

The early Upper Paleolithic human skeleton from the Abrigo do Lagar Velho (Portugal) and modern human emergence in Iberia

(Neandertals/mandible/postcrania/dentition/radiocarbon dating)

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ABSTRACT The discovery of an early Upper Paleolithic human burial at the Abrigo do Lagar Velho, Portugal, has provided evidence of early modern humans from southern Iberia. The remains, the largely complete skeleton of a ≈4-year-old child buried with pierced shell and red ochre, is dated to ca. 24,500 years B.P. The cranium, mandible, dentition, and postcrania present a mosaic of European early modern human and Neandertal features. The temporal bone has an intermediate-sized juxtamastoid eminence. The mandibular mentum osseum and the dental size and proportions, supported by mandibular ramal features, radial tuberosity orientation, and diaphyseal curvature, as well as the pubic proportions align the skeleton with early modern humans. Body proportions, reflected in femorotibial lengths and diaphyseal robusticity plus tibial condylar displacement, as well as mandibular symphyseal retreat and thoracohumeral muscle insertions, align the skeleton with the Neandertals. This morphological mosaic indicates admixture between regional Neandertals and early modern humans dispersing into southern Iberia. It establishes the complexities of the Late Pleistocene emergence of modern humans and refutes strict replacement models of modern human origins.

During the past decade it has become apparent that the human biological and cultural evolutionary transitions between late archaic (Neandertal) and early modern humans and between the Middle and Upper Paleolithic occurred relatively late throughout most of Iberia (1–4). It is now certain that the Middle Paleolithic of most of Iberia south of the Pyrenees lasted until about 30,000 years B.P., perhaps as late as 28,000 years B.P., and that the initial stages of the Upper Paleolithic known to have occurred further north (the Châtelperronian and the early Aurignacian) were never present in this region. Moreover, human paleontological evidence from Zafarraya in southeastern Spain indicates that late Middle Paleolithic technology from this region was the product of Neandertal populations (5). This evidence has led to hypotheses as to why Middle Paleolithic Neandertals endured in the cul-de-sac of Iberia between 5,000 and 10,000 years after they had been replaced (by whatever historical processes) elsewhere in Europe (4, 6, 7). The “Ebro Frontier” model (3, 6–8) suggests that the basin of the Ebro river of northern Spain represented a biogeographical and ecological barrier to the diffusion of the Upper Paleolithic innovations developed by late Neandertal populations to the north (the Châtelperronian) and, subsequently, to the dispersal of the first modern human groups in western Europe.

Even though both the late Middle Paleolithic and early Upper Paleolithic are increasingly well known and chronologically situated south of the “Ebro Frontier” (4, 6, 9), diagnostic human remains associated with early Upper Paleolithic industries in this region have been elusive. The discovery of a largely intact early Upper Paleolithic child’s burial at the Abrigo do Lagar Velho in Portugal therefore adds significantly to our knowledge of the biology and burial practices of the earliest Iberian modern humans and sheds light on the nature of the transition from Neandertals to their successors in one of the last archaic human frontiers.

THE ABRIGO DO LAGAR VELHO

The archeological site consists of deposits within horizontal fissures and along the current base of a limestone cliff on the south side of the Lapedo Valley near Leiria, central western Portugal (lat 39° 45′ 25″ N, long 8° 43′ 58″ W). The site was damaged by earth removal in 1992, exposing an Upper Paleolithic sequence and coming within a few centimeters of the burial along the base of the cliff. On November 28, 1998, the site was discovered by J.M. and P.S., who also found the left hand and forearm bones of the child in a burrow. The following week C.D. and J.Z. confirmed the presence of Paleolithic deposits and a human burial. A salvage excavation directed by J.Z. ensued from December 12 to January 7, 1999, in the framework of which the burial was excavated by C.D. Paleontological analysis by C.D. and E.T. commenced on January 4, 1999.

