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Cannibalism in the Neolithic

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Cannibalism is a provocative interpretation put forth repeatedly for practices at various prehistoric sites, yet it has been so poorly supported by objective evidence that later, more critical reviews almost invariably reject the proposal. The basic data essential to a rigorous assessment of a cannibalism hypothesis include precise contextual information, analysis of postcranial and cranial remains of humans and animals, and detailed bone modification studies. Such data are available from the Neolithic levels of the Fontbrégoua Cave (southeastern France) where several clusters of human and animal bones have been excavated. The analysis of these bones strongly suggests that humans were butchered, processed, and probably eaten in a manner that closely parallels the treatment of wild and domestic animals at Fontbrégoua.

DESPITE ABUNDANT LITERATURE ON THE SUBJECT [SEE bibliographies in (1) and (2)], the occurrence of human cannibalism in Old World prehistory remains an open question. We are concerned here with dietary cannibalism—the use of humans by humans as food—evidence for which is found in patterns of bone modification and discard. The key features of dietary cannibalism involve close, detailed similarities in the treatment of animal and human remains. If it is accepted that the animal remains in question were processed as food items, then it can be suggested by analogy that the human remains, subjected to identical processing, were also eaten.

Evidence of deliberate discard, cut marks, and bone breakage to extract marrow are criteria used to deduce that animal bones at archeological sites were food refuse; these same criteria have been used to interpret isolated and scattered human bones at various prehistoric sites as evidence of cannibalism (3). However, in many cases such an interpretation is weakened by doubts about whether humans caused the observed damage and by lack of precise contextual evidence. Poorly recorded excavation data, insufficient documentation and analysis of damage and discard patterns, and the high frequency of pre- and postdepositional disturbances by nonhuman agents at archeological sites have fueled these doubts. These are the

main reasons why explanations of cannibalism are often ignored or rejected (4–6).

It has been suggested that human bones with cut marks are not the remains of cannibal meals but the traces of funerary rites involving the handling of corpses without consumption of human tissues (2, 7). Secondary burial may mimic cannibalism if it includes active dismemberment and defleshing of the body; however, the absence of bone breakage for marrow and the mode of bone disposal will set it apart from dietary cannibalism (8).

A hypothesis of dietary cannibalism must be based on four types of evidence: (i) Similar butchering techniques in human and animal remains. Thus frequency, location, and type of verified cut marks and chop marks on human and animal bones must be similar, but we should allow for anatomical differences between humans and animals; (ii) similar patterns of long bone breakage that might facilitate marrow extraction; (iii) identical patterns of postprocessing discard of human and animal remains; (iv) evidence of cooking; if present, such evidence should indicate comparable treatment of human and animal remains.

We studied recently excavated materials from a Neolithic cave site in southeastern France. A combination of excellent bone preservation, primary depositional context, and fine excavation techniques allows us to present evidence of cannibalism at the site.

The Site and Bone Occurrences

The Fontbrégoua Cave (9) is divided into three spatially discrete areas: the porch, the main room, and the lower room (Fig. 1). All areas have yielded skeletal and cultural materials: pottery, stone tools, remains of domestic and wild faunas, carbonized seeds of domestic wheat and barley, and human remains.

Stratigraphic and cultural evidence suggest that during the 5th and 4th millennia B.C. the cave was repeatedly used as a temporary

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Table 1. Location, age, and relative depth of features.

Features			Age of level (years B.C.)	Sample*
Lower room	Main room	Porch		
	7		3150 ± 110	GSY 2432
	6		3100 ± 120; 2930 ± 110	GSY 2101, 2433
	8		End of 4th millennium	
	5		About 3700	
	H3, 9		3740 ± 190;	GSY 2757,
	10		3740 ± 130	2756
H1		H2	4300 to 3700†	
4			Late 5th millennium	
1, 2	3		4750 ± 100	GSY 2990

*Gif-sur-Yvette laboratory sample number; uncalibrated ^{14}C dates on charcoal. †The age and relative position of the two disturbed clusters, H1 and H2, are approximate.

residential camp (10). In the Early Neolithic, hunting and sheep and goat herding were of comparable importance, whereas in the Middle Neolithic hunting played a minor role (11).

Preserved habitation features include 13 clusters of bones, which occur in shallow, probably man-made, hollows of relatively small size (20 to 100 cm wide and 8 to 35 cm deep). Ten of these clusters (features 1–10) preserve the butchered remains of wild or domestic animals; three clusters [features H1 through H3; (12)] contain only human remains. The location, chronology, and relative depth of these features are given in Fig. 1 and Table 1. All clusters are judged to be intact, with the exception of two of the human clusters (H1 and H2). We verified the integrity of the features according to five criteria. (i) Bone fragments that could be conjoined were found within each feature; numerous refitting links extend across the depth of feature. Very few links with pieces outside each feature were found (Table 2). (ii) Bones within a cluster can be rearticulated to show they were derived from a single individual. (iii) The vertical and horizontal distribution of bones within each feature is restricted. (iv) Horizontal boundaries of features were sharp and clearly

demarcated. (v) Rodent or carnivore tooth marks, suggesting a nonhuman agent of collection or damage, are not present. Fresh bone surfaces with sharp fracture edges and intact anatomical segments found in six of the features (Table 3) provide further evidence of an undisturbed context.

