Radiocarbon dates from the Grotte du Renne and Saint-Césaire support a Neandertal origin for the Châtelperronian

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The transition from the Middle Paleolithic (MP) to Upper Paleolithic (UP) is marked by the replacement of late Neandertals by modern humans in Europe between 50,000 and 40,000 y ago. Châtelperronian (CP) artifact assemblages found in central France and northern Spain date to this time period. So far, it is the only such assemblage type that has yielded Neandertal remains directly associated with UP style artifacts. CP assemblages also include body ornaments, otherwise virtually unknown in the Neandertal world. However, it has been argued that instead of the CP being manufactured by Neandertals, site formation processes and layer admixture resulted in the chance association of Neanderthal remains, CP assemblages, and body ornaments. Here, we report a series of accelerator mass spectrometry radiocarbon dates on ultrafiltered bone collagen extracted from 40 well-preserved bone fragments from the late Mousterian, CP, and Protoaurignacian layers at the Grotte du Renne site (at Arcy-sur-Cure, France). Our radiocarbon results are inconsistent with the admixture hypothesis. Further, we report a direct date on the Neandertal CP skeleton from Saint-Césaire (France). This date corroborates the assignment of CP assemblages to the latest Neandertals of western Europe. Importantly, our results establish that the production of body ornaments in the CP postdates the arrival of modern humans in neighboring regions of Europe. This new behavior could therefore have been the result of cultural diffusion from modern to Neandertal groups.

stimulus diffusion | cultural modernity

Crucial to understanding the replacement processes of Neandertals by modern humans in western Eurasia at the beginning of the Upper Paleolithic (UP) is the interpretation of so-called "transitional industries." In archeological sites, these lithic assemblages are found under various types of early UP (mostly Aurignacian) and/or above genuine Middle Paleolithic (MP) assemblages. They display various proportions of UP artifacts and technologies, but in several cases, a direct origin in the local MP has been argued (1, 2). Although, in Europe, only Neandertal remains have been found in association with Mousterian industries and only anatomically modern human remains have been securely identified in Aurignacian layers, the biological identity of the makers of the transitional industries remains unclear (3).

That Neandertals made some of the transitional industries has at times been suggested based on fragmentary paleontological evidence (4, 5) or on indirect chronological arguments (6). However, to date, only the Châtelperronian (CP), a transitional assemblage from central and southwestern France, and northern Spain, has yielded well-identified and relatively abundant Neandertal remains, specifically from two French sites (La Grotte du Renne and Saint-Césaire) (7–9).

Despite this fossil evidence, the question of whether Neandertals manufactured the CP remains the topic of intense debate. This results in part from the fact that the CP is the so-called "transitional" assemblage that documents the broadest spectrum of behavioral features reminiscent of the subsequent local UP, which was undisputedly created by modern humans. These features include the production of bladelets (10), bone artifacts, and body ornaments (11, 12), all of which are virtually unknown in the Neandertal world. Furthermore, these body ornaments, often considered as an expression of advanced symbolic behavior, have only been found in the CP of the Grotte du Renne and Quinçay, both at the northernmost limit of the CP geographical distribution (Fig. S1).

When accepted, the association of these objects with Neandertals has been interpreted in two ways. For some (e.g., refs. 8 and 13–15), this new behavior demonstrates a cultural impact on the last Neandertals by contemporaneous UP modern human populations, already present further east in Europe. For others (16), it represents a Neandertal invention of their own UP-style industry independently of modern humans.

A third group of authors speculates that the Neandertal/CP association may in fact result from various site formation processes including layer admixture (17). For the Grotte du Renne specifically it has been suggested that the Neandertal remains might have been dug out of the underlying Mousterian layers by CP modern humans (17) and/or that CP body ornaments and other bone artifacts may have moved down from the overlaying UP layers (18). At Saint-Césaire, the stratigraphic integrity of the CP deposits has also been challenged (17).

Radiometric arguments are relevant to the assessment of possible mixing of younger or older intrusive material into the CP layers. The precise dating of the CP is also central to the discussion surrounding its interpretation. In particular, the notion that the development of the CP resulted from the cultural influence of modern populations implies that CP innovations postdate the arrival of modern humans in Europe. The radiometric dating of the CP at the Grotte du Renne and in other sites has long been challenging because these assemblages lay at the limit of the application range of the ^{14}C method. In particular, contamination problems have impaired most of the dates obtained

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before recent technical improvements in the pretreatment of samples, which have increased the reliability of ^{14}C dates beyond 40 ka ^{14}C BP (19–21).