The child’s skeleton, Lagar Velho 1 (Fig. 1), was on its back parallel to the cliff base, with the head to the east and left side against the cliff. The cranium and mandible were damaged by earth removal, but the preservation of the left temporal bone and mandible indicates that the head had tilted toward the cliff face. The collapse and folding *in situ* of the right ribs suggest that the thorax was similarly tilted. The pelvis was horizontal, and the feet were plantar-flexed and crossed. The skeleton and the containing sediment are heavily stained with red ochre, but the alteration of the sediment stopped at the outer border of the skeleton, suggesting a wrap around the body. Vertically oriented animal bones and stones outlined the ochre-stained sediments; radiocarbon dating of one such bone yielded a result that is consistent with the hypothesis that these represent intentional burial features and not a natural disposition of deposit components caused by digging a burial pit.

A Commentary on this article begins on page 7117.

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FIG. 1. Lagar Velho 1 *in situ*, with damaged skull and left forearm elements already removed.

The only diagnostic archeological item in the burial was a pierced *Littorina obtusata* shell found near the cervical vertebrae; it is identical to those from Level Jb of the nearby site of Gruta do Caldeirão (Tomar) dated to $26,020 \pm 320$ years B.P. (OxA-5542; ref. 6). Similar burials with pierced shells and/or teeth and a covering of ochre are known particularly from the Gravettian of Europe, especially from Britain (Paviland), Italy (Arene Candide, Barma Grande, Caviglione, Ostuni), and the Czech Republic (Brno, Dolní Věstonice; refs. 10–12).

The uppermost 2–3 m of the shelter's fill were largely removed and current ground level represents the surface of an estimated 3- to 4-m sequence of early Upper and possibly Middle Paleolithic strata. A ≈ 60 -cm thick hanging remnant is preserved within a fissure running along the back wall of the shelter and contains a Proto-Solutrean (level 6) through Middle Solutrean (level 9) sequence. In Portugal, assemblages with diagnostic laurel-leaf point fragments date to *ca.* 20,000–20,500 years B.P., and the Proto-Solutrean dates to *ca.* 21,500 years B.P. (6, 13). Radiocarbon dating of charcoal from level 9 yielded a date of $20,200 \pm 180$ years B.P. (OxA-8419), and samples of charcoal from level 6 yielded results of $21,180 \pm 240$ years B.P. (OxA-8420) and $21,380 \pm 810$ years B.P. (Sac-1561); a stratigraphically less reliable level 6 sample yielded $22,180 \pm 180$ years B.P. (OxA-8418).

The position of the burial, ≈ 2.5 m below the Proto-Solutrean remnant, as well as its archeological resemblances to Gravettian burials elsewhere, suggests an age several millennia earlier. This inference is supported by accelerator mass spectrometry radiocarbon dating of charcoal [$24,860 \pm 200$ years B.P. (GrA-13310)] and *Cervus elaphus* remains [$24,660 \pm 260$ years B.P. (OxA-8421) and $24,520 \pm 240$ years B.P. (OxA-8423)] directly associated with the burial and of a vertebra from a semiarticulated section of a *Oryctolagus cuniculus*

vertebral column [$23,920 \pm 220$ years B.P. (OxA-8422)] immediately overlying the legs. The burial therefore occurred between 24,000 and 25,000 years B.P. and probably between 24,500 and 25,000 years B.P.

AGE AND BODY SIZE

The remains are those of a juvenile (Figs. 1 & 2). All of the deciduous teeth (right di_2 to left dm_2 plus left dc^1 and dm^2) have apically closed roots, indicating a median minimum age of ≈ 3.0 years. The I_2 is almost at Cr_c ; the C^1 is $\approx C_{3/4}$; the P_4 is $\approx C_{co}$; the M^1 and M_1 are $\approx R_{1/4}$; and the M_2 is $\approx C_{oc}$ (nomenclature established by Moorrees *et al.*; ref. 14). The levels of calcification for the latter four teeth provide median ages (male/female) of 3.4/3.5, 3.9/3.9, 4.9/4.8, and 4.9/4.5 years, by using Euro-American standards (15). The average estimate is 4.2 years postnatal, and the probable range is 3.5–5.0 years.

