head start in sibling rivalry (*8*). Both increasing and decreasing amounts of testosterone with laying order of eggs have been described in different species (*6*, *8*, *9*). This has been interpreted as maternal manipulation to ameliorate or impair, respectively, the survival prospects of the last-hatched chicks. Zebra finches do show asynchronous hatching, but it is more pronounced in the lab than in the field (*20*). The amount of T and DHT that female zebra finches deposited in the egg declined with the position in the laying sequence, regardless of males' leg-band color (Fig. 2), suggesting that females are reinforcing the feeding hierarchy within the brood. This could be adaptive when food conditions are poor or very unpredictable. If the probability of brood reduction covaried with male quality—that is, if brood reduction were less likely when females were paired to attractive males—then we would expect that testosterone would be more evenly distributed within the clutches fathered by red-banded males than in those fathered by green-banded males. However, the regression slopes of androgens with egg laying order were not different between the two conditions (Fig. 2), suggesting that the conditions leading to adaptive brood reduction in this species are more dependent on environmental conditions than on male quality.

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12. On the morning that each egg was laid, it was removed and replaced with a dummy egg. Clutches were considered complete once laying had stopped for 3 days or six eggs had been laid (*20*). Each pair of birds was housed in individual cages, without visual contact with other birds. The room was lit with full-spectrum fluorescent tubes. The failure of some studies to replicate an effect of band color on male attractiveness is most likely due to inadequate housing conditions without ultraviolet (UV) light (*21*). Our experiment was done under the required conditions of UV light.
13. The whole yolk was removed, homogenized in 0.5 ml of distilled water, and frozen on the morning of laying. Free steroids were extracted twice from yolk-water homogenate with 3 ml of ether. Ether fractions were decanted from the snap-frozen egg yolk–water phase, pooled, and then dried under a stream of nitrogen. The dried extract was redissolved in 90% ethanol and kept overnight at −20°C. Precipitated proteins and lipids were separated by decanting after 5 min of centrifugation at 1300*g*, and the ethanol was dried under a stream of nitrogen. The dried extract was redissolved in 1.5 ml of assay buffer. Extraction efficiencies were assessed in each assay and were on average 70%. Testosterone (T) + 5α-dihydrotestosterone (DHT) concentrations were measured by radioimmunnoassay. The established intraassay coefficient of variation is 5.0%, and the interassay coefficient of variation is 11.3% [BIOTRAK testosterone/dihydrotestosterone (3H) assay system Code TRK 600; Amersham Pharmacia Biotech]. The measured intraassay coefficient of variation was 3.9% for T + DHT and 2.0% for DHT alone. Disintegrations per minute was used throughout.
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22. We thank S. Buckland, M. Ritchie, and P. Gardner for statistical advice and comments on the manuscript. D.G. was supported by a grant to J.G. from the School of Environmental and Evolutionary Biology, University of St. Andrews, UK.

14 April 1999; accepted 24 August 1999

Neanderthal Cannibalism at Moula-Guercy, Ardèche, France

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The cave site of Moula-Guercy, 80 meters above the modern Rhone River, was occupied by Neanderthals approximately 100,000 years ago. Excavations since 1991 have yielded rich paleontological, paleobotanical, and archaeological assemblages, including parts of six Neanderthals. The Neanderthals are contemporary with stone tools and faunal remains in the same tightly controlled stratigraphic and spatial contexts. The inference of Neanderthal cannibalism at Moula-Guercy is based on comparative analysis of hominid and ungulate bone spatial distributions, modifications by stone tools, and skeletal part representations.

Baume ("cave") Moula-Guercy is in southeastern France on the west bank of the Rhone River, in Ardèche. The stratigraphic sequence is exclusively Middle Paleolithic. A test excavation in 1991 revealed 12 hominid skeletal fragments, some with cut marks (*1*).

