocone > paracone > hypocone > metacone. In addition, the crown presents a well-developed hypoconule (Cusp 5) and a large, cusp-like Carabelli's structure. There are strong furrows defining the hypoconule on the buccal surface. The Carabelli's cusp has a free apex that is lower than those of the main cusps. Its area comprises 30% of the area of the protocone; as a result, the protocone cusp tip is

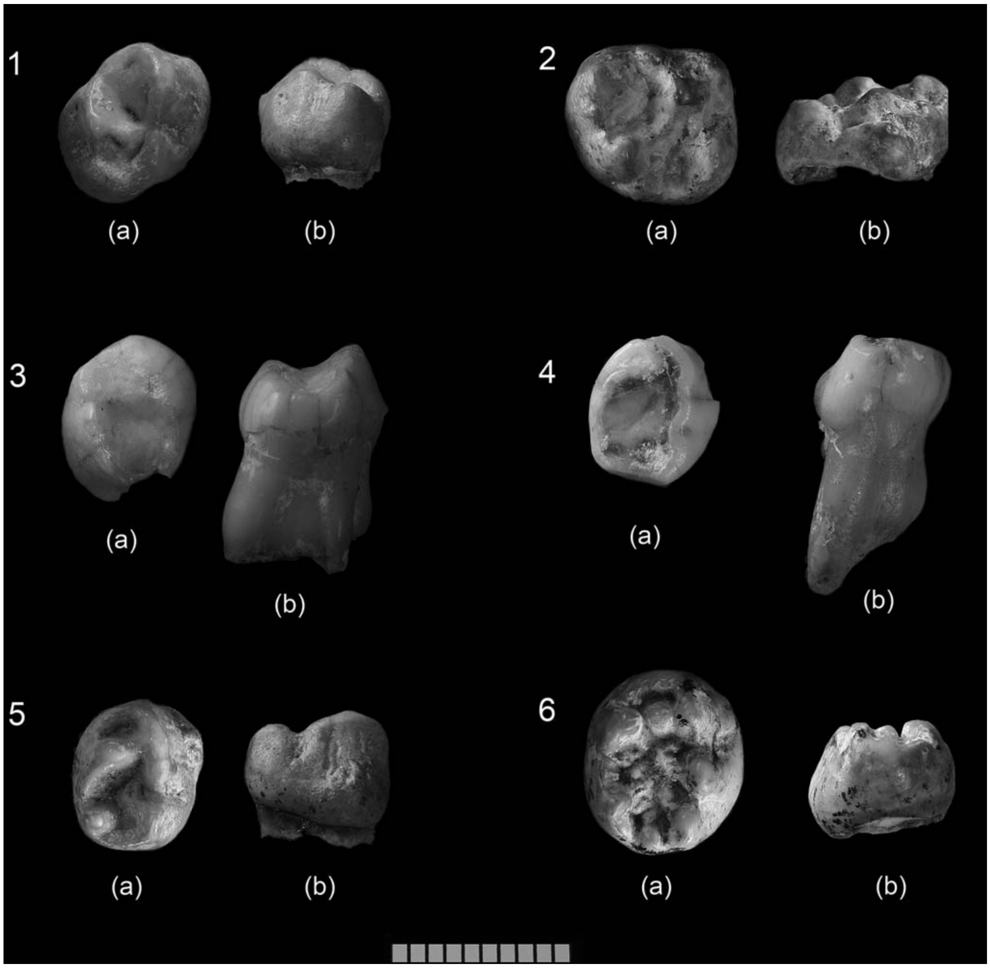

Fig. 8. Grotte du Renne, Arcy-sur-Cure deciduous molars. 1: Tooth No. 34, left dm^1 (a) occlusal (b) lingual; 2: Tooth No. 26, right dm^2 (a) occlusal (b) lingual; 3: Tooth No. 18, right dm_1 (a) occlusal (b) mesial; 4: Tooth No. 25, right dm_1 (a) occlusal (b) mesial; 5: Tooth No. 33, right dm_1 (a) occlusal (b) buccal; 6: Tooth No. 29, right dm_2 (a) occlusal (b) mesial. Scale bar in mm.

internally compressed. The essential crests of all the main cusps are apparent. A well-developed crest (*crista obliqua)* connects the protocone and metacone. The mesial marginal ridge is also well developed. The buccal and lingual profiles are strongly angled towards the occlusal basin.

Mandibular canine

Tooth No. 31: Right dc_1. Sq. Xb2.C8 (unpublished). This tooth consists of a complete crown with only a small portion of root preserved (between 0.5 and 1.5 mm). The broken root makes it impossible to determine the extent of its development. However, the lack of wear on the crown indicates that the tooth was not in functional occlusion, which suggests a developmental age of 7–15 months. No pathological conditions are noted.