The more complete right femur has an intermetaphyseal length of 198 mm plus proximal and distal epiphyseal thicknesses of 10.0 mm and 13.3 mm, respectively. Adding these and rounding up because of the absence of the epiphyseal cartilages provides an interepiphyseal length of ≈ 225 mm. Estimates from the ratios of 4- to 18-year-old modern Euro-American mean femoral lengths (16) predict adult femoral lengths of ≈ 450 mm (male) and ≈ 410 mm (female). These values are below the means for adult European earlier Upper Paleolithic males (478.0 ± 21.4 mm; $n = 13$) and females (427.3 ± 19.0 mm; $n = 9$) but within their ranges of variation; the values are close to the means for Neandertal males (443.3 ± 18.7 mm; $n = 11$) and females (400.3 ± 14.2 mm; $n = 3$).

MORPHOLOGICAL CONSIDERATIONS

Materials and Methods. This preliminary assessment of Lagar Velho 1 is concerned with its morphological affinities to northwestern Old World late archaic humans (Neandertals) versus early modern humans. The latter sample consists predominantly of Aurignacian and Gravettian remains between 20,000 and 30,000 years B.P. Given the dearth of earlier Upper Paleolithic juvenile human remains, the comparisons also involve Near Eastern Middle Paleolithic (Qafzeh-Skhul) early modern humans. Recent human comparative data are included as appropriate, the samples deriving from temperate European and North American samples (17–19). The relative positions of the fossil specimens in the postcranial proportional assessments are based on distributions of raw residuals from the reduced major axis lines for the recent human samples and are expressed as z scores.



FIG. 2. Lingual view of the mandible and dentition, showing the degrees of dental development, the symphyseal retreat, and the prominent right tuberculum laterale. (Black bar and white bar = 1 cm each.)

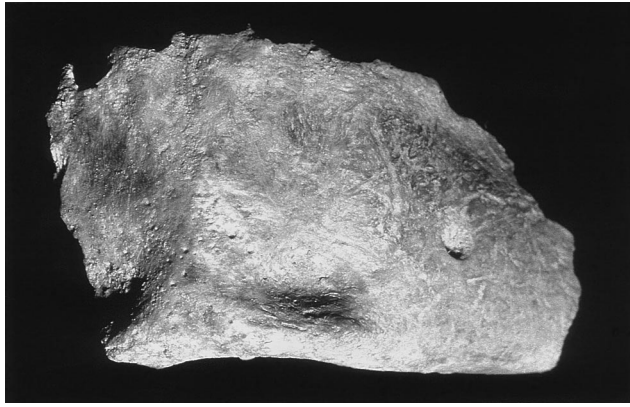


FIG. 3. Anterior view of the mandibular symphysis showing the development of the mentum osseum. Symphyseal height = 24.7 mm.

The Temporal Bone. The mastoid region in the left temporal bone is preserved with little damage. It has a clear juxtama-stoid eminence, which extends to the same level as the mastoid process tip. The relative sizes of these two processes is intermediate between Neandertal juveniles with their larger juxtama-stoid eminences (20) and early modern humans with their more projecting mastoid processes (21, 22).

The Mandible. The anterior mandibular symphysis has the full development of a mentum osseum (Fig. 3). There is a very prominent tuber symphyseos with an exceptionally protruding tuberculum laterale on each side. These combine to create a deeply excavated incisura mandibulae anterior. The midline of the tuber symphyseos extends superiorly toward the alveoli. By any criteria, this symphyseal configuration is a prominent development of a “chin,” clearly distinct from the modest development of these elements in similarly aged Neandertals (19, 23) and pronounced even for a developmentally comparable modern human (21, 24).