Clusters of Animal Bones (Features 1–10)

Four features contained the remains of several wild animals, either wild boars (features 1, 9, and 10) or animals of several different species (feature 3). Features 4, 5, 6, and 7 each contained a partial skeleton of a domestic sheep (*Ovis aries*). All analyzed features are judged to have resulted from single episodes of butchering and discard.

Three features with animal bones (features 2, 3, and 8) have been excluded from detailed analysis of the body parts represented in each feature. Feature 8 contained a cluster of sheep bones found under a heavy stone; most bones were very fragmented, some pulverized. Feature 3, which contained the skulls and some shoulder blades of six red deer, one roe deer, five marten, two badgers, one fox, and one wolf, is at the edge of an unexcavated area, at the base of the Neolithic sequence; only half of the feature has been uncovered. Feature 2 differs from others because it is not a discard cluster containing several bones. It consists of a circle of stones (diameter, 75 cm) surrounding a single left frontal bone and horn of a domestic ox with skinning marks above the orbit. This is the only feature that may be qualified as "ritual." Cut marks and location data from features 2, 3, and 8 have been studied.

Clusters of Human Bones (Features H1–H3)

Feature H3 in the main room is a shallow depression (80 by 40 cm wide and 15 cm deep) containing 134 fragments of postcranial bones that lack most of the articular ends. These bones are from a minimum of six individuals: three adults, two children, and one individual of indeterminate age. Also in the feature were eight stone

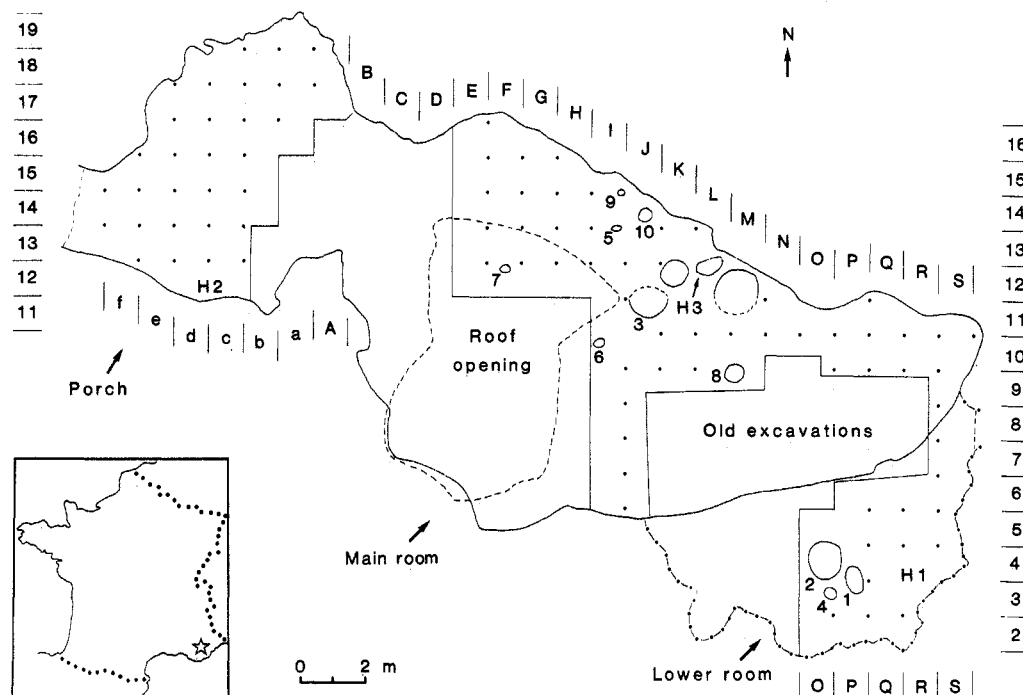


Fig. 1. Plan of Fontbrégoua Cave with features. The two unnumbered features near H3 are storage pits.

bracelet fragments that conjoin to form two round bracelets. In addition, H3 contained one broken, small polished ax, with a chopping edge of 1.1 cm, which was probably used for butchering the axial skeleton (I3).

Refitting links combined with vertical plots of elements (Fig. 2 and Table 2) show that feature H3, like the animal bone clusters, represents a single event. The bones of the six individuals were processed and discarded at the same time.