Lingually, the crown presents trace marginal ridges and a weakly developed medial ridge. The cingulum is only slightly developed and no lingual tubercles are present. The labial crown surface is both mesiodistally and superioinferiorly convex. Distally, the crown has a well-developed occlusal tubercle, and a slight furrow is associated with this feature on the buccal surface.

Mandibular molars

Tooth No. 18: Right dm_1. Sq. Xb1.D10 (unpublished). The crown and roots of this tooth are completely formed. The tooth enamel is chipped in several places. The largest chip (5.5 mm × 2.3 mm at the distobuccal corner) affects the occlusal surface; two others occur mesio-lingually (4.4 mm × 1.8 mm) and mesio-buccally (3.9 mm × 2.2 mm) near the crown base. The occlusal wear is moderate with a single dentin facet exposed on the protocone (stage 1). A small mesial interproximal facet (3.0 mm × 2.2 mm) is observable, but crown damage precludes detecting a distal interproximal facet. Enamel fractures also occur in an inferior-superior direction along the circumference of the crown. Both mesial and distal roots are broken inferiorly, although they may also have begun resorption. The completed root development and degree of occlusal wear suggest an age between 4–7 years. No pathological conditions are noted.

The crown bulges slightly at the cingulum, and there is a well-developed mesiobuccal projection near the crown base (*tuberculum molare*). Occlusal wear obscures much of the morphology, but the shape of the tooth suggests there were at least four cusps. The mesial cusps make up the bulk of the tooth, with the protoconid larger and higher than the metaconid. These two cusps are connected by a transverse crest. Occlusal wear makes it impossible to determine if an anterior fovea was present. The sagittal sulcus is deep and terminates mesially at the transverse crest. No accessory ridges or crests are observed.

The tooth also possesses two widely splayed roots. The mesial root has lingual and buccal components that are connected by a dentin plate ~6.7 mm. The lingual component is larger than the buccal. The smaller distal root (5.7 mm wide) is comprised of a single component.

Tooth No. 25: Right dm_1. Sq. Xb2.B11.3191 (unpublished). The crown and roots of this tooth are completely formed. The crown is worn with dentine exposed on all cusps (stage 1), and there is a large chip (3.0 mm × 3.8 mm) missing from the buccal surface near the base. The roots are undamaged. A small mesial interproximal facet (1.8 mm × 1.0 mm) and a much larger distal interproximal facet (3.7 mm × 1.9 mm) are present. In modern humans, the roots of the dm_1 are fully formed by 4 years and begin resorption at about 7 years. Root development, lack of resorption, and crown wear point to an age of about 5–7 years. No pathological conditions are noted.

The shape of the crown suggests at least four cusps were present. The base of the protoconid presents a well-developed mesiobuccal projection (*tuberculum molare*). Although the occlusal surface is worn, a moderately developed transverse crest connecting protoconid and metaconid, together with a small anterior fovea, are still observable. From the mesial aspect, the marginal ridge is lower than the transverse crest. Buccally, two furrows are present: one on the protoconid, and the other likely separated the protoconid and hypoconid.

There are two roots present. The mesial root has distinct buccal and lingual components. The buccal root component is much longer than the lingual root component. The distal root has a single component. A 1.5 mm nodule of dentine is present on the buccal aspect between the mesial and distal roots.

Tooth No. 33: Right dm_1. Sq. Xb2.C8 (unpublished). This tooth consists of a well-preserved, completely developed, unworn crown with 1.1–1.7 mm of root development. The absence of occlusal wear and degree of root formation suggest a developmental age of 6–11 months. No pathological conditions are noted.

The crown presents four cusps. The protoconid is the largest cusp, followed by the metaconid and hypoconid, which are subequal in size, and finally the entoconulid. Together, the mesial cusps comprise a larger portion of the crown than do the distal cusps. The protoconid and metaconid are nearly equal in height and are connected by a strong transverse crest. This transverse crest and a well-developed mesial marginal ridge enclose a moderately sized anterior fovea. From the mesial aspect, the marginal ridge is lower than the transverse crest. The metaconid is in contact with the hypoconid. The essential crest of the hypoconid is bifurcated, while the other cusps present single essential crests. Two furrows exist on the buccal surface: one occurs on the protoconid and the other occurs between the protoconid and entoconid. A small conule is present at the base of this more distal furrow. A mesiobuccal projection at the base of the protoconid (*tuberculum molare*) is well developed with accessory furrows and ridges near its base.

Tooth No. 29: Right dm_2. Sq. Xb2.C8 (unpublished). This tooth is represented by a completely formed, unworn tooth cap with less than 1 mm of root development. The absence of occlusal wear and degree of root formation indicate a developmental age of 7–15 months. No pathological conditions are noted.