In this context, a series of 31 accelerator mass spectrometry (AMS) ultrafiltered dates on bones, antlers, bone artifacts, and teeth from key archaeological layers of the Grotte du Renne have been published (22). This study showed an unexpectedly high degree of intralayer variation in the radiometric ages and brought some support to the admixture hypothesis.

In contrast, a subsequent reinvestigation of the horizontal and vertical distribution of various categories of archaeologically diagnostic objects at the Grotte du Renne did not support the hypothesis of large or small scale post depositional mixing. It instead suggested that incomplete sample decontamination is the most parsimonious explanation for the observed radiometric anomalies (11). In a response, the authors of the AMS dates did not dispute this spatial evidence but also found no ground for the claim of contamination by consolidants (23). The debate also focused on the definition of the stratigraphic units to be used in the Bayesian modeling of the radiocarbon dates (24, 25).

To test these alternative interpretations of the association at Grotte du Renne of Neandertals with the CP and UP type artifacts, we produced a series of radiocarbon ages from the different archaeological layers of the site using the same pretreatment protocols but a different sampling strategy. We also compared these ages with a direct date of the Neandertal human remains from the site of Saint-Césaire (Fig. S2).

Grotte du Renne Stratigraphy

The Grotte du Renne is one of the richest known CP sites. It was deposited at the end of a small karstic gallery, forming a cave open toward the south, over the Cure River. On an extension of approximately 10 m, from the back of the cave to the upper limit of a steep talus falling toward the river, the site contains subhorizontal, stratified deposits (Fig. S3). In the upper part of the talus, this stratigraphy can still be followed, but it is reduced to a sequence of thin oblique layers. The site was excavated between 1949 and 1963 by A. Leroi-Gourhan using advanced excavation techniques for this time period. Among other innovations, the team attempted to recognize and expose occupation surfaces. The archeological material, and the observed structures, were spatially recorded and the sediments systematically sieved.

At the Grotte du Renne, 14 stratigraphic units were originally recognized (26), of which 5 were the source of the dated material reported in this paper. Layer XI is the uppermost Mousterian layer. Layers X and IX yielded most of the CP material from the site and also contain several hearths of various sizes. These two layers are formed by an accumulation of limestone slabs. In one area in the back of the cave, they reach a thickness of 80 cm but are in general much thinner, especially close to the talus. Layer IX, in particular, is quite irregular as it displays a thickness of only 3 cm in some areas (Fig. S3). In layer X, occupation floors (sublayers) were tentatively identified and numbered (27). However, their identification and recognition was not always straightforward and several artifact refits were detected between the sublayers of X (28) (Fig. S4). Two have also been detected between layers X and IX (Fig. S4). In contrast to layers X–IX, the uppermost CP layer (VIII) displays a lower density of artifacts. It is composed of yellow clayish gravel, without hearths, and has yielded numerous bones of hyenas and cave bears, suggesting only intermittent human occupation (26). Over CP layer VIII, layer VII has yielded a Protoaurignacian assemblage, which is to date the northernmost assemblage of this type identified in western Europe (29).

Methods

We selected 40 bone samples from layers XI–VII of the Grotte du Renne (Table 1), all from different areas of the horizontal section of the site. We especially

targeted those areas that yielded CP body ornaments or diagnostic Neandertal remains (Fig. S5). Thirty-one samples are from the CP deposits, 4 are from the underlying Mousterian and 5 are from the Protoaurignacian.

Our primary selection criterion was good bone preservation. Thus, we did not sample worked elements because they often have little well-preserved compact bone and may have been treated with unrecorded consolidants, which can alter the radiocarbon age. We sampled a large number of thick, untreated pieces of compact bone from shafts, mostly of reindeer and horse, to assess possible movements of material between stratigraphic layers and to compare their ages to those of worked artifacts published for the site (22). Additionally, 35% of the selected fragments displayed anthropogenic marks (cut-marks or percussion marks).