Clusters H1 and H2 were disturbed. We define a disturbed cluster as a group of bones that were originally deposited together but were later displaced vertically and horizontally by other agents. The former existence of a cluster is indicated by pieces that can be refitted and by a higher density of pieces within a restricted area, as shown

by horizontal and vertical plots of their observed positions (Fig. 3).

The H1 cluster in the lower room contains mostly cranial bones (five incomplete crania, isolated fragments of two others, and six mandibles) and 34 postcranial elements. The minimum number of individuals (MNI) is seven, that is, three adults and four children. One H1 bone shows rodent tooth marks and another shows carnivore tooth marks similar to those produced by wolves or dogs. The H1 bones were found in a zone 8 m long and 2.5 m wide, parallel to the cave wall. The maximum vertical distance between pieces that refit is 70 cm; the longest horizontal link is 4.6 m.

Four observations suggest that most of the bones deposited in H1 have been recovered in the present excavation. (i) The densest patch

Table 2. Link frequencies in features. Genus and minimum number of individuals in each feature are in parentheses. Abbreviations: NA, not applicable; NISP, number of identified specimens, after refitting.

Link descriptors	Features								
	H1 (7 <i>Homo</i>)	H3 (6 <i>Homo</i>)	1 (3 <i>Sus</i>)	9 (4 <i>Sus</i>)	10 (2 <i>Sus</i>)	4 (1 <i>Ovis</i>)	5 (1 <i>Ovis</i>)	6 (1 <i>Ovis</i>)	7 (1 <i>Ovis</i>)
Conjoined groups (<i>n</i>)	18	20	38	61	36	9	2	13	4
Conjoined pieces (<i>n</i>)	116	59	102	154	116	35	16	65	36
Conjoined pieces (%) [*]	62.7	33.9	32.8	65.3	60.4	36.8	72.7	45.1	46.1
Outside links (<i>n</i>) [†]									
Horizontal	NA	0	1	4	2	0	0	0	0
Vertical	NA	0	3	0	0	0	0	0	0
Pieces in outside links (%)	NA	0	5.5	2.1	1.0	0	0	0	0
NISP	84	134	240	149	87	81	8	57	49

^{*}Number of conjoined fragments divided by the total number of bone fragments, excluding unidentified splinters. [†]Outside horizontal links are with pieces that were never deposited in the feature or were displaced. Vertical links indicate displacement.

Table 3. Percentage of element representation. Abbreviations: MNE, minimum number of elements; CUT (%), number of bones with cut marks divided by the number of identified specimens, excluding teeth; AU, anatomical units found intact in situ; total number of pieces in anatomical units are in parentheses.

Element	Features								
	H1 (7 <i>Homo</i>)	H3 (6 <i>Homo</i>)	1 (3 <i>Sus</i>)	9 (4 <i>Sus</i>)	10 (2 <i>Sus</i>)	4 (1 <i>Ovis</i>)	5 (1 <i>Ovis</i>)	6 (1 <i>Ovis</i>)	7 (1 <i>Ovis</i>)
Cranium	100.0	0	100.0	0	50.0	0*	0	0	0†
Mandibles	85.7	0	66.7	0	50.0	100.0	0	100.0	50.0
Cervical vertebrae	8.2		4.8	0	42.9	0	0	0	0
Thoracic vertebrae	0	1.4‡	38.1	0	53.6	0	0	76.9	69.2
Lumbar vertebrae	0		83.3	0	50.0	0	0	100.0	42.9
Sacrum	0	16.7	0	0	50.0	0	0	100.0	0
Caudal vertebrae	0§	0§	8.3	0	15.0	43.7	0	14.3	0
Clavicle	21.4	25.0							
Ribs	0	6.2	25.0	0	35.7	57.7	0	53.8	57.7
Scapula	14.3	50.0	16.7	0	50.0	50.0	0	0	0
Humerus	21.4	50.0	66.7	0	50.0	50.0	0	50.0	100.0
Ulna	0		33.3	62.5	50.0	50.0	0	50.0	100.0
Radius	14.3	37.5	33.3	50.0	50.0	50.0	0	50.0	100.0
Pelvis	0	8.0	0	0	25.0	50.0	50.0	100.0	100.0
Femur	21.4	33.0	66.7	50.0	25.0	50.0	50.0	100.0	50.0
Patella	0	0	0	25.0	0	50.0	50.0	50.0	0
Tibia	14.3	75.0	16.7	37.5	0	50.0	50.0	100.0	50.0
Fibula	25.0	25.0	33.3	12.5	0	50.0¶	0¶	0¶	50.0¶
Carpals	0	0	37.5	40.6	0	100.0	0	60.0	50.0
Tarsals	2.0	0	30.9	3.6	3.6	70.0	50.0	62.5	20.0
Metacarpals	0	0			18.7	100.0	0	0	0
Metatarsals	0	0	70.8#	48.4#	6.2	100.0	0	0	0
Hand phalanges	3.6	1.2				100.0	0	0	0
Foot phalanges	1.0	0				100.0	0	0	0
Total MNE	45	55	216	144	76	81	8	57	48
CUT (%)	45.6	30.3	15.4	11.4	57.5	23.5	37.5	50.9	49.0
AU	0	0	12 (37)	3 (6)	6 (15)	6 (25)	2 (5)	0	5 (37)