This anterior symphyseal configuration is combined with a posterior retreat of the anterior symphysis, indicated by an anterior symphyseal angle (of the alveolar plane to the infra-dentale–pogonion line) of 89° . It is close to the mean for early juvenile Neandertals ($90.3^\circ \pm 4.4^\circ$; $n = 7$) and below that of similarly aged recent humans ($101.5^\circ \pm 4.7^\circ$; $n = 15$; ref. 18).

The corpus and ramus have a modest planum alveolare, a mental foramen below the dm_1 , an open (V shaped) mandibular foramen, a symmetrical mandibular incisure, and an absence of a superior medial pterygoid tubercle (despite rugosity for the medial pterygoid muscle). These features either align the specimen with recent humans or do not discriminate between the two groups (25).

The Dentition. The deciduous dental remains have no macroscopic pathological alterations and minimal incisor attrition. The first molar crown diameters (Table 1) are similar to those of Neandertals and early modern humans, who are not significantly different in these dimensions. The I_2 breadth shows a gradual decrease from Neandertals to Qafzeh-Skhul humans to earlier Upper Paleolithic humans to recent Europeans, and Lagar Velho 1 falls between the means of the last two samples. Late archaic and early modern humans differ

more in their anterior-to-posterior dental proportions than in absolute dental dimensions (26), and the relative I_2 versus M_1 breadths of Lagar Velho 1 fall with the early modern humans and separate from the Neandertals.

The Postcranial Remains. At least one of each of the major long bones was preserved in the appendicular skeleton of Lagar Velho 1, with only the radius lacking a complete intermetaphyseal length (Fig. 4). The intermetaphyseal maximum lengths (left side for all but the femur) are, for the humerus, 143 mm; for the ulna, 122.5 mm; for the femur, 198 mm; and for the tibia, 155 mm. The clavicles are not sufficiently preserved to provide lengths, and major portions of the pelvis remain.

The right femur has a neck-shaft angle of $\approx 128^\circ$. This value is similar to the values of juvenile (Roc de Marsal 1, 130° ; La Ferrassie 6, 132°) and early adolescent (Teshik-Tash 1, 128°) Neandertals and the juvenile Skhul 1 early modern human (131°). Neck-shaft angles decrease with normal locomotor loading during development (27), such that (based on a recent Native American sample; ref. 28) it should decrease $\approx 2\%$ between the juvenile and adult years. The predicted adult value for Lagar Velho 1 (125°) is similar to the values of Neandertals ($121.0^\circ \pm 4.7^\circ$; $n = 9$) and earlier Upper Paleolithic Europeans ($118.8^\circ \pm 6.0^\circ$; $n = 13$) but below the Qafzeh-Skhul values ($133.2^\circ \pm 2.6^\circ$; $n = 6$). The right femur has a metaphyseal bicondylar angle (29) of 8° . The greater medial distal epiphyseal thickness (13.3 mm versus 12.7 mm) suggests that the articular bicondylar angle was slightly higher. These values are attained by recent humans at about 4–5 years of age (29). This pattern is echoed in the proximal tibial metaphyseal orientation; the medial metaphyseal retroversion angle (12°) is close to articular angles of mature Neandertal ($15.0^\circ \pm 2.2^\circ$; $n = 5$) and earlier Upper Paleolithic ($15.8^\circ \pm 5.3^\circ$; $n = 8$) tibiae.

These angles indicate that locomotor loading levels were similar to those of European Late Pleistocene hominids and nonurban recent humans (29, 30). In combination with the apparent absence of pathological lesions on the dental and leg remains, these angles imply normal and active locomotor behavior for Lagar Velho 1 in the context of little or no systemic developmental stress. As a result, it is possible to consider other proportions of its lower limbs as reflections of normal skeletal morphology.

Early and recent modern humans are largely distinct from archaic humans in the relative mediolateral shortness of their pubic bones (31), and this contrast appears early in development (18). A comparison of pubic (acetabulosymphyseal) breadth to femoral length shows a regular pattern of development ($r^2 = 0.857$) with the La Ferrassie 6 Neandertal falling significantly above the recent human distribution (Table 2). The Lagar Velho 1 pubic length is within the recent human distribution but is still relatively high for a modern human.

