1 November 1985, Volume 230, Number 4725

SCIENCE

Stone Age Prehistory of Northern Spain

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Research into the prehistory of Vasco-Cantabrian Spain has been going on steadily since the 1870's when M. Sanz de Sautuola excavated and discovered rock art in Altamira Cave (*1*). Few regions provide fairly complete and detailed records of human adaptations during the period spanning the Upper Pleistocene and Holocene (~125,000 years)—among them are coastal South Africa, the Nile Valley, the Levant, southern France, and Cantabrian Spain. Because of good archeological preservation conditions and long histories of research, these regions have produced significant bodies of information on the physical and cultural evolution of *Homo sapiens*.

Summary. The Vasco-Cantabrian region of Spain is one of the few areas of the world where a large sample of archeological sites has yielded a detailed record of the changes in the human condition in the period spanning Neanderthal times from about 125,000 years ago until the adoption of food production, less than 6000 years ago in this area. During this time, human adaptations underwent a series of crucial transformations involving profound changes in cultural systems and perhaps also in aspects of the biological basis for culture.

The Cantabrian region provides chronological, industrial, faunal, and environmental evidence about several of the major adaptive transitions: between the Mousterian (Neanderthal period) and the early Upper Paleolithic, between the early and the late Upper Paleolithic and the Mesolithic, and between the Mesolithic and the Neolithic. Both the earliest and latest periods—the Acheulean (the later Lower Paleolithic) and the Neolithic—are still poorly known, and hominid fossils are rare. Best known for its spectacular Upper Paleolithic cave art, the region is also rich in evidence for the long-term prehistoric intensification of the food quest, from opportunistic foraging to sophisticated hunting, fishing, gathering, and ultimately to animal husbandry and agriculture.

Composed of the provinces of Guipúzcoa, Vizcaya, Cantabria (Santander) and Asturias, the Cantabrian region is bounded to the north by the Bay of Biscay, to the south by the Cantabrian Cordillera (maximum elevation, 2650 meters in the Picos de Europa) behind which lies the high Meseta del Norte, to the east by the Pyrenees, and to the west by the Galician granitic shield. Although about 400 kilometers long, this region is never more than 50 km wide (and often much less) (Fig. 1).

At present, this coastal region, warmed by a branch of the Gulf Stream, has a temperate, moist climate and luxuriant vegetation (mixed deciduous forest and artificial pastureland). However, maximum glacial conditions during the late Pleistocene were radically different, with arctic waters in the Bay of Biscay, glaciers along the Cordillera, and open grassland and heath vegetation along the coastal zone; some arboreal refugia survived in hilly areas (*2–4*). Interstadial conditions (intermediate between full glacial and interglacial conditions) permitted only limited reforestation of the coastal zone chiefly with pines, birch, hazel, and oaks (*3*). Periglacial processes such as cryoturbation, congelifraction, and solifluxion have been documented both in archeological cave sites and at open-air geological localities (*3, 5*). Ice age ungulate faunas were dominated by red deer (*Cervus elaphus*), ibex (*Capra pyrenaica*), chamois (*Rupicapra rupicapra*), wisent (*Bison bison*), and horse (*Equus caballus*), but also included occasional reindeer (*Rangifer tarandus*), giant elk (*Megaloceros*), aurochs (*Bos primigenius*), mammoth (*Mammuthus primigenius*), and various rhinoceros taxa (*Dicerorhinus kirchbergensis, D. hemitoechus, Coelodonta antiquitatis*). During interglacial periods, roe deer (*Capreolus capreolus*) and boar (*Sus scrofa*) increased (*6–8*). Probably because of differential preservation, virtually all the known Pleistocene archeological sites are in karstic caves, open-air sites having either been eroded or deeply buried in this region of steep slopes.

Lower and Middle Paleolithic

Evidence of Acheulean occupation in northern Spain is scant and tenuous, consisting principally of the basal levels in Castillo cave (Cantabria) (*9*). Although no hominid material from this period has been found in the Vasco-Cantabrian region, two mandibles and several isolated teeth assigned to late *Homo erectus* or early *H. sapiens* have been discovered at Atapuerca (Burgos), 80 km south of the Cordilleran crest (*10*). The basal deposits at El Castillo, excavated between 1911 and 1914, are thought to have been formed during the Last Interglacial (oxygen isotope stage 5e) (*4*). The stone tools are mostly sawtooth-edged denticulates and sidescrapers, with several choppers and chopping tools and a few bifaces. This industry was associated with remains of red deer, possibly fallow deer, horse, bovines, ibex, cave bear, a proboscidian, and a rhinoceros (*4, 9*).