Extraction of collagen, isotopic measurements, and graphitization were performed at the Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, in Leipzig, Germany. All bone samples presented here were subject to the following pretreatment procedures (19). Samples were first cleaned by sand blasting, and then 500 mg of bone powder was taken. The samples were decalcified in 0.5 M HCl at room temperature. Later, 0.1 M NaOH was added to remove humics, and the treatment was completed with the addition of 0.5 M HCl. The resulting solid was gelatinized after Longin (30, 31) at pH 3 in a heater block at 75 °C. The gelatin was filtered in an Eeze-Filter (Elkay Laboratory Products) to remove small (<8 μm) particles and then ultrafiltered with a Sartorius "Vivaspin 15" 30-kDa ultrafilter. Before use, the filter was cleaned to remove carbon containing humectants. Finally, the samples were lyophilized.

The collagen extracts were measured for their C:N ratios, %C and %N, and carbon and nitrogen stable isotope values by using a ThermiFinnigan Flash EA coupled to a Delta V isotope ratio mass spectrometer. The criteria for determining whether the collagen was well-preserved and, therefore, could be radiocarbon dated was a collagen yield of above 1% and a C:N ratio between 2.9 and 3.6 (32–35). After this determination, the collagen samples were graphitized.

The graphite was sent to the Klaus-Tschira-Accelerator-Mass-Spectrometry (AMS) facility of the Curt-Engelhorn Centre in Mannheim, Germany, for AMS measurements. All dates were corrected for a residual preparation background estimated from pretreated ^{14}C-free bone samples, kindly provided by the Oxford Radiocarbon Accelerator Unit (ORAU).

A tibial fragment of compact bone from the Saint-Césaire Neanderthal was obtained to perform isotopic and paleogenetic studies. Its isotopic values and C:N ratio were first determined at the Max-Planck Institute for Evolutionary Anthropology and were found to be in acceptable ranges. Subsequently a subsample of the bone was sent to the ORAU for commercial radiocarbon dating, and pretreatment of the bone was undertaken there using their standard procedures (21). The isotopic values and radiocarbon dates are given in Table 1.

Using the stratigraphic information and the OxCal 4.1 program, which calibrates the dates by using IntCal09 (36, 37), we built a Bayesian model for the distribution of ages. This model is based on the distinction of four separate phases at the Grotte du Renne site, which take into account the archeological observations and the artifact refits. These phases are the Mousterian (layer XI), the CP (combining layers X and IX), the later CP (layer VIII), and the Protoaurignacian (layer VII). The uniform distribution of the radiocarbon ages was tested by using agreement indices. This index shows how the simple calibrated distribution agrees with the distribution after Bayesian modeling and is expected to be more than 60% when the dates are in agreement with the stratigraphy (37). The t-type outlier detection with prior probabilities set at 0.05 within the Bayesian model (37) was also used to detect problematic samples.

Results

At the Grotte-du-Renne, all of the isotopic values and the C:N ratio are well within the accepted ranges (32–35) and most of our samples display high yields of collagen, ranging between 2 and 7% (Table 1). One of the 40 samples had a collagen yield of slightly less than 1%. However, it displayed a normal C:N ratio, was sent for dating, and provided a date in good agreement with samples from the same layer.

Obtained dates range between 40,900 and 43,230 ^{14}C BP ($n = 4$) for the Mousterian phase, 35,500 and 40,970 ^{14}C BP ($n = 26$) for the CP phase, 35,380 and 37,710 ^{14}C BP ($n = 5$) for the later CP phase, and 29,930 and 34,810 ^{14}C BP ($n = 5$) for the Protoaurignacian phase. The calibrated ranges of boundaries and their confidence intervals are listed in Dataset S1. CP and later CP

Table 1. Radiocarbon dates of the Grotte du Renne layers and Saint-Césaire Neandertal