Neandertals and European early modern humans contrast in the length of the tibia relative to the femur (32). Moreover, differences in this ecogeographically patterned body proportion (in which the Neandertals are hyperarctic and the earlier Upper Paleolithic humans subtropical) appear early in development among recent humans (33, 34) and Neandertals (18, 35–37) and remain stable over multiple millennia (32). Tibial metaphyseal length versus femoral diaphyseal intermetaphy-

Table 1. Comparative permanent dental metrics

Sample	I_2 breadth, mm	M^1 length, mm	M^1 breadth, mm	M_1 length, mm	M_1 breadth, mm
Lagar Velho 1	(6.6)*	10.5	11.8	12.0	10.9
Neandertals	7.8 ± 0.4 [27]	11.2 ± 0.7 [26]	12.0 ± 0.8 [26]	11.4 ± 0.7 [44]	10.9 ± 0.5 [44]
Qafzeh-Skhul	7.2 ± 0.6 [8]	11.3 ± 0.6 [13]	12.2 ± 0.7 [13]	11.7 ± 0.8 [8]	11.4 ± 0.6 [9]
Early Upper Paleolithic	6.9 ± 0.5 [22]	10.8 ± 0.8 [29]	12.1 ± 0.8 [29]	11.5 ± 0.8 [35]	11.0 ± 0.9 [38]
Recent Europeans	6.3 ± 0.4 [106]	10.0 ± 0.6 [104]	11.3 ± 0.5 [104]	10.7 ± 0.6 [106]	10.3 ± 0.5 [106]

Data are shown as means \pm SD [n].

*Includes estimated additional crown formation, as is indicated by the parentheses.



FIG. 4. Anterior view of the long bones. (Black and white bars = 1 cm each.)

seal length provides a tight linear fit between the variables for the age range ($\approx 2\text{--}8$ years) in a cool-temperate modern human sample ($r^2 = 0.983$), with Skhul 1 falling above the line and both La Ferrassie 6 and Lagar Velho 1 falling significantly below the recent humans (Table 2). Given the hyperarctic versus tropical proportions of Neandertal versus Qafzeh-Skhul adult remains (38), the separation of the La Ferrassie and Skhul specimens is expected. However, the low position of Lagar Velho 1 is unexpected, given the relatively long tibiae of all known European earlier Upper Paleolithic humans (32).

These contrasts in adult limb-segment proportions are combined with the Neandertals having very broad trunks and the Qafzeh-Skhul and European earlier Upper Paleolithic trunks being quite slender (32, 38). As a result of the contrasting body masses (and hence baseline weight-bearing loads) relative to femoral and especially tibial lengths, Neandertals seem to have robust leg diaphyses, whereas these early modern humans seem gracile (39). The apparent differences in structural hypertrophy, however, disappear once body proportions are taken into account (40–43). Consequently, given that mature

diaphyseal hypertrophy reflects in large part developmental trajectories (44), it is expected that immature Neandertals and early modern humans had similar femoral and tibial diaphyseal hypertrophy once body proportions were incorporated into the analysis. In other words, any significant differences in diaphyseal hypertrophy should primarily reflect contrasts in body proportions (relative trunk size for the femur and relative trunk size plus leg segment proportions for the tibia) and only secondarily differences in lower limb robusticity.

In the comparison of femoral midshaft circumference to length (Fig. 5), Lagar Velho 1 and the three Neandertal specimens (La Ferrassie 6, Roc de Marsal 1, and Teshik-Tash 1) fall significantly above the recent human distribution (Table 2). The Qafzeh-Skhul early modern humans are more modest in their positions. In the tibial comparison (Fig. 5), the early modern Skhul 1 is in the middle of the recent human distribution (reflecting the competing effects of linear body proportions and Pleistocene *Homo* hypertrophy), and La Ferrassie 6 is well above the recent human distribution (reflecting the combination of hypertrophy and hyperarctic body proportions). Lagar Velho 1 is beyond the Neandertal specimen, clearly separate from the recent humans. Therefore, either Lagar Velho 1 had exceptionally robust femora and tibiae, or more likely, it shared the hyperarctic trunk and lower limb proportions of the Neandertals.