*The maxillae and premaxillae are present. †The right occipital condyle is present. ‡Total percentage of cervical, thoracic, and lumbar vertebrae. §Coccyx. ||Total percentage of ulnae and radii. ¶Lateral malleolus. #Total percentages for metacarpals and metatarsals. **Total percentages for hand and foot phalanges.

of bones is 3 m away from the edge of older excavations, so it is unlikely that any H1 bones were previously excavated. (ii) All bone fragments from every level in the lower room have been thoroughly sorted in search of additional human material. (iii) Although some bones may have been destroyed by mechanical attrition or carnivore damage, visible damage on the preserved human bones is rare (1.5% of the specimens, excluding teeth). (iv) Animal bones in the same deposits also show limited carnivore damage (2%).

Finally, the high proportion of refitting links (Table 2) and their spatial pattern suggest that most H1 bones were originally in association. Therefore, we include the H1 material in the analysis, except in the study of fracture patterns, since breakage might have occurred during postdepositional disturbances.

The H2 pieces were scattered along the cave wall in a strip 1.7 m long and 10 cm wide. The vertical spread was 74 cm. Of 20 fragments, 15 have been conjoined in five groups. No carnivore or rodent marks appear on the bones; of ten bones, three have cut marks. The number of postcranial bones ($n = 2$) is too small to be informative, and we cannot be sure that all the bones have been recovered. Thus, only cut marks and location data have been considered.

Analyses of Fontbrégoua (10) suggest that there were initially more discard clusters than found during this excavation; presumably many such clusters were disturbed by various agents, including the inhabitants' own digging activities. It is notable that there are no graves at the site. The mode of burial in Provence for this time period was individual inhumation; however, documentation of this practice is not extensive (14).

Location and Mode of Discard

Human and animal clusters are found in all parts of the cave; there is no special area reserved for features with the human bones (Fig. 1 and Table 1). This is especially evident in feature H3, which is in the same level as features 9 and 10 and spatially close to them. The absence of animal bone clusters in the porch is not significant because deposits are very disturbed.

In size and shape, H3 (80 by 40 by 15 cm) is similar to other clusters, especially feature 1 (70 by 40 by 7 cm), which contained the partial skeletons of three wild boars.

Table 3 shows the frequencies of body parts present in each cluster. Each figure is obtained by dividing the observed minimum number of a skeletal element by the expected number of the same element, based on the MNI; the ratio is expressed as a percentage (15). This statistic is often used to express patterns of differential survival. Here, since these clusters (with the exception of H1) are intact and have undergone no postdepositional destruction, the percentage of element representation reflects discard patterns.

Data in Table 3 suggest the following observations: (i) In all clusters animals or humans are represented by selected anatomical parts; other parts are missing or are present in lower than expected frequencies. For example, in feature 4 the left foreleg and the right hindleg are missing, yet all four limb extremities (metapodials and phalanges) are present and intact. Crania and limb extremities are missing from features 5, 6, 7, and H3 (16). Feature 9 contains the manus and pes of four wild boars plus some leg bones; all other body parts are missing. In H3 only six scapulae and six humeri are present out of the 12 expected for each; in feature 1 there are only four humeri out of the six expected. (ii) Sometimes only a small portion of an anatomical segment is present. Thus in feature 6 the braincase is missing, but the muzzle bones are present; the right foreleg from scapula to phalanges is missing, but the right carpals are present. In feature 7 the cranium and the neck are missing, but

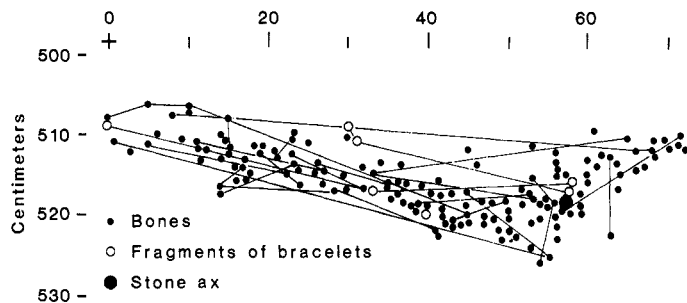


Fig. 2. Feature H3: vertical projections and refitting links (short links omitted).

the right occipital condyle is present. In H3 the sacrum and pelvis are represented by only small fragments of one element. In features 1 and 4 sacra are absent, but caudal vertebrae are present.