Sample no.	Samples (with spatial and stratigraphic origin)	% Coll.	δ ^{13}C	δ ^{15}N	%C	%N	C:N	^{14}C age B.P.	+/− 1σ Err
Grotte du Renne									
Proto-Aurignacian									
EVA-79	Arcy 58 R VII C7 b	3.7	−20.6	6.2	27.6	10	3.2	29,930	208
EVA-81*	Arcy 58 VII C9 (178)	4.4	−20.5	8.4	22.8	8.1	3.3	33,850	311
EVA-92	Arcy 58 RVII b C10 (348)	5.3	−20.6	7.6	24.2	8.7	3.3	31,610	131
EVA-93	Arcy 58 RVII C11 (452)	4.6	−21.3	3.4	28.6	10.7	3.1	33,010	182
EVA-95	Arcy 58 RVII D10 (254)	6.2	−20.7	6.3	28.4	10.6	3.1	34,810	210
Later CP									
EVA-52	Arcy VIII B15 (24)	1.8	−20	5.5	44.5	14.4	3.6	35,980	432
EVA-53	Arcy VIII 59.C15 (38)	0.9	−19.1	3.8	38.9	14.2	3.2	36,230	435
EVA-54	Arcy VIII 59.Y10(50)	2.2	−18.5	3.4	35.4	13.1	3.2	35,380	390
EVA-55*	Arcy VIII 59.C15 (36)	1.2	−19.3	3.2	41	15	3.2	36,630	452
EVA-56*	Arcy VIII 58.C8 (92)	1.4	−20.4	7	37.4	13.8	3.2	37,710	533
CP									
EVA-44	Arcy IXa B15 (20)	1.6	−20.7	6.1	35.2	13	3.2	39,280	351
EVA-46	Arcy IXa 58.B11	2.7	−21	5.6	48	17.6	3.2	39,930	361
EVA-47	Arcy IXa B14 (106)	4	−21.3	4.7	39.4	14.6	3.2	39,750	360
EVA-33*	Arcy IXb Y13 (43)	4.4	−18.7	3.6	39.1	14.5	3.1	40,970	424
EVA-34*	Arcy IXb B13(110)	4.5	−19	4.6	39.3	14.5	3.2	40,520	389
EVA-35	Arcy IXb B12(134)	3.4	−18.6	3.1	39.5	14.5	3.2	39,240	341
EVA-36	Arcy IXb C12(70)	3.5	−19.3	3.3	45.6	16.7	3.2	37,740	307
EVA-37	Arcy IXb B12 (21)	4.3	−18.5	3.7	42	15.4	3.2	39,450	340
EVA-38	Arcy Xa A11 (3412)	1.5	−20.8	5.7	38.6	14.3	3.2	36,540	248
EVA-40	Arcy Xa A12 (42)	3.4	−19.1	4.1	39.1	14.5	3.1	37,510	275
EVA-41*	Arcy Xa A12 (75)	2.5	−19.1	7.8	41.1	15.1	3.2	38,730	333
EVA-42*	Arcy Xa B12 (36)	4	−19.2	3.5	50.2	18.5	3.2	38,070	311
EVA-43	Arcy Xa 59.C9 (68)	4.1	−18.9	3.1	37.8	13.9	3.2	39,020	352
EVA-23	Arcy Xb1 61.C7 (464)	2.6	−21.1	5.9	42.5	15.8	3.1	36,840	335
EVA-24	Arcy Xb1 61.D11 (60)	5.2	−19.1	8.9	40.2	15	3.1	38,400	317
EVA-25	Arcy Xb1 61.D11 (87)	2.2	−19.6	3.6	41.3	15.2	3.2	36,210	250
EVA-26*	Arcy Xb1 61.Z11 (180)	4	−18.7	3.6	41.3	15.2	3.2	39,390	334
EVA-27	Arcy Xb1 61.D11 (93)	4.4	−18.7	3.5	41.9	15.4	3.2	40,230	395
EVA-28	Arcy Xb1 61.C12 (274)	4.5	−18.7	2.5	39.2	14.5	3.2	40,930	393
EVA-29*	Arcy Xb2 61.Z11 (213)	1.7	−20.9	5.6	40.4	14.8	3.2	35,500	216
EVA-30*	Arcy Xb2 61.B9 (327)	2.2	−21	5.3	40.3	14.9	3.2	37,980	284
EVA-31	Arcy Xb2 61.A11 (2641)	2.5	−19.8	5.5	40.1	14.7	3.2	39,290	334
EVA-32	Arcy Xb2 61.C9 (336)	5.1	−21	5.1	40.6	15	3.2	36,820	257
EVA-48	Arcy Xb2 62.C9 (102)	3.5	−18.6	3	43.2	15.4	3.3	39,070	332
EVA-49	Arcy Xb2 62.C9 (103)	4.4	−18.9	3.9	41.9	15.5	3.1	40,830	778
EVA-51	Arcy Xb2 62.Z10 (2)	3.8	−18.6	7.7	39.8	14.6	3.2	39,960	702
Mousterian									
EVA-77*	Arcy 56 R XI A12	6.2	−20	6.9	29.6	10.9	3.2	42,120	805
EVA-83*	Arcy 59 R XI B12 (25)	5.9	−20.4	9.1	29.6	10.9	3.2	41,980	821
EVA-84	Arcy 60 R XI C15 (133)	6.4	−20.3	9.3	25.7	9.5	3.2	43,270	929
EVA-85*	Arcy 60 R XI C15 (428)	5.1	−20.7	8.8	25.8	9.5	3.2	40,900	719
Saint-Césaire									
OxA- 18099	SP 28; Neanderthal tibia	0.77	−19.3	11.7	27.3	9.6	3.3	36,200	750