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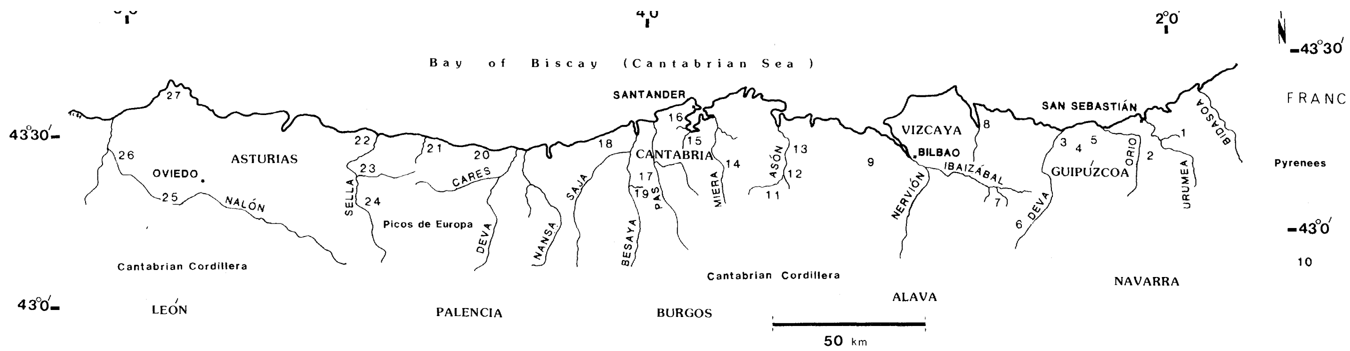

Fig. 1. Vasco-Cantabrian region, showing the sites referred to in the text. Guipúzcoa province: 1, Aitzbitarte; 2, Marizulo; 3, Urtiaga, Ermittia; 4, Ekain; 5, Altxerri; and 6, Lezetxiki. Vizcaya province: 7, Bolinkoba; 8, Santimamiñe; and 9, Arenaza. Navarra province: 10, Zatoya, Abauñtz. Cantabria province: 11, Tarreron; 12, Covalanas, La Haza; 13, El Valle; 14, El Rascaño; 15, Cueva Morín; 16, El Pendo, El Juyo, Camargo; 17, El Castillo, La Flecha, La Pasiega; 18, Altamira; and 19, Hornos de la Peña. Asturias province: 20, Mazaculos, Cuartamentero, El Molino de Gasparín; 21, La Riera, Cueto de la Mina, Balmori; 22, Tito Bustillo; 23, Los Azules; 24, Collubil; 25, Las Caldas, El Conde; 26, La Paloma, Peña de Candamo; and 27, Bañugues.

The Mousterian is better known in Vasco-Cantabrian Spain, with a total of 14 sites, although the number of modern excavations is still small and only one Neanderthal (*Homo sapiens neanderthalensis*) fossil—a humerus from Lezetxiki (Guipúzcoa)—has been found (*6*). The Mousterian probably spans oxygen isotope stages 5c through 3, which may be equivalent to Würm I and II in the Aquitaine chronostratigraphy (*4*). A terminal Mousterian date of about 35,000 years ago seems reasonable (*11*).

The Mousterian lithic artifact assemblages from Cueva Morín, El Pendo, El Castillo, La Fecha, and Hornos de la Peña in Cantabria and from El Conde in Asturias show a pattern of continuous intergradation in terms of their relative frequency composition, with assemblages rich in denticulates at one extreme and rich in sidescrapers at the other. In addition, some assemblages contain highly variable numbers of bifaces and cleaver flakes, which were used to define a special Mousterian facies, the Vasconian, for this and the French Basque region (*12, 13*). That the relative frequencies of different tool types is likely to reflect functional differences among occupations is supported by the discovery of two "activity areas" marked by different assemblages and separated by a possible stone wall within Cueva Morín level 17 (*14, 15*).

Faunal remains from several Mousterian cave sites suggest that the caves served alternately as carnivore lairs and for human occupation. Remains of cave bears (*Ursus spelaeus*) are especially prominent in and between Mousterian levels both here and in the French Basque region, along with remains of hyena (*Crocuta crocuta*), wolf (*Canis lupus*), lion (*Panthera leo*), leopard (*Panthera pardus*), and a number of small carnivores (*16*). The Mousterian ungulate faunal assemblages are generally small and are composed of red deer, bovines, and horses. The animals, particularly the large species, are represented by few individuals and relatively few body parts (*6–8*). In some cases, parts of carcasses may have been scavenged and the long bones cracked for their marrow (*17*). There is no evidence of hunting of the dangerous boar, and the cliff-dwelling ibex and chamois are rare. True mountain sites are nonexistent; most Mousterian sites are located along the edge of the rolling coastal plain (*7*). There is no indication of significant exploitation of marine resources, even though the shore would not have been much farther north of its present position, particularly during the many major interstadials of the early last glacial time.