The crown presents complex occlusal morphology. In addition to the four major cusps, it possesses a large hypoconulid and smaller Cusp 6. The fissures form a Y pattern, with the metaconid and hypoconid in contact. Each major cusp presents a strong essential crest. The essential crest of the protoconid is especially marked and cusp-like; it meets and joins the metaconid essential crest to form the distal border of a wide and deep anterior fovea. Mesially, the anterior fovea is defined by a thick mesial marginal ridge. The cusp tips are high and internally compressed, with the buccal side sloping strongly inward. The convex lingual, mesial, and (especially) distal profiles contribute to the internal compression of the cusp tips. The buccal groove between the protoconid and hypoconid is wide and deep. There is also a small, unconnected furrow on the protoconid, but the crown lacks a true protostylid (as defined by the ASUDAS). An additional buccal furrow occurs between the hypoconid and hypoconulid and extends half the height of the crown.

Taxonomy and interpretation of dental morphology and metrics

Permanent maxillary incisors

The maxillary incisors (especially I^1) are among the most useful teeth for distinguishing between Neandertals and anatomically modern humans. Upper central incisors are lacking at the Grotte du Renne. However, the two I^2s exhibit strong expression of lingual marginal ridges (shovel shape), lingual tubercles (*tuberculum dentale*), and labial convexity. The combination of these three traits is particularly distinctive of Neandertal maxillary incisors (Crummett, 1995).

Frequency data for shovel-shaped incisors and lingual tubercles show marked differences between Neandertals and Upper Paleolithic modern humans (Table 8). In Neandertals, the frequency of I^2 shoveling is 93% and the frequency of lingual tubercles is 100%. In contrast, in Upper Paleolithic samples the frequencies are 38% and 13%, respectively. More importantly, the frequency of finding these two traits in combination is much higher in Neandertals than in Upper Paleolithic modern humans.

In addition, Neandertals tend to possess anterior teeth with robust buccolingual diameters. The Grotte du Renne I^2s not

Table 8
Morphological comparison of teeth from the Grotte du Renne, Neandertals, and Upper Paleolithic Europeans. Traits listed are those for which Neandertals and Upper Paleolithic modern humans differ substantially

Tooth	Trait	Trait presence	Grotte du Renne	Mousterian Neandertal % present (n)	Upper Paleolithic Modern % present (n)
I^2 (n = 2)					
	Shoveling	Grade 3+	present	93 (27)	38 (8)
	Lingual tubercles (*tuberculum dentale*)	Grade 1+	present	100 (25)	20 (8)
	Two of the above		present	100 (24)	20 (8)
P^3 (n = 2)					
	Essential crest	Grade 1+	present	100 (19)	57 (8)
	Maxillary premolar accessory ridges	Grade 1+	present (1/2)	69 (16)	20 (5)
	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	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)	22 (9)
P_4 (n = 1)					
	>1 lingual cusp	Grade 2+	present	90 (30)	44 (16)
	Transverse crest	Grade 2+	absent	77 (27)	6 (17)
	Asymmetry	Grade 1+	present	92 (25)	22 (13)
	Two of the above (distolingual cusp + asymmetry)		present	91 (22)	8 (13)
M_1 (n = 2)					
	Mid-trigonid crest	Grade 1+	present	96 (28)	4 (25)
	Cusp 6	Grade 1+	present	26 (19)	17 (23)
	Two of the above		present (1/2)	57 (7)	0 (15)
M_2 (n = 2)					
	Y-pattern	Y	present (1/2)	79 (34)	44 (27)
	Cusp 6	Grade 1+	present	55 (20)	24 (17)
	Mid-trigonid crest	Grade 1+	Present	91 (24)	8 (24)
	Anterior fovea	Grade 2+	present	88 (24)	50 (20)
	Three of the above (Cusp 6+ mid-trigonid crest + anterior fovea)		present	63	0
M_3 (n = 1)					
	Four cusps		absent	0 (23)	32 (19)

only exceed the average buccolingual breadths of both Neandertal and Upper Paleolithic samples, but are either outside the range of or near the upper limit of the range of Upper Paleolithic modern humans (Table 5).

Permanent maxillary premolars

Maxillary premolar morphology, by itself, is not particularly useful in distinguishing among Middle-Late Pleistocene hominins. Neandertals and other archaic humans tend to present maxillary premolars with relatively complex morphology, including well-developed protocone and paracone essential crests and mesial and distal accessory ridges. The essential crests show a tendency for bifurcation, especially on the paracone, and accessory cusplets are not uncommon. This morphology is usually more pronounced on P^4 than it is on P^3 (Bailey, 2002b).