C:N ratios, %C, %N, and amount of collagen extracted (%Coll) refer to the >30-kDa fraction. δ^{13}C values are reported relative to the vPDB standard and δ^{15}N values are reported relative to the AIR standard.
*Bones with anthropogenic modifications.

together represent a period twice as short as the Protoaurignacian. The later CP alone lasted only approximately 500 y, which may also explain overlaps in dates between our two CP phases.

OxCal finds an excellent agreement index (A_overall = 113.5%, when the prior probability of two outliers discussed below is set to 100) between the full set of dates and the stratigraphic information (Fig. 1). The results of the outlier detection method are shown in Fig. 1 (as well as Dataset S2). Only two samples, EVA-29 and EVA-56, although well within the accepted range for collagen yield and C:N ratio, display a significant posterior probability indicative of outliers. They are both cut-marked and

chronologically correspond to the limit between CP and later CP. Their occurrence may result from a decontamination problem for the younger of the two, from human or carnivore activity during the later CP phase, or simply from excavation errors.

The direct date obtained for the Saint-Césaire skeleton (Fig. S6) can be accepted with some caution, because its collagen yield is 0.8%. However, the C:N ratio is fully within the accepted range. Its age of between 41,950 and 40,660 calBP with a probability of 86% (1σ) corresponds to the transition from CP to later CP at the Grotte du Renne and is consistent with the CP assignment of the specimen.
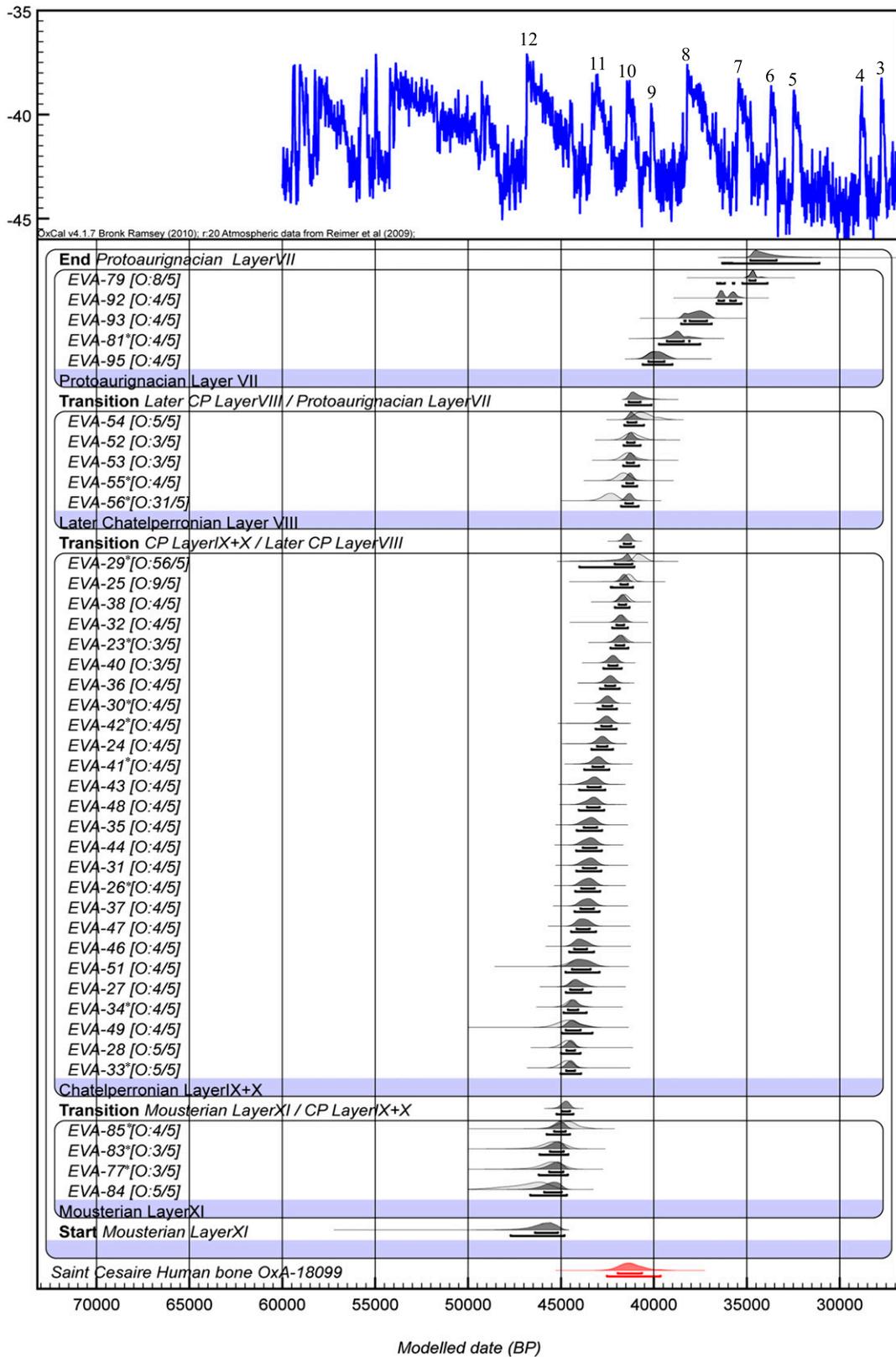
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Fig. 1. Calibrated ages and boundaries calculated by using OxCal 4.1 (37) and IntCal09 (36). The Grotte du Renne ages are in black and are compared with the Saint-Césaire human bone date in red. Asterisk indicates anthropogenically modified bones. The results are linked with the (NGRIP) δ18O climate record.