Mousterian inhabitants seem to have subsisted in an opportunistic fashion, acquiring small numbers of middle- to large-sized ungulates of the coastal plain and hinterland valleys through a combination of scavenging and perhaps some hunting. Sites do not appear to have been located with an eye to their strategic advantages, and weapons would have at best been simple, since there is no evidence of hafted points, traps, or nets. Controversy has arisen over collections of broken and retouched bones from Cueva Morín and El Pendo. Some investigators see evidence of deliberate bone tool manufacture (imitative of stone-flaking techniques), others of carnivore gnawing (*13, 14, 18, 19*). Even if they were tools, these bones would not indicate advanced bone-working ability. The Vasco-Cantabrian Mousterian lacks any credible evidence of art or adornment, and the lithic industries show a remarkable stasis in technology and composition range throughout a period of more than 35,000 years. As elsewhere in the Old World, the Middle Paleolithic here represents an adaptive mode in which the role of culture was still fairly limited, and direct physical solutions to problems were common.

Early Upper Paleolithic

Industries classified as Perigordian and Aurignacian appear in Cantabrian Spain some 35,000 years ago and last until about 21,000 years ago. Upper Paleolithic stone artifact assemblages are defined by the consistent use of blade production techniques and the conversion of blade blanks into a wide variety of increasingly specialized types of tools such as burins, endscrapers, backed knives, perforators, and points. However, since large, good quality flint nodules are scarce, particularly in the western part of this region, many tools continued to be made on flakes, and heavy-duty quartzite tools persist through the Upper Paleolithic and Mesolithic (*20*). The two principal Chatelperronian (Lower Perigordian) levels in the region (at Cueva Morín and El Pendo) lack bone and antler artifacts. However, bone points, awls, and polishers as well as engraved bones, perforated teeth, and shells are fairly common in Gravettian (Upper Perigordian) and especially Aurignacian levels (*21*) (Fig. 2).

Human skeletal remains are scarce in northern Spain, but whenever Upper Paleolithic finds have been made (notably in the Aurignacian of El Castillo and Camargo in Cantabria), they have been of robust, anatomically modern *Homo sapiens* (*22*).

The mechanism of replacement of Neanderthal in Europe with modern populations is a controversial issue, particularly with the discovery of a Neanderthal skeleton in association with Chatelperronian artifacts at Saint-Césaire, Charente-Maritime (southwestern France). Competing proposals about replacement include independent in situ evolution of modern morphology from the local Neanderthal form, physical replacement of the local Neanderthal populations by intrusive anatomically modern populations originating in Africa and southwest Asia, and evolution of Neanderthal populations as an adaptive response and through genetic contact with anatomically modern populations whose morphological characteristics had earlier evolved outside of Europe (*23*).

The number (18) and distribution of sites in the Aurignaco-Perigordian periods does not change radically from those of the Mousterian (*8, 24*). The archeological differences between the two early Upper Paleolithic complexes, assemblages of which are interstratified at El Pendo and Morín, are mainly in the relative frequencies of thick endscrapers, burins, backed pieces, and a variety of other supposedly diagnostic tool types. There are two basic assemblages: one is dominated by scrapers and the other by backed pieces and burins (*15, 25, 26*). This could reflect some basic functional differences between site occupations, although the data on seasonality, lithic microwear, chipping debris, and faunal body parts needed to test this are lacking.

Some early Upper Paleolithic faunal assemblages are still fairly rich in carnivore remains, but most are not, suggesting an increased human presence in the caves and role in the acquisition of ungulate carcasses, probably by hunting (*16, 27*). The size and diversity of the overall ungulate faunas from these levels are small. There is no evidence of intensive specialization in the mass hunting of particular species at given sites, although the Gravettian of Bolinkoba (Vizcaya) shows an early systematic exploitation of ibex and use of a strategic cliffside cave location (*8*). There is still virtually no evidence for the use of shellfish or other marine food sources.

We lack positive evidence to link the Aurignacian or Perigordian with any of the abundant cave art in the region (except for the presence of some mobile art objects in archeological deposits and the presence of such deposits in the mouths of decorated caves such as El Castillo and El Pendo). There is, however, substantial evidence of human construction activity about 29,000 years ago in Cueva Morín—a large dugout feature with associated hearth and row of postholes and a pair of mound-topped graves with putative casts of bodies with possible offerings (*14, 28*). Such construction and mortuary behavior is reminiscent of roughly contemporaneous evidence from sites in Moravia. Thus although the early Upper Paleolithic shows only modest evidence of differentiation compared to the Mousterian in terms of subsistence activity, there is evidence of lithic technological change, innovation in the systematic shaping of bone and antler, artistic activity, and sophisticated funerary and possibly residential construction that distinguish it from the Middle Paleolithic. The Cantabrian evidence reinforces the impressions formed elsewhere in Europe and in Africa that the early Upper Paleolithic was a time of growth in the roles of technology, social organization, and planning in human adaptive strategies.