The pattern that emerges from all human and animal clusters shows discard of selectively butchered parts. Two facts are intriguing. First, missing anatomical segments are represented by isolated elements or scraps of little food value, for example, carpals, occipital condyle, minute bits of sacrum, or, as in feature 4, intact lower leg parts. Second, these isolated elements are near or at points of disjuncting and segmentation. We conclude that the missing anatomical segments have been culled from essentially complete carcasses at the cave itself. After disarticulation, selected body parts were set aside for separate processing and consumption; thus they are missing from the features. If segmentation had taken place outside the cave, it is unlikely that scraps from the culled units would have been collected and transported inside the cave for the purpose of discarding them.

Two observations support this view of butchering in the cave. (i) Sheep were penned at the site (17); thus we infer that they were killed and butchered at the site. (ii) All types of bones from wild boar and human skeletons are present in the cave bone assemblage, including parts of low utility such as heads, necks, caudal vertebrae, and phalanges (10).

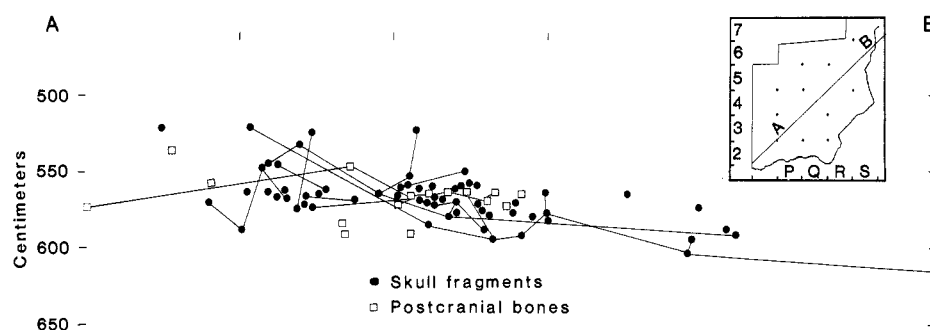
It is possible that filleting (defleshing) and marrow fracturing were done on a skin; the residue was then discarded in a single pile. The use of a skin would explain why the bones are tightly packed in well-defined clusters and why so many fragments can be conjoined. It would also explain the presence in each cluster of many small unidentifiable splinters resulting from the operations of marrow fracturing (18) and the presence of bits of culled units.

In sum, it is clear that human and animal carcasses were processed and discarded according to the same pattern of selective butchering (19). Segmentation and selection of parts for differential use or distribution are normally practiced when butchering animals (20); their occurrence in the processing of human carcasses is significant. Although domestic sheep were butchered one at a time, wild animals were captured and butchered in groups. Interestingly, two of the three clusters of human bones correspond to the wild animal pattern of butchering.

Cut Marks

Cut marks on human bones have been compared to marks on homologous animal bones. Of 223 bones bearing 246 cut marks (21), we verified a sample of 27 bones with 31 cut marks by scanning electron microscope (SEM) studies, using procedures described in (22). The verified sample includes 29% of the observed cut marks on the human bones (25 of 85) and 4% of the marks on

Fig. 3. Disturbed feature H1: vertical projections and refitting links (some peripheral links omitted). Inset shows cave area where H1 bones were found. The A-B line is the axis of maximum dispersal.



the animal bones (6 of 161). All putative cut marks replicated for microscopic study (23) were confirmed as cut marks. Nearly all types of human bones bearing observed cut marks have at least one verified cut mark. The fine-grained substratum (24) and undisturbed context of the features and the placement and patterns of cut marks (25) are further evidence that these are purposive toolmarks and are not due to carnivores or trampling (26). The interpretation of activity is based on descriptions by Binford (5) and on our experimental butchering of a sheep and a goat with flint blades and a stone ax.

All cut marks, regardless of the taxonomic identity of the bones, show features suggesting that they were made shortly after death (immediate processing), rather than a year or more after death (delayed processing). This assessment of the timing of processing is based on SEM comparisons of the Fontbrégoua material and experimentally altered bones (27). Immediate processing is consistent with an interpretation that both animals and humans were processed for use as food.

There are strong similarities in frequencies of marked bones and types of cut marks (Tables 3 and 4). Especially significant is the abundance of filleting marks on both human and animal bones, indicating that meat was routinely removed from the bones. Frequencies of filleting versus dismembering marks on long bones are: 80.0% in H3, 70.6% in feature 1, 75.0% in 4 and 6, 54.5% in 7, 80.0% in 9, and 75.0% in 10 (28).