The tibial plateau is dorsally displaced 20 mm from the midcondyles to the anterior tibial tuberosity, a pattern seen among the Neandertals and associated with increasing the quadriceps femoris moment arm to compensate for elevated body-mass to leg-length proportions (45). This pattern further supports the inference of elevated relative trunk mass in Lagar Velho 1.

The left humerus has clear diaphyseal torsion and a prominent ridge along the pectoralis major insertion leading up to the anterior greater tubercle. There is rugosity for the pectoralis major attachment, and the ridge creates a marked inter-tubercular sulcus and an anterolateral to posteromedial elongation of the diaphyseal cross section. This proximal humeral diaphyseal morphology implies hypertrophy of the thoracohumeral musculature, a pattern seen in Neandertals but usually little developed among early modern humans (39, 46).

The radius has an interosseus crest in line with the dorsal third of radial tuberosity. The resultant anteromedial position of the radial tuberosity contrasts with the directly medial position of most Neandertals, such that the orientation found here is present in 26.9% of Neandertals ($n = 13$) but in 100% of European earlier Upper Paleolithic humans ($n = 23$; refs. 47, 48). At the same time, the radius has little lateral curvature, characteristic of early modern human radii but unlike most mature and immature Neandertal radii (46, 49).

DISCUSSION

These morphological considerations provide a mixed impression of the Lagar Velho 1 juvenile early Upper Paleolithic

Table 2. z scores based on raw residuals from the reduced major axis line of the recent human cool-temperate sample for immature Lagar Velho 1, Neandertal, and Qafzeh-Skhul early modern human femora and tibiae

Sample	z Scores			
	Public breadth/femur length	Tibia/femur length	Femur circumference/length	Tibia circumference/length
Lagar Velho 1	1.247	-2.044	2.815	2.582
Neandertals				
La Ferrassie 6	2.119	-2.415	2.501	2.402
Roc de Marsal 1	—	—	2.032	—
Teshik-Tash 1	—	—	2.643	—
Early modern humans				
Qafzeh 10	—	—	1.646	—
Skhul 1	—	0.493	1.148	0.037

A z score > 1.95 indicates that $P < 0.05$.