Discussion

At the Grotte du Renne, our radiocarbon results are notably consistent with the stratigraphic divisions. Most importantly, of

31 samples documenting the CP and later CP deposits not a single one yielded a date in the ranges observed for the overlying Protoaurignacian or underlying Mousterian layers. Considering
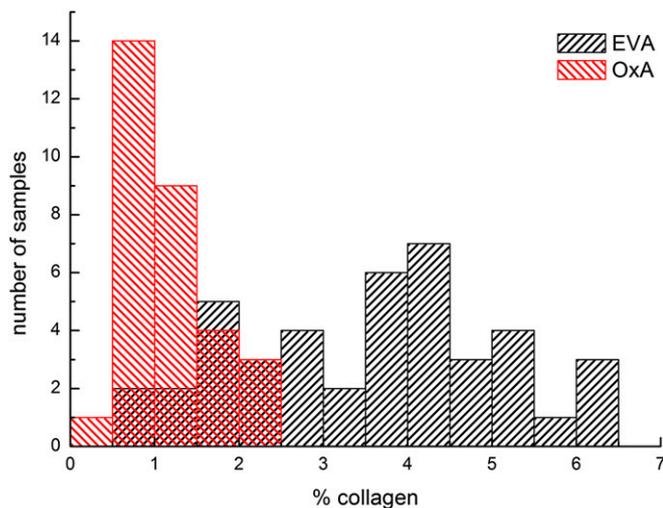
Fig. 2. Distribution of the collagen yields in the samples used in the current study (in black, EVA samples) and in previous radiometric measurements of the same sequence (22) (in red, OxA samples).

the number of analyzed samples and their spatial distribution, it seems therefore unlikely that major contamination of the CP and later CP could have occurred in the portion of the site with horizontal layers.

These observations are at odds with the previous radiometric measurements on the same sequence (22). In that study, nine outliers were detected in a series of 31 dates, and in the CP layers alone, eight samples yielded dates outside the known chronological range of the CP. In our view, this high degree of intralayer variation in the radiometric ages results not from layer admixture but rather from the sample selection criteria. In particular, the emphasis put on directly dating anthropogenically modified bones, including bone tools and body ornaments, may at times have biased the sampling toward poorly preserved bones. After an initial screening of the 59 collected samples, the previous study discarded 19 samples because of insufficient collagen quality (22) (none were discarded in our study). Still, as a whole, the remaining samples displayed low collagen yields, in some cases between 0.3 and 0.5% (Fig. 2). In this situation, contamination is a huge issue. Significantly, none of the CP pendants, and only three CP awls could be dated, one of them with a younger age than the youngest Gravettian documented in the site.