Meat may have been filleted from still-articulated units, as is suggested by some of the anatomical segments found intact in situ. These units include: distal tibia, tarsals or lateral malleolus or both (features 4, 5, and 7); distal radius, ulna, and sometimes carpals (features 7 and 10); distal femur and proximal tibia (feature 4); tarsals (features 1 and 5); vertebral segments (features 1, 4, 7, and 10); and phalanges or metapodials or both (features 1, 4, and 9). Articulated units were not observed in features 6 and H3, which contained only highly fragmented bones.

With respect to cut mark location and morphology, a remarkable degree of concordance can be observed between animal and human bones. Of 33 cut mark varieties on human cranial and postcranial bones, 23 can be matched with similar marks on homologous animal bones (25).

Differences in cut mark location between animal and human remains are important for two elements, the scapula and the cranium. The greater variety of dismembering cut marks on human scapulae (Table 4) can be attributed to the greater complexity of the shoulder joint in humans, who possess a clavicle, unlike suids and ruminants. Although the treatment of human crania closely parallels that of animal crania with respect to sagittal skinning marks (29), the human material bears cut marks in locations that are undamaged on animal bones. Thus, for example, human crania show cut marks near the insertion of the sternocleidomastoideus muscle on the mastoid process, on the vault bones in areas normally covered by the temporalis muscle, and on the facial bones overlaid by musculature.

These marks are interpreted as defleshing marks. In contrast, the only defleshing marks observed on animal skulls in the features, and in a larger sample from the Early Neolithic deposits, are associated with removal of the tongue. These cut marks occur on the hyoid and on the internal face of the mandibular corpus. It is possible that human crania were more extensively defleshed because they were kept as trophies or ritual objects, as is documented in later periods in the same region (30). However, in all other ways the frequencies and types of marks on the Fontbrégoua bones are consistent with a conclusion that human and animal carcasses were treated similarly.

Marrow Fracturing

All marrow bones in the features and all bones in the H3 cluster are broken, each in several fragments. Although some damage is

Table 4. Frequencies of bones with cut marks from all features. Only homologous bones present in both animal and human samples are listed. Small samples with combined N less than 20 (radii, vertebrae) are not included. Abbreviations: N, number of specimens after refitting; for crania we have used the MNE to avoid problems related to the high degree of fragmentation; CUT, percentages of bones with cut marks; F, Sk, and D, percentages of bones with filleting, skinning, or dismembering marks, respectively; one bone may have two types of marks.

Bone sample	N	CUT	F	Sk	D
Postcranial					
		<i>Humerus</i>			
Human	12	41.7	41.7		0
Animal	20	40.0	40.0		10.0
		<i>Femur</i>			
Human	13	38.5	23.1		38.5
Animal	29	41.4	27.6		24.1
		<i>Tibia and fibula</i>			
Human	25	32.8	28.0		4.0
Animal	13	38.5	38.5		7.6
		<i>Scapula</i>			
Human	16	50.0	18.7		50.0
Animal	9	44.4	22.2		22.2
		<i>Ribs</i>			
Human	38	26.3*	21.0		13.2*
Animal	88	59.1	32.9		36.4
Cranial					
		<i>Mandibles</i>			
Human	9	88.9		66.7	55.6
Animal	14	78.6		57.1	54.5
		<i>Cranium</i>			
Human	8	100.0		75.0	25.0
Animal	13	84.6		76.9	30.8

*Significantly different from the corresponding value in the animal group (χ^2 test on raw frequencies, $P < 0.05$). The low frequency of cut marks and, more specifically, of D marks on human ribs is due to a scarcity of proximal fragments. No significant differences are found in other groups, according to χ^2 or Fisher's exact probability tests. Skinning marks are not found on the listed postcranial bones; possible defleshing marks on skulls are discussed in the text.

likely due to postdepositional alteration and sediment pressure, the high degree of fragmentation of the long bones is primarily attributed to deliberate breakage for marrow. In H3 most of the long bone fragments (88 of 107) are thin, elongate shaft splinters, and many can be identified only by refitting them into larger pieces. Their mean length is 9.4 cm with a range of 2 to 28 cm (and a standard deviation of 4.5). Some attributes indicate fresh bone breakage: fracture edges are smooth in 73% of the cases; 71% have acute or obtuse angles (31). Perhaps the most significant criteria of dynamic loading (by a blow) are wide impact scars with radiating fissure lines. They are present in 20.7% of the long bone fragments in H3; half of these are characterized by broad, thin spalls still attached to the bone, with platforms bounded by arcuate fissure lines behind the point of impact (5, 32). The frequency of impact scars on human long bones compares well with values observed on animal bones from features 1, 4, 7, and 10 (23.4, 12.5, 13.3, and 15.0%, respectively) and with ethnographic observations (5).