The lowest exposed units (levels XVI to XX) represent a cold period that is biochronologically dated to the terminal Middle Pleistocene (isotope stage 6). The upper units (levels IV to XI) represent a cool period corresponding to isotope stage 4. Level VI is volcanic tephra dated to 72,000 ± 12,000 years ago (*2*). A thick and homogenous deposit (levels XII through XV) between the upper and lower units contains an abundant fauna representative of a temperate forest. We interpret the data to indicate an Eemian age for the latter deposits (isotope stage 5, 80,000 to 120,000 years ago) (*2*). The Neanderthal fossils all derive from level XV, a temporary Mousterian (Middle Paleolithic) occupation thought to date to between 100,000 and 120,000 years ago on the basis of biochronologies of large and small mammals (*2*). Approximately 30% of the estimated volume of this unit has been excavated (Fig. 1). Contemporary European sites are rare. Moula-Guercy's detailed paleoenvironmental and behavioral records complement its Neanderthal remains in illuminating the transition from the Middle to the Upper Pleistocene.

Level XV contains a lithic assemblage attributable to the Ferrassie Mousterian, a lithic tradition based on a high frequency of

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scrapers and Levallois [prepared core (*3*)] debitage. The lithics are not abundant in this unit, being mainly represented by tools rather than debitage and cores. This layer contains structural evidence in the form of three hearths and a stone wall (Fig. 1). As of August 1998, there were 78 identified, unconjoined hominid fragments from level XV. Additionally, there were 392 taxonomically and anatomically identified nonhominid remains [number of identifiable specimens present (NISP)] among the 1527 cataloged macromammalian faunal specimens. The red deer *Cervus elaphus* is represented by least five individuals [minimum number of individuals (MNI)]. The hominid and cervid remains evince parallel discard histories based on their spatial and stratigraphic commingling (Fig. 1). The subsequent occupation (level XIV) was very different. There, the same kind of Mousterian assemblage is present but with abundant fauna and lithics and without hominid remains.

Preservation of the osteological remains from level XV is excellent. Even fetal ungulate remains were recovered. *Cervus elaphus* is the dominant taxon, followed by *Homo* and *Capra* (Fig. 1). The 78 certain hominid fossils include cranial, dental, and postcranial remains that are attributable to a minimum number of six individuals. The only intact hominid bones are those of the hand and foot.