Considering the comparable sizes of some of the artifacts dated in the previous study (22) and of our samples, it seems improbable that the diverging results are the consequence of a selective migration through the stratigraphy of worked bones and artifacts. Our samples with anthropogenic modifications provided ages in perfect agreement with those of bone fragments without modifications. Additionally, the possible selective migration of body ornaments from the Protoaurignacian layers into the lowermost CP layer (X), where most of the ornaments were discovered, is inconsistent with the absence of any undisputable Protoaurignacian stone artifacts of similar size in these CP layers.

An upward selective migration of Neandertal remains toward the CP layers is equally difficult to conceive. Although the CP and later CP deposits yielded 29 isolated teeth and one temporal bone displaying clear Neandertal features (7, 8), the underlying Mousterian layer (XI) is archeologically poor (the area directly under the excavated CP deposits yielded only three human teeth from an excavation area of 30 m^2). Furthermore, two teeth, most likely Neandertal (7), come from the later CP deposits immediately underlying the Protoaurignacian.

Another issue that may explain some of the mismatches previously observed between stratigraphy and radiometric results relates to the distinction of stratigraphic units. The discovery of some refits between CP layers and sublayers led us to group the CP into only two chronostratigraphic units. According to our results, these units represent 3,300 and 500 y of deposit, respectively. Considering documented human and animal activities in the site during these two periods (38), considering the challenging situation of recognizing occupation floors during excavation on large surfaces of a cave deposit, and considering the limits of radiocarbon precision in this time period, further refinements in the chronostratigraphy presented here are unlikely.

The direct date obtained for the Saint-Césaire skeleton does not falsify the null hypothesis that the Neandertals found in the CP deposits of the Grotte du Renne were actually the makers of this assemblage. Other CP sites have yielded a range of dates of which most predate the use of AMS and advanced pretreatment procedures in radiocarbon dating and are therefore highly problematic (39). To date, the Grotte du Renne sequence is the only one documented by a large number of AMS radiocarbon dates obtained on ultrafiltered samples. These dates are quite similar to the CP dates recently obtained with the same technique at Les Cottés (France), also in the northern part of the CP extent (40).

The Protoaurignacian of the Grotte du Renne and Les Cottés is much younger that the oldest occurrence of this assemblage in northern Italy (41) and southern France (42), suggesting a later arrival of their likely modern makers in central France. The time range of the Protoaurignacian is also wider than found for this period in the southern sites and encompasses the Early Aurignacian radiocarbon dates from Les Cottés. If contamination is not an issue then layer VII might be a palimpsest of Proto- and Early Aurignacian. The exact age of the Early Aurignacian in central and northern France remains, to date, poorly known. However, the lithic assemblage of layer VII primarily displays a Protoaurignacian pattern (29).

Finally, according to our results, the CP Neandertals of the Grotte du Renne, Saint-Césaire, and Les Cottés clearly postdate the earliest likely modern humans remains documented in western Europe (43) and largely overlap in time with the early Aurignacian in the Swabian area (44) and in southwestern France (42). This evidence is fully compatible with a model of stimulus diffusion (45), accounting for the emergence of behavioral novelties among the CP Neandertals (8, 10).

Conclusion

On radiometric grounds, we find no evidence to support the previous arguments for major movements of material occurring between archeological layers at the Grotte du Renne in the section of the site between the cliff and talus, the area which yielded the bulk of the archaeological material. This result confirms previous studies on the spatial distribution of the paleontological (46) and archeological material (11).

As a whole, the CP and later CP layers of this site represent a rather short time period. This rapid deposition, the difficulty in separating sublayers at the time of the excavation, some limited movement of material between CP sublayers, and the limited resolution of radiocarbon dates make finer chronological distinctions difficult.

Although major progress has been made in the reliability and calibration of ^{14}C dates beyond 40,000 Cal BP (47), a comparison of our results and those previously obtained for this site also suggests that bone preservation remains a crucial issue when radiocarbon dating is applied to this type of material. This issue represents a major technological challenge for the dating of small artifacts and very fragmentary human remains.

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Based on the stratigraphic evidence and on our radiometric results at the Grotte du Renne and Saint-Césaire, the most parsimonious hypothesis remains that Neandertals were the makers of the CP. They produced body ornaments in the northernmost part of CP's geographical distribution only after modern humans arrived in western Europe and Protoaurignacian or Early Aurignacian populations occupied neighboring regions.

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