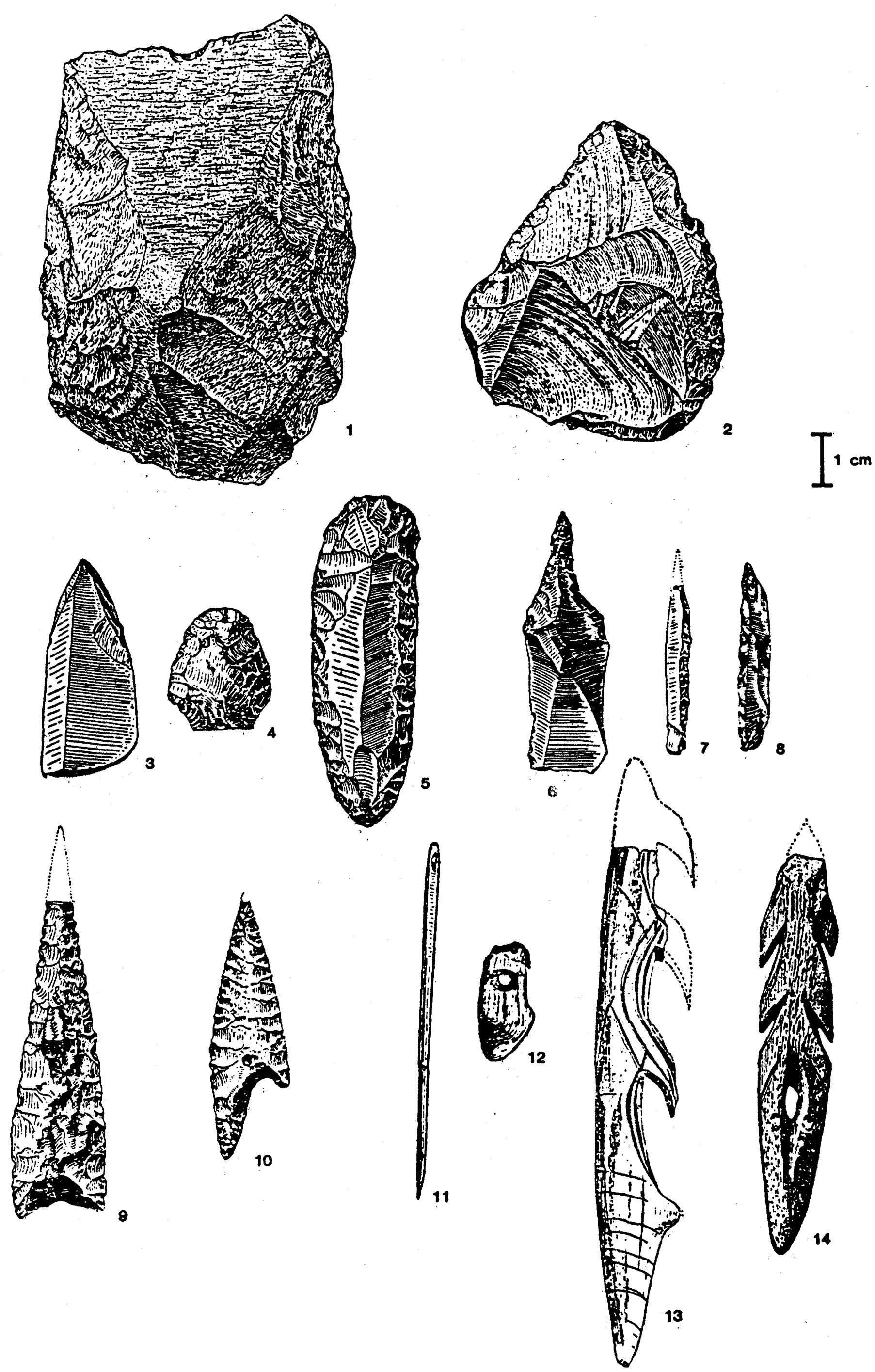

Fig. 2. Mousterian (1 and 2) and Upper Paleolithic (3 through 14) artifacts from Cueva Morín and Cueto de la Mina. 1, cleaver; 2, sidescraper; 3, burin; 4 and 5, endscrapers; 6, perforator; 7 and 8, backed bladelets; 9 and 10, Solutrean points; 11, bone needle; 12, red deer canine pendant; 13, Magdalenian harpoon; and 14, Azilian harpoon (*58*).