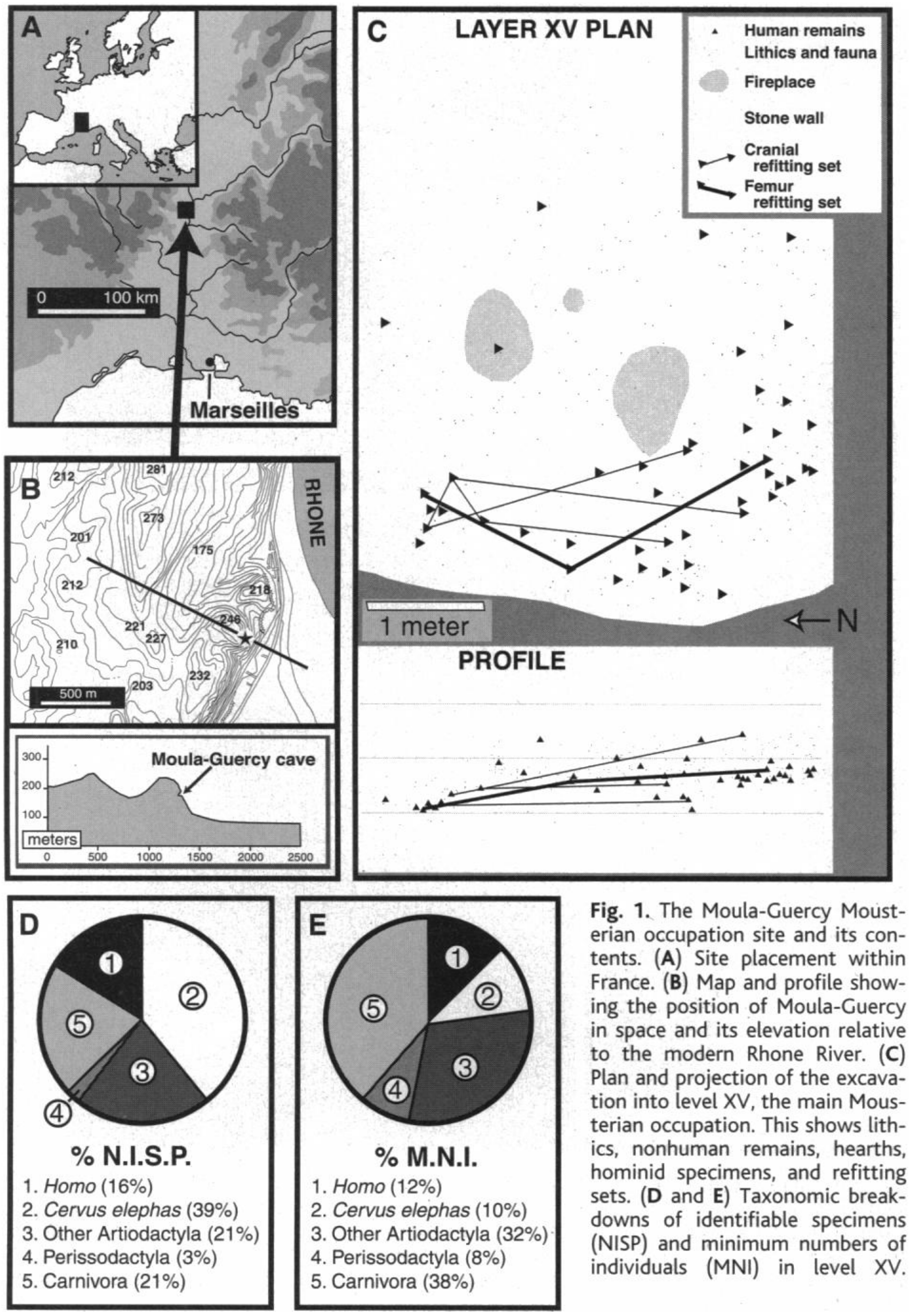

Fig. 1. The Moula-Guercy Mousterian occupation site and its contents. (**A**) Site placement within France. (**B**) Map and profile showing the position of Moula-Guercy in space and its elevation relative to the modern Rhone River. (**C**) Plan and projection of the excavation into level XV, the main Mousterian occupation. This shows lithics, nonhuman remains, hearths, hominid specimens, and refitting sets. (**D** and **E**) Taxonomic breakdowns of identifiable specimens (NISP) and minimum numbers of individuals (MNI) in level XV.

Determining individual ages for such broken and isolated remains is difficult. At least one large and one smaller adult Neanderthal are represented by clavicles and calcaneal fragments. Two immature specimens are aged at 15 to 16 years, based on dental eruption. Two additional individuals aged 6 to 7 years are also present.

European fossil hominids recovered from deposits of similar antiquity are all Neanderthals. In regard to all anatomical areas in which character assessment can be accomplished, the Moula-Guercy level XV hominid remains represent Neanderthals. Neanderthal characters that are evident among the fragmentary remains currently include a double occipital suprainiac fossa; an occipital torus that fades laterally and is depressed near the midline; a posteriorly originating mandibular ascending ramus; incisor hypertrophy; taurodont molars and premolars; a long, thin, crested superior pubic ramus; hand and foot phalanx robusticity; wide terminal phalangeal

Table 1. Comparison of hominid-induced modifications on different skeletal parts of *Homo* (Neanderthal) and *Cervus* (deer). The anatomical differences between these taxa, particularly the larger crania and smaller metapodials of the Neanderthals, result in the observed differences in modification frequencies and element counts. Except where denoted as percentage values, the first number in each column is the number of specimens (NISP) with the modification. The second number is the total number of specimens observed.