Each of the three premolars from Grotte du Renne shows strong protocone and paracone essential crests, and an accessory cusp along the distal margin. One of the P^3s and the P^4 presents accessory ridges as well. Upper Paleolithic modern humans may also present this morphology, albeit at lower frequencies. More importantly, the combination of traits such as a well-developed essential crest and accessory crests in a P^3 is common in Neandertals but has yet to be observed in a small sample of Upper Paleolithic modern humans (Table 8).

The buccolingual measurements for these teeth also favor a Neandertal affiliation. The two P^3s are large, falling within the Neandertal range but outside the Upper

Paleolithic range (Table 5). The P^4 falls within the range of both Neandertals and Upper Paleolithic modern humans, although it is at the upper end of the Upper Paleolithic range. The length of the P^4 root is within the range of Neandertals and much longer than the two Upper Paleolithic P^4 roots that could be measured (Table 7).

Permanent mandibular incisors

In Neandertals, mandibular incisors tend to have moderate-to-strong median ridge development, trace-to-moderate shoveling, and occasionally a cingulum shelf. This primitive morphology is also observed in other archaic (non-Neandertal) humans. The single I_2 from the Grotte du Renne also possesses these features. The buccolingual dimension of this tooth falls within the range of Neandertals and outside that of Upper Paleolithic modern humans (Table 5).

Permanent mandibular canine

Neandertal mandibular canines show higher frequencies for the canine distal accessory ridge than do Upper Paleolithic modern humans (Table 8), but in and of itself this feature is not particularly diagnostic. The Grotte du Renne mandibular canine shows marked expression of the distal accessory ridge and moderate shoveling.

Canine size is a better discriminator; Neandertals tend to have larger crowns than modern humans. The buccolingual diameter of the Grotte du Renne canine falls at the high end of the Neandertal range and just above the Upper Paleolithic range. The root is somewhat short relative to that of Neandertal mandibular canines. However, because there is evidence suggesting impaction, we caution against using root length in the interpretation.

Leroi-Gourhan (1958) saw similarities between this canine and the canines found in much older Mousterian-associated strata (Layer 20). In particular, he noted the robust crown dimensions and the double-channeled root. He also believed that the crown morphology—the marked cingulum, shoveling, and a distolingual tubercle—were similar to that seen in the La Chaise Neandertal.

Permanent mandibular second premolar

Neandertals and anatomically modern humans show marked differences in P_4 crown morphology (Bailey, 2002a; Bailey and Lynch, 2005). Most Neandertals posses P_4s with a large mesially placed metaconid that is attached to the protoconid via an uninterrupted transverse crest. In addition, Neandertal P_4s tend to have multiple lingual cusps and an asymmetrical occlusal outline. The P_4 of anatomically modern humans tend to be more symmetrical, with a smaller, more medially placed metaconid, lower frequencies of multiple lingual cusps, and no transverse crest.

Like most Neandertals, the single P_4 from the Grotte du Renne presents a large mesially placed metaconid, multiple lingual cusps, and marked occlusal crown asymmetry. The essential crests of the protoconid and metaconid are very well developed; however, they do not form a transverse crest. The combination of a distolingual cusp and an asymmetrical crown is much more common in Neandertals than in Upper Paleolithic modern humans (Table 8).

Metrically, the buccolingual breadth of the P_4 is within the range of Neandertals, but more than two standard deviations above that of Upper Paleolithic modern humans (Table 5). The root length is also within the range for Neandertals but above the range of the Upper Paleolithic modern human sample (Table 7).

Leroi-Gourhan (1958) made similar observations of this premolar. He was particularly struck by the crown's robust dimensions, the marked inclination of the lingual margin, as well as the developed distolingual cusp, which he believed contributed to the tooth's strong asymmetry. He also believed that the root morphology was archaic in its possession of three lobes.

Permanent mandibular molars

Neandertal mandibular molars tend to posses five or more cusps and a well-developed mid-trigonid crest associated with a large anterior fovea. The frequency of Cusp 6 and the mid-trigonid crest is much higher in Neandertals than Upper Paleolithic modern humans. Both of the M_1s from the Grotte du Renne possess a Cusp 6 and a mid-trigonid crest. The frequency of the combination of these two characters is 57% for Neandertals but 0% for Upper Paleolithic modern humans (Table 8).

In M_2, the Y pattern, mid-trigonid crest, large anterior fovea, and Cusp 6 *(tuberculum sextum)* are traits found with higher frequency in Neandertals than Upper Paleolithic modern humans. The Grotte du Renne M_2s both possess Cusp 6, mid-trigonid crests, and large anterior fovea. One of the two has a Y pattern. The combination of the three traits shared by these two teeth (Cusp 6/mid-trigonid crest/large anterior fovea) is found in 59% of Neandertals but in no Upper Paleolithic modern humans (Table 8).