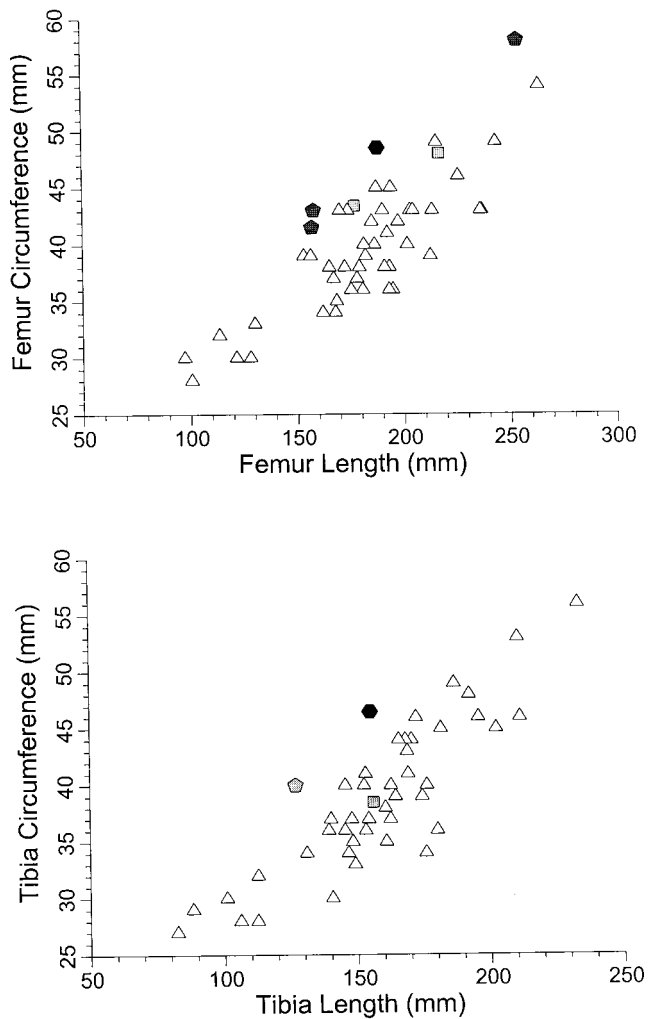


FIG. 5. Midshaft circumference versus femoral intermetaphyseal diaphyseal length (*Upper*) and versus tibial intermetaphyseal length (*Lower*). Black hexagon, Lagar Velho 1; gray pentagons, European Neandertals; gray squares, Qafzeh-Skhul humans; open triangles, cool-temperate recent humans.

human skeleton relative to northwestern Old World Neandertals and early modern humans. It is buried in a distinctively early Upper Paleolithic pattern, but its morphology is a mosaic of Neandertal and early modern human features.

The temporal juxtastoid eminence development is intermediate between these two groups. The mandibular mentum osseum and dental proportions align it completely with the early modern humans. This alignment is supported by mandibular ramal discrete traits, orientation of the radial tuberosity, radial curvature, and relative pubic breadth. The femorotibial length proportions and lower limb hypertrophy (femoral and tibial diaphyseal robusticity and tibial condylar posterior displacement) indicate hyperarctic Neandertal body proportions distinct from those of European earlier Upper Paleolithic humans. In addition, the mandibular symphysis retreats at an archaic angle, and the thoracohumeral muscle insertions are most similar to those of the Neandertals.

The body proportions of Iberian Neandertals are not known, but all European Neandertals, including the Châtelperronian St. Césaire 1, have hyperarctic body proportions (41, 50). It is therefore likely that the Iberian Neandertals either had similar body proportions or, given the more temperate glacial climate of coastal southern Iberia (6), had less extreme cold-adapted proportions. All of the European earlier Upper Paleolithic human remains have subtropical body proportions, whether

measured directly or inferred from femoral and tibial diaphyseal scaling (32, 42, 43). The more moderate oxygen-isotope stage 3 climate of southern Iberia versus the climate known for southwestern France or central Europe makes it unlikely that the inferred cold-adapted body proportions of Lagar Velho 1 were the product of regional climatic selection. They can only indicate affinities to the Neandertals.

Although some of these features are developmentally plastic, the mandibular and dental patterns as well as the ecogeographically related body proportions seem to be resistant to environmental perturbations and to be evolutionarily stable over at least the millennia of concern. They are therefore appropriate markers for assessing the ancestry of Lagar Velho 1.

There are two logical explanations for the morphological mosaic seen in Lagar Velho 1. It could represent the ancestral (plesiomorphic) pattern for Late Pleistocene European humans, or it could be the result of admixture between European late archaic and early modern humans. The first explanation can be rejected by the presence of a uniquely derived (autapomorphic) feature of modern humans, its mentum osseum development, supported by its chronological position after the presence of both Neandertals and early modern humans in Europe.

The morphological mosaic of the Lagar Velho 1 child therefore indicates admixture between early modern humans spreading through Iberia and local Neandertal populations. Such morphological mosaics, with character states distinctive to each parental group (directional dominance), plus intermediate (additive) or divergent (overdominance or underdominance) configurations, characterize hybrids between subspecies, species, and genera of primates and carnivores (51–55). It is not known whether any one mosaic pattern would be expected, given specified ancestral morphological patterns, nor is it known how stable the pattern is likely to have been over time. However, the mosaic seen in Lagar Velho 1 conforms to the known patterns of hybridization.