	Cut marks		Fracture for marrow or brains	
	Hominid	Deer	Hominid	Deer
	Cut marks and fracture			
Cranium	15/23	0/1	23/23	1/1
Mandible	2/2	1/5	2/2	5/5
Vertebrae	0/2	1/12	–	–
Ribs	2/2	1/8	–	–
Pelvis	0/3	0/0	–	–
Scapula	0/0	0/2	–	–
Humerus	0/0	4/9	–	–
Radius	1/2	–	–	–
Ulna	1/2	–	–	–
Radioulna	–	2/7	–	–
Carpal	0/1	0/3	–	–
Tarsal	1/7	1/5	–	–
Metapodial	1/3	9/36	0/3	43/43
Femur	3/5	7/15	–	–
Tibia/fibula	1/4	2/9	–	–
Phalanx	4/9	1/20	2/9	13/17
Clavicle	3/3	–	–	–
Limb bones	6/13	15/40	13/13	40/40
	Inner conchoidal scars			
Total pieces	7.4%	10.7%		
	Percussion pits			
Total pieces	2.9%	2.0%		
	Adhering flakes			
Total pieces	1.5%	1.0%		
	Anvil striae			
Total pieces	1.5%	0.5%		

apical tufts; a superoinferiorly flattened clavicular shaft; a relatively short third metacarpal styloid process; and thick long bone cortices in both adults and immatures. The larger adult individual is one of the largest Neanderthals known.

Qualitative and quantitative studies of modifications to the hominid and nonhominid faunal assemblages from the Moula-Guercy