Finally, although the single M_3 is quite worn, we are fairly certain that it possessed more than four cusps. In Neandertals, more than four cusps are present in 100% of the M_3s. In Upper Paleolithic modern humans, the frequency is lower (68%) (Table 8).

Morphologically, the mandibular molars show clear Neandertal affinity. Tooth measurements provide no additional information as there is nearly complete overlap in tooth size between Upper Paleolithic modern humans and Neandertals. Not surprisingly, the Grotte du Renne mandibular molars fall within the ranges of both groups (Table 5).

Leroi-Gourhan's (1958) assessment of the mandibular molars (Nos. 5 and 6) was that they were archaic. Crown and root size played an important part in his diagnoses, but he also considered morphology to be important. In particular, he noted the marked anterior fovea, Y-5 fissure pattern, the presence of the hypoconulid (Cusp 5), and what he thought was a possible Cusp 6 on the M_2. For the M_3, he felt that the rounded occlusal outline and the large hypoconulid pointed to an archaic, rather than anatomically modern, individual.

Deciduous teeth

There has been no systematic and comparative study of the tooth crown morphology of deciduous Neandertal teeth using standards similar to the Arizona State University dental anthropology system. Therefore, trait frequencies cannot be reported. However, we can make broad comparisons between the deciduous teeth from the Grotte du Renne and those of Mousterian Neandertals and Upper Paleolithic modern humans (see Table 3). While it has been claimed that Neandertal deciduous teeth '*ne presentment pas de différences morphologiques fondamentales avec celles des subjects europeens actuels*' (Tillier, 1979) [do not present fundamental differences from those of European modern humans], this assertion needs to be systematically tested with comparative data. At this point, only qualitative comparisons are possible.

Deciduous maxillary incisors

Among Neandertal deciduous maxillary incisors there is variation in the expression of traits that are more consistently expressed in adult incisors. Some deciduous maxillary incisors show moderate (especially mesial) marginal ridge development (e.g., Dederiyeh, Pech de l'Azé). In others, the marginal ridges are distinct but more weakly expressed (Roc du Marsal). Tillier (1983) describes Shanidar 7 and Subalyuk Neandertals as having shovel-shaped incisors, and Kebara as not. Upper Paleolithic modern humans tend to have labially flat incisors that exhibit only minor traces of marginal ridge development, if any (e.g., Madeleine).

The morphology of the Grotte du Renne incisors is similar to that observed at Roc de Marsal, which shows marked labial convexity, slight shoveling (especially mesially on di^1), and slight lingual tubercle development on the di^1 but not di^2. The Grotte du Renne di^1s exhibit marked labial convexity, slight lingual shoveling, and some expression of a lingual tubercle. Like those of Roc de Marsal, the di^2s show weaker shoveling and lack distinct lingual tubercles.

Metrically, the buccolingual breadths of the maxillary incisors with complete crowns fall within the range of Neandertals (Table 6). Both complete di^1s are larger than the two Upper Paleolithic modern human teeth to which they can be compared. The di^2s are also within the Neandertal range. The smaller of the two is equal in size to the largest of the three di^2s of Upper Paleolithic modern humans.

Deciduous maxillary canines

Morphologically, the Grotte du Renne dc^1s are very similar to those of the Roc de Marsal and Dederiyeh 1 Neandertals, which also possess two lingual tubercles, a cingulum shelf, and a symmetrical diamond-like shape. They are also similar to those of the Châteauneuf Neandertal described by Tillier (1979). The doubling of the lingual tubercle has been described as a feature that exists in other Neandertals and not in early (Skhūl I and Qafzeh 4) or recent modern humans (Tillier, 1979). This morphology is not present on any of the comparative Upper Paleolithic modern human specimens analyzed in this study. Like Neandertals, the Grotte du Renne specimens have a more sharply-angled buccal outline when viewed from the mesial or distal aspects than do the Upper Paleolithic modern human specimens.

Metrically, the Grotte du Renne dc^1s are large. The buccolingual breadths fall at the middle-high end of the range for Neandertals and are larger than the three Upper Paleolithic modern human maxillary canines to which they can be compared.