The timing of the transitions from archaic to modern *Homo sapiens* morphology and from Middle to Upper Paleolithic differs slightly from region to region, but the results are broadly similar in all cases.

Late Upper Paleolithic

This period is traditionally divided into the Solutrean and Magdalenian culture-stratigraphic units; these are based on the presence of leaf-shaped, invasively retouched points and shouldered points in the Solutrean and round section antler harpoons in the Upper Magdalenian, as well as the absence of such artifact types in the intervening Lower Magdalenian (*29*). The Solutrean and Magdalenian are well dated; from 20,500 to 17,000 years ago and 17,000 to 11,000 years ago, respectively, corresponding to the height of Würm Upper Pleniglacial and to the period of irregular but accelerating deglaciation and warming that culminated in the Tardiglacial (*30*).

In this period, lithic technology was also extended into the production of backed bladelets, thought to be elements in composite (hafted) tools and weapons. Numerous specialized artifact types were invented, both in stone and in bone and antler, the latter including the eyed needle and a wide variety of point types that presumably served as tips for spears, leisters, and even propelled weapons such as the atl-atl dart, harpoon, and arrow. Grinding stones are sometimes found; some were clearly used for pulverizing ochre, but others could have been used in the preparation of nuts, roots, or grains (*31*). Analyses of Solutrean and Magdalenian lithic artifact assemblages show that there are regular nontemporal and nonstylistic differences among them that are probably related to differences in activities conducted at different sites or in occupation horizons at individual sites. There is a dichotomous relationship within the Solutrean and within the Magdalenian between assemblages dominated by scrapers and others dominated by burins and backed pieces, just as there was between the contemporaneous Aurignacian and Perigordian units (*25, 32*).

In the late Upper Paleolithic, subsistence activities show intensification with both a generalized diversification of resources and specialization in the exploitation of certain species that had already been present in limited quantities in Mousterian assemblages (*7, 8*). Recent excavations have confirmed indications of massive hunting of medium-sized ungulates in this period. At Tito Bustillo, in certain levels at La Riera (both in Asturias), at El Castillo and El Juyo (Cantabria), and in certain levels at Ekain (Guipúzcoa), for example, large numbers of red deer have been found in thin strata within limited excavation areas (*27, 33–35*). Dental and osteological studies suggest that herds of *Cervus* hinds and fawns were hunted. Many sites are now at strategic topographic locations such as gorges and steep-sided blind valleys. Several sites located on or near mountainsides have faunal assemblages heavily dominated by ibex. These include Rascaño (Cantabria) and certain levels at La Riera and Ekain, as well as sites excavated in the past, such as Collubil (Asturias) and Ermittia (Guipúzcoa) (*6, 8, 22, 33, 36, 37*). The swift, wary, rocky slope-adapted ibex was also hunted in herds by the use of such tactics as drives toward hidden hunters (*7*).

In addition to the two specially targeted species, *Cervus* and *Capra*, Solutrean and Magdalenian hunters also regularly took bovines, horses, chamois, some reindeer, roe deer, and boar. Foxes, mustelids, and lagomorphs were also trapped, apparently for the first time. Birds, including some large, edible species, appear with increasing frequency in archeofaunal assemblages and seem to have been actively hunted by humans, probably with nets. People in this period also occasionally exploited seals, possibly beached ones (*7, 8, 33, 36*).

The early appearance and growth in importance of fish and shellfish are documented particularly well through the course of the long late Upper Paleolithic stratigraphic sequence in La Riera Cave. Here large specimens of estuarine forms of limpets (*Patella vulgata*) and periwinkles (*Littorina littorea*) and anadromous salmonids (*Salmo* spp.) in 20,000-year-old occupations are joined through time by increasing numbers of molluscan and fish species, including open littoral and ocean ones, although the seacoast would have been some 10 km from the cave then as compared to the 1.5 km today (*33*). Overexploitation of the limpets may have been one of the principal causes of a marked decrease in shell size through time in this region (since large limpets exist today along shores that are not subject to gathering). This is a trend observed not only at La Riera but also at other Upper Paleolithic sites (*38*).