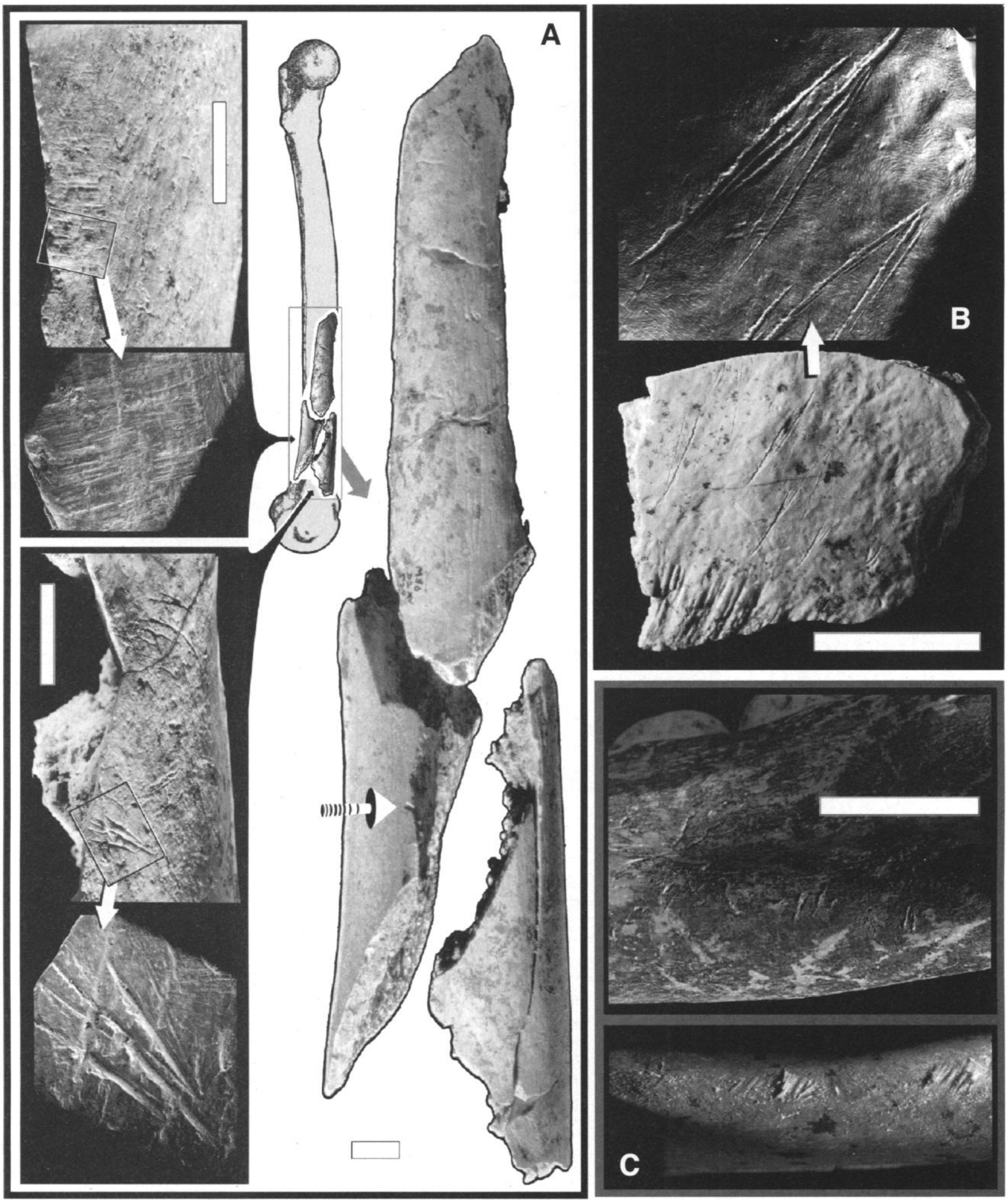

Fig. 2. Modifications to the Neanderthal skeletal remains illustrated by photographic and scanning electron microscope images. Scale bars equal 1.0 cm. (**A**) Refitting set CS-2, a distal left femur. The cut marks (lower left), percussion impact scar (white arrow), anvil striae on the opposite side (upper left), and internal conchoidal scars indicate defleshing before fracture by directed percussion by a hammerstone atop an anvil. (**B**) Ectocranial surface of the left parietal bone with cut marks. Note the successive signatures of the same stone tool edge, indicating filleting of the temporalis muscle. (**C**) The mandibular corpus of a juvenile Neanderthal (top) and a red deer (bottom) to show the similar position and form of cut marks made by a stone tool.

level XV demonstrate parallels in processing. The antiquity of modification of both faunal and hominid remains is demonstrated by matrix cover and manganese rosettes superimposed on cut marks, as well as by multiple cut marks crossing ancient fracture edges of refit pieces discovered in different parts of the cave. Only one identifiable *Cervus* specimen shows carnivore modification. None of the hominid remains do. In contrast, both hominid and deer bones show abundant and unequivocal evidence of hominid-induced modification. These modifications were studied and quantified according to criteria established elsewhere (*4*). Cut marks, percussion pits, anvil striae, adhering flakes, internal vault release, inner conchoidal scars, crushing of spongy bone, and peeling are all found on both the ungulate and hominid remains. In some instances, the cut and percussion marks show signature criteria to indicate successive strokes of the same implement in defleshing and percussing (Fig. 2). There is similar post-discard polish on the hominid and nonhominid assemblages, possibly indicating that occupation of the cave continued after the butchery event or events had occurred. Refitting studies establish that fragments of fractured human bones were spread across 3 m of the cave and were distributed through ~30 to 40 cm of deposit (Fig. 1).

The assessment of cannibalism in a prehistoric context depends on the demonstration that faunal and hominid remains were subjected to similar treatment (*4*, *5*). In the case of Moula-Guercy, there is clear evidence to this effect. Table 1 provides quantitative data on the representation and modifications of deer and Neanderthal bones. All crania and limb bones of both taxa are broken. There is an elevated frequency of hominid vault fragments relative to those of deer, presumably because fracture of the much larger hominid cranial vault produces more pieces. Furthermore, fracture of deer metapodials yields more marrow than does fracture of hominid metacarpals or metatarsals, generating differential fragmentation between the two taxa for these elements. Bone fracture is presumably related to processing for marrow and brains in both *Homo* and *Cervus*. The patterns of bone modification observed on the hominid and deer assemblages are also in parallel, except for functional differences between the taxa. For example, deer lack clavicles.