Deciduous maxillary molars

The Grotte du Renne dm^1 is most similar to those of Neandertals in its possession of four cusps. According to Tillier (1979), the dm^1s of Châteauneuf, Gibraltar II, Subalyuk, and Shanidar 7 Neandertals also have four cusps. Recent modern humans typically have two or three cusps but early modern humans are reported to be variable. Skhūl I is reported to have four cusps and Qafzeh 4 three (Tillier, 1979). The configuration of dm^1s of Upper Paleolithic modern humans is more premolar-like than those of Neandertals, in that they possess two or three cusps, a well-defined sagittal sulcus dividing lingual and buccal cusps, and a more mesially oriented lingual cusp. The presence of Carabelli's structure on the lingual surface of the Grotte du Renne dm^1 may be particularly diagnostic; this character is said to be absent in modern (contemporary) humans (Carlsen, 1987) but is present on some Neandertal dm^1s. The crest connecting the paracone and metacone (*crista obliqua*) observed in the Grotte du Renne tooth is similar to that in Pech de l'Azé and Roc du Marsal dm^1s.

The Grotte du Renne dm^2 is similar to those of Neandertals, which mirror the morphology of the permanent M^1 in relative cusp size, cusp configuration, and crown traits. Like Neandertal dm^2s (and permanent M^1s), the Grotte du Renne specimen possesses a hypocone that is larger than the metacone, and a metacone that is mesially and lingually oriented. In contrast, Upper Paleolithic dm^2s present a metacone that is often larger than (rather than smaller than) the hypocone. The Grotte du Renne dm^2 also possesses a large Carabelli's cusp that is nearly as high as the other cusps. Like those observed on the dm^2s of Roc de Marsal, La Quina, and Dederiyeh 2, this accessory cusp is so large that it displaces the protocone toward the occlusal basin. In comparison, Upper Paleolithic modern human dm^2s show only weak expression of Carabelli's structure if at all, and in no specimen does it form a genuine cusp. Finally, the mesial and distal accessory cusps observed on the Grotte du Renne dm^2 are similar to those of the Châteauneuf dm^2 described by Tillier (1979).

Metrically, the buccolingual breadth for the Grotte du Renne dm^1 and dm^2 are within the range observed in Neandertals and slightly below the range observed in Upper Paleolithic modern humans.

Deciduous mandibular canine

The morphology of the dc_1 is not particularly diagnostic in Neandertals. The Grotte du Renne dc_1 resembles that of Pech de l'Azé and differs from those of Upper Paleolithic modern humans in its marked labial convexity and in the degree of marginal ridge development. The buccolingual breadth is within the range of Neandertals and slightly larger than the two Upper Paleolithic specimens to which it can be compared.

Deciduous mandibular molars

The deciduous mandibular molars of Neandertals differ from those of anatomically modern humans in ways similar to the permanent P_4 and M_1. The primary difference is in their possession of a strong crest that connects the mesial cusps (the transverse crest in P_4 and the mid-trigonid crest in mandibular molars).

The Grotte du Renne dm_1s closely resemble those of Neandertals and they differ from those in the Upper Paleolithic sample by having a mesial marginal ridge that is continuous with the metaconid and a strong transverse crest joining the protoconid and metaconid cusps. These two features outline a deep and wide anterior fovea. In contrast, the Upper Paleolithic teeth present either a mesiolingual groove that extends from the anterior fovea (St. Germain, Solutre, and Isturitz) or accessory cusps where the anterior fovea would be (Bruniquel and Madeleine). Finally, the dm_1s from the Grotte du Renne, like those of Neandertals, show a more mesial placement of the lingual cusp compared to those of Upper Paleolithic modern humans.

The Grotte du Renne dm_2 is very similar to those of Neandertals in its possession of an ovoid occlusal outline, internally compressed cusps, and a wide anterior fovea bordered by a well-defined mesial marginal ridge and a substantial mid-trigonid crest. In contrast, Upper Paleolithic dm_2s have a rectangular occlusal outline, with more widely spaced cusps and no mid-trigonid crest. Although two Upper Paleolithic-associated dm_2s from Isturitz show marked development of the essential and mesial accessory crests of the protoconid and metaconid, these crests do not join to form a continuous crest between the cusps.

Demography and disease at the Grotte du Renne

None of the teeth from the Châtelperronian layers at the Grotte du Renne are found in their associated jaws. Therefore, it is unclear exactly how many individuals are represented in the assemblage. However, an estimate of the minimum number of individuals can be made based on repeated teeth, developmental age, and wear status. Based on these criteria, we have estimated that a minimum number of six individuals are represented, including one neonate, one infant (9–15 months), three subadults (two aged 4–8 years and one aged 12–18), and one adult. As none of the teeth must belong to the same individual, a maximum of 29 individuals is possible. In a few cases, it is possible to hypothesize that several teeth belong to the same individual based on their provenience, preservation, wear status, and/or probable developmental age. If this is the case, the maximum would be reduced by 10 individuals.