Nevertheless, neither fracture morphology nor impact scars with splintered margins are exclusively associated with human marrow fracturing, and they may be produced by carnivores (31, 33). The absence of gnaw marks on the bones from all features (with the exception of H1) will not hold as a valid argument against carnivore damage since the analyst's ability to identify such marks may be doubted. Evidence against carnivore damage and for the human origin of bone breakage is provided, instead, by the repetitive spatial patterns of the bone clusters: sharp horizontal boundaries and localized densities of homogeneous items, abundant refitting links within each feature, and few or no outside links. These patterns provide evidence that the clusters are intact and man-made.

Evidence of Cooking

Two indicators of cooking that might be found on archeological bones are changes in collagen chromatographs (34) and changes in the microscopic morphology of bone surfaces (35). Both were absent from the Fontbrégoua bones. Amino acid analyses of bone collagen in nine samples from H1, H3, feature 1, and the main room deposits show that these bones were not exposed to temperatures greater than 150°C; SEM inspection of various bone samples did not reveal changes in microscopic morphology known to occur at 185°C. However, temperatures achieved by meat-covered bones during boiling or roasting are lower than these thresholds, as experimental studies confirm (35, 36).

Additional evidence that casts doubt on the idea of cooking is provided by the abundant filleting marks and intact anatomical units, both features that one would not expect to find in roasted or boiled remains. Clearly, there is no good evidence showing that cooking of meat-on-bone occurred. However, the treatment of animal and human remains does not differ in this regard; in both cases uncooked bones were discarded after filleting and marrow fracturing.

Conclusions

Our inference that animal and human meat was eaten is based on the evidence of ordinary butchering practices and unceremonial patterns of discard in a domestic setting. Similarities in the treatment of animal and human remains are striking. The evidence of breakage to extract marrow and the mode of discard contrast strongly with known secondary burial practices (8). Elements of rituals seem to be present in the treatment of human skulls, but they are consistent with an interpretation of exocannibalism. Feature 2

suggests that *Bos* skulls could also be an object of special consideration.

We believe that cannibalism is the only satisfactory explanation for the evidence found at Fontbrégoua Cave. Taphonomic studies of human bones at additional Stone Age French sites should help to establish whether our findings represent isolated events or institutionalized practices (37).

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12. The letter H stands for human.
13. Fontbrégoua's Neolithic levels have yielded 15 polished axes with edge widths of 1.1 to 4.8 cm. We believe one of the uses of these small axes was butchering. Chop marks, made with an ax, are present on a human rib and a vertebral fragment in feature H3; others are found on wild boar vertebrae in features 1 and 10. Experimental butchering with a 2.5-cm-wide polished stone blade set in a wooden handle has produced similar marks on vertebrae and pelvis of a sheep and goat.
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15. For example, in feature H1 there is a minimum number of three humeri; the expected number of humeri is 14 since the minimum number of individuals is seven. The percentage of representation is $(3/14) \times 100 = 21.4$. See C. K. Brain, in *Human Origins*, G. L. Isaac and E. R. McCown, Eds. (Benjamin, Menlo Park, CA, 1976), pp. 97–116; ———, *The Hunters or the Hunted?* (Univ. of Chicago Press, Chicago, 1981), p. 21; D. P. Gifford-Gonzalez, in *Proceedings of the First International Conference on Bone Modification*, R. Bonnicksen, Ed. (Center for the Study of Early Man, Orono, ME, in press).
16. The H1 cluster may contain the skulls that are missing from the H3 cluster; however, we can neither prove nor refute this idea. No refitting links have been found between the two clusters; the postcranial bones are too fragmented to be matched for size and age with some degree of confidence. The two clusters are in deposits of broadly equivalent age, but the gap left by the older excavations forbids any assessment of stratigraphic continuity between the two areas.
17. The Fontbrégoua's deposits contain two diagnostic traces of cave herding. The first is abnormally high frequencies of ovicaprine milk teeth with maximum degree of wear and totally resorbed roots. These teeth were lost naturally, and their abundance suggests that the animals were kept in pens inside the cave [D. Helmer, in *Animals and Archaeology*, J. Clutton-Brock and C. Grigson, Ed. (British Archaeological Reports, International Series 204, London, 1984), vol. 3, pp. 39–45]. The second is large quantities of calcite spherulites, representing the mineral residue of ovicaprine dung. Similar traces are found in other Neolithic caves [J. Brochier, *Bull. Soc. Préhist. Franç.* **80**, 143 (1983)].
18. For example, feature H3 contained 154 indeterminate bone fragments >2 cm and 133 g of small bone chips recovered through water sieving; feature 10 had 61 indeterminate bone fragments >2 cm and 470 g of smaller ones.
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23. Replicas of marked surfaces are used to avoid transporting of and damage to the originals.
24. Predominantly fine sand and silt; J. Brochier, in preparation.
25. Photos, drawings, and lists of cut marks are provided in (10) and in P. Villa et al., *Gallia Préhistoire*, in press.