Similar changes in archeofaunas did not occur under broadly similar environmental conditions during the Lower Pleniglacial. Furthermore, all the described faunal changes continued for a period of some 15,000 years, under both full glacial and increasingly more temperate conditions, culminating in the Holocene interglacial. It can therefore be argued that these subsistence intensification trends—indicated by faunal remains, direct and indirect technological data, and site location information—constitute evidence of long-term adaptive responses to cumulative regional human population pressure (*8, 33, 39*). Despite their relatively brief time spans, the Solutrean and Lower and Upper Magdalenian culture-stratigraphic units are represented by 34, 35, and 36 sites, respectively; each represents about twice as many as have been preserved and found for the whole 15,000-year period of the early Upper Paleolithic and more than twice the number for the more than 35,000-year span of the Mousterian.

Although these site numbers are obviously partial samples, it seems clear that regional human population was much larger in the late Upper Paleolithic than in earlier periods. Part of the increase in site numbers may have been the result of the development of complex logistical settlement-subsistence systems; this very development probably resulted from the need for a fuller exploration of all habitats and all wild food resources in the region in order to permit survival of more densely packed hunter-gatherer groups in this topographically confined region.

Along with increasingly sophisticated food-gathering strategies and technologies, late Upper Paleolithic people developed elaborate uses of fire, including various sorts of hearths and roasting pits, as shown by discoveries at Las Caldas, Tito Bustillo, Cueto de la Mina, La Riera in Asturias, Abauntz in Navarra, and Rascaño in Cantabria (*40, 33*). The most elaborate late Upper Paleolithic structural complex yet uncovered in northern Spain was recently found in Magdalenian 14,000-year-old deposits in El Juyo Cave (*41*).

It is to the Solutrean and especially the Magdalenian to which the majority of the mobile art works from the region belong, mostly engraved bones and carved antlers, along with engraved stone plaquettes, perforated shells, and teeth. Many of these objects are concentrated in only a few sites, however, notably La Paloma and Cueto de la Mina (Asturias), El Pendo, Altamira, El Rascaño, El Castillo, and El Valle (Cantabria), Aitzbitarte and Urtiaga (Guipúzcoa) (*42*). Some of the engravings on bones, such as the deer scapulae from Castillo and Altamira, bear striking similarities to engravings on cave walls and ceilings (*43*).

Much if not most of the cave art in this region was also probably done during the late Upper Paleolithic. To date, more than 60 caves with Paleolithic art have been discovered in the four provinces (*44*). These range from numerous instances with only one or a few poor paintings or engravings to such classic art sanctuary complexes as Altamira, La Pasiega, El Castillo, Peña de Candamo, and such recent spectacular discoveries as Ekain, Altxerri, and Tito Bustillo, with many caves of intermediate rank lying between the extremes in terms of quantity, quality, and complexity of their animal and geometric representations.

Vasco-Cantabrian cave and mobile art share many general stylistic and thematic similarities with the Paleolithic art of Aquitaine and the French Pyrenees. Individual sanctuaries seem to share even closer similarities, despite broad geographic separation, such as Santimamiñe (Vizcaya) and Niaux (Ariège) with their black bison and horses (*45*). On the other hand, subregional (territorial) stylistic similarities are apparent, as among the relatively nearby groups of Arenaza (Vizcaya), La Haza, Covalanas, and La Pasiega (Cantabria), with their red tampon outline hinds (*46*).

It has been suggested that cave art sanctuaries may have played a role as centers of band aggregation within larger group territories (*47*). The sanctuaries and the ceremonial activities possibly associated with them would have served to strengthen the sense of group identity and association with a particular territory, concepts made useful under conditions of increased regional population density and resource competition. Aggregations at such sanctuaries could also have served more immediate purposes, such as seasonal collective hunts and exchange of information, mates, and exotic goods. The increased use of composite technologies, projectile weapons, and intensive food procurement techniques, coupled with indirect evidence of sophisticated social relations in northern Spain, as elsewhere, testify to the complex nature of hunter-gatherer adaptations in the few millennia from the height of the Last Glacial to its end. The Cantabrian Upper Paleolithic tool assemblages and art styles generally resemble those of southwestern France. But, although subsistence intensification is evident in both regions, the Cantabrian record is distinctive for its early broad-spectrum subsistence base, with increasing dependence on marine resources, whereas in France, a heavy dependence on reindeer hunting developed until the extirpation of this species at the end of the Pleistocene.

Mesolithic

Culturally the end of the Old Stone Age is marked by the appearance of the Azilian, whose technology represents a continuation of Magdalenian trends toward microlithic compound tools and is traditionally defined by the presence of flat section antler harpoons. This transitional industry spans the time from the end of the Würm Tardiglacial (Dryas III) and the initial Postglacial (Preboreal) period from slightly before 11,000 years ago to slightly after 9000 years ago (*30*, *48*, *49*). This corresponds to the beginnings of massive Holocene reforestation and rise in sea level. There are about the same number of sites in this period as there were in each of the preceding three late Upper Paleolithic subdivisions. The topographic distribution of the sites also seems to be similar, with the existence of many in the mountainous interior.