Three teeth from square D10 [Nos. 18 (Rdm_1), 19 (LI^2), and 20 (LP^3)] likely belong to one individual. The development of the permanent teeth I^2 and P^3 agree in a developmental age of about 4–7 years. The dm_1 has fully formed roots, was in functional occlusion, and exhibits only moderate wear, suggesting that it also belonged to an individual approximately 4–7 years old.

Three teeth from square B5/B6 [Nos. 22 (Rdi^2), 23 (LI^2), and 24 (LP^3)] likely belong to one individual. Both the incompletely formed I^2 and P^3 conform to an age of 5–8 years. The crown of the di^2 is fairly worn and the root was beginning to undergo resorption, suggesting an age of 4–6 years.

Four of the five teeth from square C7 [Nos. 17 ($M_{1,2}$), 26 (Rdm^2), 27 (Rdi^1), 28 (Rdi^2), and 34 (Ldm^1)] likely belong to one individual. All but No. 17 are unworn deciduous teeth. Although the root apices of the incisors have been broken, the frailty of the root sheaths suggests that they were incomplete. The extent of root formation of the dm^1 and dm^2 suggests developmental ages of 7–11 and 9–12 months, respectively; the lack of wear and the presumed root development of the incisors are consistent with that age. Tooth No. 17 is from a much older individual (>15 years).

Four of the five teeth from square C8 [Nos. 29 (Rdm_2), 30 (RM_1), 31 (Rdc_1), 32 (Ldi^1), and 33 (Rdm_1)] likely belong to the same individual. The crown and root development of the deciduous molars and the canine all correspond to a developmental age between 6 and 18 months. The degree of development of the RM_1 is consistent with this age. The di^1 must have come from a second individual, however. The degree of wear suggests that it belongs to a much older child (>5 years).

Nearly all of the deciduous teeth in this sample were deposited when the individual died, as opposed to being shed naturally. This indicates that most of the individuals were quite young when they died. The two molars showing marked and unusually oriented occlusal wear (Nos. 6 and 16) may be indicative of antemortem tooth loss of one or more teeth (causing malpositioning), which could be a sign of poor dental health and/or old age. However, without their associated jaw(s), it is impossible to be certain what the cause of the unusual tooth wear was. The high proportion of children to adults observed in this sample is not particular to Arcy-sur-Cure and seems to be typical of Pleistocene humans (Trinkaus, 1995; Bermudez De Castro and Nicolás, 1997). Although, Caspari and Lee (2004) have noted higher old-to-young ratios in Upper Paleolithic relative to Neandertal samples.

Enamel hypoplasia is a developmental defect related to generalized disturbances (Lukacs, 1989; Hillson, 1996). In this study, the type of hypoplasia (furrow, pit, planar) and number of events was recorded. Seven of the fifteen permanent teeth (46%) exhibit some form of enamel hypoplasia, predominantly in the form of random pitting (Table 9). This frequency is slightly higher than the frequency of linear enamel hypoplasia (LEH or furrow form) in anterior teeth reported for Neandertals by Guatelli-Steinberg et al. (2004), and similar to frequencies reported by Ogilvie et al. (1989: 46.4% for maxillary and 37.8% for mandibular teeth), which included both pit and furrow types. Two teeth show evidence of multiple

Table 9
Teeth exhibiting hypoplasia in the Grotte du Renne sample

Tooth	Specimen No.	Defect type	Location
I^2	23	Pits (bands) (2)	2.8 mm and 4.9 mm from cusp tip
P^3	20	Pits (random)	Buccal surface
P_4	4	Pits (vertical)	Protoconid buccal only
M_3	6	Pit (single)	Protocone (mesiobuccal)
C	7	Furrows (2)	7.7 mm and 9.9 mm from cusp tip
$M_{1,2}$	17	Pits (random)	Buccal near cusp apices
M_2	21	Pits (random)	Superior third of crown, especially distal, buccal, and near cusp apices

stress events. In one tooth (No. 23, an I^2) they are manifest as bands of pits, and in the other (No. 7, a C_1) they are of the furrow type. The remaining teeth show single (No. 6) and multiple (Nos. 4, 20, 21, and 27) pit-type defects arranged in a non-linear fashion. Thus, with the exception of the C_1 (No. 7), hypoplastic defects are expressed entirely as pits. None of the deciduous teeth exhibited enamel hypoplasia, which agrees with the low incidence (3.3%) reported for Neandertal deciduous teeth reported by Ogilvie et al. (1989). The high incidence of enamel hypoplasia in permanent teeth of Neandertals has been interpreted as being a sign of nutritional deficiency caused by inefficient foraging (Ogilvie et al., 1989). However, a more recent study has shown that the incidence of LEH in Neandertals is similar to that in modern human Inuits, which, according to the author, does not support the inefficient foraging hypothesis (Guatelli-Steinberg et al., 2004).