Anatomical assessment of the hominid bone modification leads to an understanding of the butchery practices used. For example, all three Neanderthals represented by the distal clavicle display cut marks on the lateral inferior surface of this bone, indicating disarticulation at the shoulder. In at least one individual each, the Achilles' tendon, pedal phalangeal flexor tendons, and tendon of brachialis were cut transversely at the ankle, metatarsophalangeal, and elbow joints, respectively. The temporalis muscle was removed from two of the immature cranial vaults. Cut marks on the lingual surface of the juvenile mandible show that the tongue was cut out. Cut marks on the femoral shafts show that the thigh musculature was removed.

These bone modifications indicate that the human individuals were defleshed and disarticulated. After this, the marrow cavity was exposed by a hammer-on-anvil technique. Refitting of femoral pieces shows that the medial distal femoral shaft surface was struck with a percussor and fractured while supported on an anvil [conjoining set 2 (CS-2): three fragments of a very large adult's femur]. Cut marks, percussion pitting, inner conchoidal scars, and anvil striations on the contra-coup surface of this refitted specimen are evidence of marrow processing (Fig. 2). Discarded conjoint shaft fragments were found, separated by 3 m (Fig. 1).

The cervid and hominid remains at Moula-Guercy show parallel spatial distribution (discard history), element representation, and bone modifications. We interpret these data to indicate that the hominid and deer carcasses were butchered in a similar way, with the objective being the removal of soft tissues and marrow. An inference of cannibalism is therefore warranted for Moula-Guercy level XV. We find no evidence that modifications to the hominid or deer bones from Moula-Guercy represent any form of mortuary ritual for either species. Whether the cannibalism was motivated by resource stress or other social factors will require further investigation here and at other sites.

Cannibalism has been attributed to Neanderthals for nearly a century (*6*) and is a recurrent theme in considerations of their mortuary practices. Perimortem modifications are known from other Pleistocene localities, such as Krapina, Vindija (*7*), Marillac (*8*), Combe Grenal (*9*), Macassargues (*10*), Zafarraya (*11*), and even Europe's earliest occupation site, the Lower Pleistocene TD6 occurrence at Atapuerca's Dolina (*12*). Inferences of paleolithic cannibalism have been questioned on the basis of insecure spatial and stratigraphic data, as well as insecure identification of bone modifications. The largest skeletal series interpreted as evidence of cannibalism among Neanderthals is the Krapina assemblage from Croatia (*13*). The cannibalism interpretation was questioned by Trinkaus (*14*), who attributed the assemblage to other taphonomic factors. A subsequent analysis of perimortem cut marks on the Krapina Neanderthal bones by Russell (*15*) led her to conclude that there was: "postmortem processing of corpses with stone tools, probably in preparation for burial of cleaned bones" (p. 381). Both investigators deny any evidence of marrow processing of the Krapina Neanderthal limb bones (*14*, *16*).

Moula-Guercy is a key site for understanding Mousterian occupation in Europe at the beginning of the Upper Pleistocene. It has now yielded spatial and associational data critical to the accurate assessment of prehistoric behavior. As a result, the Moula-Guercy fossils and their context are now the best evidence that some Neanderthals practiced cannibalism.

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17. We thank the Ministère de la Culture et de la Communication; le Service Régional de l'Archéologie (DRAC Rhône-Alpes); Monsieur le Président du Conseil Général de l'Ardèche et le Vice-Président chargé de la Culture; Monsieur le Maire de Soyons et Monsieur le Conservateur du Musée Municipal; Fondation Singer-Polignac; Académie des Sciences de Paris; and D. DeGusta, H. Gilbert, L. Hlusko, J.-L. Arsuaga, J.-M. Carretero, F. C. Howell, N. Toth, and Y. Coppens.

21 June 1999; accepted 26 August 1999