Faunal remains indicate continued extensive exploitation of red deer together with ibex, roe deer, and boar, as well as small quantities of bovines, horses, chamois, and birds. Some fish and shellfish remains as well as land snails are also found associated with Azilian artifact assemblages (*8*, *48*).

Azilian art works are few in this region. They include two extremely similar, perforated, and elaborately decorated bones from Los Azules Cave (Asturias) and El Rascaño (Cantabria) (*48*, *50*). In Cantabrian Spain there are few painted pebbles—the hallmark of this culture-stratigraphic unit at the French-type site of Mas d'Azil. The best Cantabrian examples have been found at Los Azules, where some were associated with a human burial, located in the midst of occupation horizons dating to 9500 years ago (*48*). Along with painted (and engraved) pebbles, other apparent offerings included flat section harpoons, lithic artifacts, and sea shells in a fill stained with red ochre.

A second culture-stratigraphic unit, the Asturian, is of entirely Postglacial age, although its beginning at around 9300 years ago, according to the basal date from Mazaculos Cave (Asturias), overlaps with the most recent Azilian (*51*). The Asturian industry is characterized by simple cobble picks, often found with choppers and other heavy duty tools together with limited quantities of flaking debris (*52*, *53*). The picks are usually, but not always, found in the context of large shell middens (*concheros*). These shell heaps, which are clearly not habitation layers because they reach to the ceilings of already nearly filled cave mouths, are composed mainly of small limpets (*Patella* spp.) and top shells (*Monodonta lineata*), along with a wide variety of other mollusks, sea urchin and crab carapaces, fish bones, and remains of red deer, roe deer, and boar (*52*, *53*). All are near to the early Holocene shore.

Bi-pointed bone objects interpreted as fish gorges have been found at Mazaculos and La Riera (*53*). A couple of painted pebbles have been found in association with the Mazaculos *conchero*, and small numbers of backed bladelets have been found at several Asturian sites. These finds, together with the radiocarbon overlap, suggest that some early Asturian middens represent a functional pose of the late Azilian, namely intensive shellfish exploitation and resultant bulk deposition (*51*). Oxygen isotope analyses of Asturian shells from La Riera, Balmori, and Mazaculos show exclusive winter gathering, which would indicate that exploitation was conducted as a "tiding-over" strategy (*54*). On the other hand, some *concheros* have much more recent radiocarbon dates (5000 to 4500 years), and some even contain small numbers of potsherds (*53*). This might indicate that "Neolithic" subsistence continued to rely in part on marine resource exploitation at least in a supplementary fashion. The picks, which have been found in contexts other than *concheros* (including a few at interior sites), may have been used in plant collection as well as for some limpet gathering (*51*). Deliberate human burials associated with Asturian materials have been found in the Molino de Gasparín rock-shelter and (apparently) in Cuartamentero Cave (Asturias) (*52*, *53*).

There are a few other Mesolithic assemblages, principally from eastern Cantabria and the Basque country, with numerous geometric microliths. These are variously classified as Tardenoisian or Sauveterrian, but little is known about the associated adaptive patterns other than that red deer, roe deer, and boar were the principal game animals at sites like Marizulo (Guipúzcoa), Arenaza (Vizcaya), and Zatoya (northern Navarra) (*6*, *55*). However, it is noteworthy that remains of domesticated dog (*Canis familiaris*) have been identified in intact terminal Mesolithic deposits (without ceramics or other domesticated animals) in Marizulo (>5300 years ago) and Arenaza caves, although the dog remains in late Azilian deposits at Ekain and Urtiaga may be intrusive (*6*, *56*). The broad-spectrum hunting, gathering, and fishing of the Cantabrian Mesolithic is similar to the adaptations of early post-Paleolithic cultures in other areas of Eurasia and

Africa (and the American Archaic), although in other regions, notably the Near East, domestication economies were already developing.