25. Photos, drawings, and lists of cut marks are provided in (10) and in P. Villa *et al.*, *Gallia Préhistoire*, in press.
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28. Total counts of filleting and dismembering marks on long bones from features H3, 1, 4, 6, 7, 9, and 10 are: 35, 17, 4, 8, 11, 10, and 8, respectively. See (21) for counting procedures.
29. Five human and seven animal crania have long sagittal marks along the midline, frontal to occipital.
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36. Amino acid analyses of two modern samples (a sheep pelvis boiled for 4 hours and a sheep humerus from a shoulder roast cooked until well-done on an open fire for 1 hour and 15 minutes) show chromatographs identical to those of modern unheated bones and to those of the archeological bones. Temperatures achieved by meat during roasting are less than 100°C [J. Child, L. Bertholle, S. Beck, *Mastering the Art of French Cooking* (Knopf, New York, 1968), p. 379].
37. Bone fragments from feature H3 have been dated by the Lyon laboratory to 3930 ± 130 B.C. (uncalibrated ¹⁴C date on bone; Ly 3748).
38. Supported by grants from the Wenner Gren Foundation, the American Council of Learned Societies, and the Leakey Foundation to P.V. The Fontbrégoua excavations are funded by French Ministry of Culture grants to J. C.

Molecular Biology of the H-2 Histocompatibility Complex

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The H-2 histocompatibility complex of the mouse is a multigene family, some members of which are essential for the immune response to foreign antigens. The structure and organization of these genes have been established by molecular cloning, and their regulation and function is being defined by expression of the cloned genes.

THE MAJOR HISTOCOMPATIBILITY COMPLEX (MHC) OF mammals is a multigene family whose members encode cell surface glycoproteins involved in the recognition and immune response to foreign antigens. The MHC has been conserved throughout vertebrate evolution, and the MHC's of mouse (H-2) and human (HLA) have been studied extensively. The H-2 complex, located on mouse chromosome 17, has been divided into class I and class II genes on the basis of structural and functional similarities (1-5).

The class I genes are located at four genetic loci defined by serologic analyses of recombinant inbred mice: H-2K, H-2D/H-2L, Qa-2,3, and Tla (Fig. 1). These genes encode heavy chains of a molecular size of approximately 45,000 (45 kD) that are noncovalently associated as heterodimers with a β_2 -microglobulin (β_2m), a 12-kD polypeptide encoded by a gene on mouse chromosome 2 (6). The 45-kD polypeptide has three extracellular domains (here called α_1 , α_2 , and α_3) anchored in the membrane by a short transmembrane segment, and a cytoplasmic peptide of some 35 amino acids (Fig. 2a).

The K, D, and L molecules are highly polymorphic (7), are expressed on the surface of virtually all cells, and appear to direct the recognition of virus-infected and neoplastic cells by cytotoxic T lymphocytes (CTL) (8, 9). The antigen-specific receptors of CTL recognize viral glycoproteins only when they are associated with these class I molecules on the cell surface. In contrast, products of the Qa-2,3 region (Qa-2,3) and the Tla region (TL) are less

polymorphic and their expression is limited to certain tissues (10-13). The Qa-2,3 and TL molecules are not involved in associative recognition by CTL, and their function is unknown.

The class II genes are located at two genetic loci (I-A and I-E) that map between H-2K and H-2D/H-2L (Fig. 1). The I-A region contains the A_β , A_α , and E_β genes and the I-E region contains the E_α gene. These genes encode heterodimers (Ia molecules) consisting of a 35-kD α chain noncovalently associated with a 29-kD β chain (14). Both α and β chains consist of two extracellular domains, a transmembrane segment, and a cytoplasmic region (Fig. 2a). The Ia molecules are highly polymorphic and are expressed primarily on the surface of B lymphocytes, macrophages, dendritic cells, and certain epithelial cells. The antigen-specific receptors of helper T cells that are required for the generation of CTL and for antibody production by B cells recognize foreign antigen only when it is associated with Ia molecules (15, 16).

The domain organization of class I and class II molecules is reflected by the exon-intron organization of the corresponding genes. The α_3 domain of class I molecules and the α_2 and β_2 domains of class II molecules have strong sequence homology to domains of immunoglobulin-constant regions and thus belong to the immunoglobulin supergene family (17).

Organization of Class I Genes

The organization of class I genes of the BALB/c (H-2^d) and C57BL/10, or B10 (H-2^b), haplotypes is known in detail, and the

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