Cement is deposited throughout life and tends to build up on root apices and the bifurcation of roots in multi-rooted teeth (Hillson, 1996). Two teeth, a P^4 (No. 13) and an M_3 (No. 6), show this type of 'normal' cementum build up. In the M_3, it most likely associated with continual eruption to compensate for the effects of the marked occlusal wear. In the P^4, the reason for the build up is less clear, as the tooth is only minimally worn. A C_1 (No. 7) exhibits cementum covering the entire root and marked hypercementosis on the lower half of the root. The cause of hypercementosis is unknown. However, in recent humans it is known to be related to over or under use, to Paget's Disease, hyperpituitarism, or chronic infection in the adjacent area (Hillson, 1996). Based on the evidence that this tooth was probably impacted (e.g., absence of crown wear but a fully formed root), the most likely explanation is that the hypercementosis is associated with the impaction and lack of use.

Discussion

To Leroi-Gourhan (1958), it was clear that the teeth from the Châtelperronian layers were "archaic". He was most impressed by the crown and root size, but also believed that crown morphology supported their archaic taxonomic status. In particular, he noted the presence of strong lingual tubercles on the anterior teeth and well-developed talons or talonids of the molars. He saw clear similarities between the teeth from the Châtelperronian layers and those from the Mousterian layers, as well as with Neandertals like Saccopastore. He claimed that if the teeth had been found in a Mousterian context, there would be no question of the taxonomic affinity. The only 'problem' was that the teeth were found with Upper Paleolithic tools.

At the time of the first publication, Leroi-Gourhan (1958) had only nine teeth on which to base his assessment (two of these, it turns out, are non-human). Since then, many more teeth have been found in both the Châtelperronian and Mousterian layers at the Grotte du Renne. Therefore, a more robust statement can be made about the taxonomic affiliation of the individuals they represent. Moreover, many more teeth of Neandertals are known in general and it is possible to base a taxonomic assessment on a large comparative database. Bailey (2002b) has demonstrated that the permanent dentition of Neandertals show distinct differences from that of anatomically modern humans, especially when combinations of traits are considered. In some cases the high frequencies of certain traits, and trait combinations, may be a derived condition (Bailey, 2002a, 2004; Bailey and Lynch, 2005).

Based on our comparative study of the entire Châtelperronian dental sample at Arcy-sur-Cure, both permanent and deciduous, we find that Leroi-Gourhan's (1958) original taxonomic assessment was likely correct. Some of the most diagnostic permanent teeth are present in the sample (P_4, I^2, mandibular molars). Morphologically, these teeth show clear Neandertal affinity in their combination of traits or in the presence of traits that are rare or absent in Upper Paleolithic modern human samples. These include the asymmetrical P_4 with a large, mesially oriented metaconid and multiple lingual cusps, the mandibular molars with mid-trigonid crest, and the markedly shovel shaped, labially convex maxillary incisors with marked lingual tubercle expression. The deciduous teeth also show closer similarity to those of Neandertals than they do to those of Upper Paleolithic modern humans. For the most part, their morphology mirrors that observed in Neandertal permanent teeth, for example, the dm_1 transverse (metaconid/protoconid) crest, the dm_2 mid-trigonid crest, the shovel-shaped and labially convex maxillary incisors, and a maxillary dm^2 with the configuration of a Neandertal permanent M^1.

Metrically, each tooth fits comfortably within the Neandertal range. In the cases where the teeth also fall within the range of Upper Paleolithic modern humans, this is because the ranges of the two groups overlap.

It is important to underline that when looking at the spatial distribution of the teeth from the Châtelperronian layers of Arcy-sur-Cure, the teeth displaying the clearest Neandertal morphology do not come preferentially from the portions of the site where the archaeological layers are thinner and sloping, and where possible admixture with underlying Mousterian layers could have occurred. They are found in portions of the site where the archaeological layers are thick and horizontal. They are also found in the lower-most Châtelperronian layer (Xb) as well as in the upper-most (VIII). In our view, these considerations refute the possibility that the entire series of Neandertal teeth from the Grotte du Renne Châtelperronian layers could result from contamination through contact with the Mousterian layers. Finally, it should be noted that these layers have not yielded a single tooth which displays a suite of features diagnostic of modern humans.

The preponderance of evidence, therefore, supports Neandertal affinity for the Châtelperronian-associated teeth at the Grotte du Renne, Arcy-sur-Cure. These teeth are fully Neandertal in their morphology, with no indication of evolution towards or admixture with anatomically modern humans. Dentally, at least, it appears as though the late surviving Neandertals were as 'Neandertal' as the Mousterian Neandertals from earlier layers (Leroi-Gourhan, 1958) and from other sites (Bailey, 2002b; Tillier, 1979).

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