Neolithic

The Neolithic in northern Spain is defined by the presence of ceramics and remains of domesticated caprines, cattle, and pigs (*56*). Virtually nothing is known of any possible cereal agriculture in the Neolithic. The earliest dates for levels tentatively assigned to the Neolithic are in excess of 5000 years old (Arenaza, Abauntz, and Marizulo) (*56*). Even levels with domesticated animals and ceramics contain Mesolithic-type microliths and abundant wild game remains, plus marine and terrestrial mollusks. Some levels (for example, Zatoya level I) with a few sherds have no domesticated animals (*55*). Others (Tarrerón level III and several "Asturian"-type *concheros*) are classified as terminal Mesolithic because of the lack of both ceramics and domesticates, although radiocarbon dating indicates a temporal overlap with the early Neolithic (*53, 57*). Inhabitants of northern Spain added sheep and goat, cattle, and pig herding to their broad-spectrum subsistence repertoire which involved intensive hunting of red and roe deer, boar, and other game and collection of mollusks (and certainly plant foods). Ceramics are few and poor in quality, lithics are at least initially like those of the Mesolithic, and habitation continues to be in caves, with no evidence of houses or villages. The base of level I at Marizulo yielded a prepared human grave which also contained skeletons of a dog and a lamb, but we know of nothing more elaborate from the Neolithic of Vasco-Cantabrian Spain (*6, 56*). Thus the initial impact of Neolithic attributes seems to have been slight in this region. Domesticates simply permitted a further expansion of the resource base without apparently causing significant changes in overall human adaptations. These were only to begin much later, in the Bronze Age.

Conclusions

The Stone Age prehistory of Vasco-Cantabrian Spain spans a long period of which about the last 70,000 years are relatively well known. During much of this time glacial environmental conditions far different than the mild conditions of the present prevailed in this coastal region. Nevertheless it was a region rich in terrestrial and marine resources and was always far more hospitable than the northern Meseta lying just beyond the Cantabrian Cordillera. From meager beginnings in the late Acheulean, the small human populations at first survived with rather simple, redundant technology and a combination of opportunistic hunting and scavenging of a few obvious large- and medium-sized ungulate species in the Mousterian.

Beginning in the early Upper Paleolithic, with a manifestly expanded regional population—now of anatomically modern *Homo sapiens*—more elaborate technologies based in part on blades and bone and antler tools make their appearance, along with the first manifestations of art and elaborate construction, although there is scant evidence for significant changes in subsistence patterns. Major change does appear to come relatively quickly in the late Upper Paleolithic, however. By this time regional human population density had apparently grown to the point of favoring development not only of increasingly diversified subsistence bases and specialized food acquisition strategies and technologies, but probably also territorially based information exchange networks, visible evidence for which may include the numerous cave art sanctuaries of this period. The trend toward full use of the wild terrestrial and aquatic food resources of the region culminated in the millennia marking the end of the Last Glacial and beginning of the Postglacial with a series of partly contemporaneous Mesolithic cultures. To this were added a few domesticated animals and ceramic vessels in the Neolithic, without at first fundamentally altering the man-land relationships that had been developing for so long in this region.

This record parallels in general adaptive developments in other Old World regions, albeit with differences in timing and in emphasis, due to differences in regional location, topography, climate, resources, and population levels. Specific differences in adaptive strategies through time and between regions during particular periods of the late Quaternary still require documentation. Such new information should reveal the options eventually followed by various populations of *Homo sapiens*, leading from a hypothetically simple foraging subsistence to complex hunting and gathering and, finally, to food production in most regions of the world.

References and Notes

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59. My research in northern Spain and southwestern France has been largely supported by a number of NSF grants. I thank G. Isaac and E. Trinkaus, as well as P. Arias, E. Cartwright, and B. Seligman for helpful comments on an early draft of this article.

The Changing View of Neural Specificity

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Since the introduction of the "neuron doctrine"—the concept that the nervous system consists of separate cellular units interconnected by a complex axonal and dendritic network (*1*)—neurobiologists have wondered how this complex machinery is assembled. We now summarize evidence obtained from a variety of animals and neural regions that has gradually led to a major shift in the way many neurobiologists view the formation of the detailed yet stereotyped patterns of connections that characterize the nervous systems of virtually all animals.

The Classical View of Specific Nerve Cell Connections

Most neurobiologists 10 or 15 years ago thought that the explanation of neural specificity was nerve cell recognition. This consensus grew out of the pioneering work of Sperry and his collaborators in the early 1940's, work that culminated in 1963 with Sperry's definitive statement of the "chemoaffinity theory" (*2*). The essence of this hypothesis is that pre- and postsynaptic elements bear specific surface labels that recognize each other by mutual affinity during the process of axon outgrowth and synapse formation. Such labels were thought to promote both accurate axon trajectories and the formation of appropriate synaptic connections.

This idea, of course, was not entirely new—for example, S. Ramón y Cajal and J. N. Langley had suggested much the same concept at the end of the 19th century (*3*)—but Sperry supported the notion with compelling experiments on the neural connections between the eye and the brain and raised these earlier suggestions to the level of a central tenet of developmental neurobiology. Sperry's key experiment involved rotating the eye through 180° after having severed the optic nerve in amphibians (*4*). These animals, unlike mammals, have retinal axons that are able to grow back to the

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