Moreover, the dating of the burial to several millennia after the probable period of transition from Neandertal to early modern human in southern Iberia (28,000–30,000 years B.P.), and hence the persistence of a morphological mosaic for that time period, indicates that this child was not the result of a rare Neandertal/early modern interbreeding but the descendant of extensively admixed populations. There does not seem to be a better means of explaining why, in spite of sharing a similar material culture and identical burial practices with the Gravettian elsewhere in Europe, Lagar Velho 1 is anatomically so distinct.

The presence of such admixture supports the hypothesis (56, 57) of variable admixture between early modern humans dispersing into Europe and local Neandertal populations. It runs counter to the interpretation (58, 59) that, in western Europe, this transition involved the extinction without descent of the Neandertals and their complete replacement by dispersing early modern humans with more elaborate technological and sociocultural systems.

The broader implications of this finding are multiple. First, it means that the degree of abruptness in sociocultural and technological complexes around the time of the transition from the Middle to Upper Paleolithic need say little about the degree of human biological population continuity. Second, the geographical location and temporal position of the transition need not constrain the degree to which there was admixture between local archaic and early modern human populations. Third, it is inappropriate to apply a species distinction with strict implications of reproductive isolation to the Neandertals versus early modern humans. And fourth, hypotheses (60–63) that full population replacement of late archaic humans by early modern humans took place everywhere outside of the (presumably African) core area of modern humans can be

rejected. It is therefore necessary to go beyond the categorical models that have been used commonly to characterize the late archaic to early modern human and the Middle to Upper Paleolithic transitions and to recognize the complex regional, temporal, human biological, and cultural processes as well as historical trajectories that took place.

CONCLUSION

The early Upper Paleolithic human burial at Lagar Velho, Portugal, provides evidence of the burial practices and human biology of these Late Pleistocene human populations. The burial, with pierced shell ornamentation and red ochre, is similar to Gravettian ones elsewhere in Europe. The facial and appendicular remains provide a morphological mosaic, with the mandibular mentum osseum and dental proportions, as well as mandibular ramal, antebrachial features, and pubic size, aligning the specimen with European early modern humans. The mastoid region is intermediate; however, the femorotibial length proportions and lower limb hypertrophy reflect arctic body proportions, and these features, along with the mandibular symphyseal retreat and thoracohumeral muscle hypertrophy, indicate affinities to the Neandertals. This mosaic indicates admixture between late archaic and early modern humans in Iberia, refuting hypotheses of complete replacement of the Neandertals by early modern humans and underlining the complexities of the cultural and biological processes and events that were involved in modern human emergence.

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- Vega Toscano, L. G. (1990) *Mem. Mus. Prehist. Ile France* **3**, 169–176.
- Villaverde, V. & Fumanal, M. P. (1990) *Mem. Mus. Prehist. Ile France* **3**, 177–183.
- Zilhão, J. (1993) in *El Origen del Hombre Moderno en el Suroeste de Europa*, ed. Cabrera, V. (Univ. Nacl. Educ. Distancia, Madrid), pp. 127–145.
- Hublin, J. J., Barroso Ruiz, C., Lara, P. M., Fontugne, M. & Reyss, J. L. (1995) *C. R. Acad. Sci. Ser. II* **321**, 931–937.
- Garcia Sanchez, M. (1986) *Homenaje a Luis Siret*, (Consejería Cult. Junta Andalucía, Granada, Spain), pp. 49–56.
- Zilhão, J. (1997) *O Paleolítico Superior da Estremadura Portuguesa* (Colibri, Lisbon).
- d'Errico, F., Zilhão, J., Julien, M., Baffier, D. & Pelegrin, J. (1998) *Curr. Anthropol.* **39**, S1–S44.
- Zilhão, J. (1998) in *XIII International Congress of Prehistoric and Protohistoric Sciences: Proceedings*, eds. Facchini, F., Palma di Cesnola, A., Piperno, M. & Peretto, C. (Abaco, Forli, Italy), Vol. 2, 299–312.
- Zilhão, J. (1999) in *Gibraltar and the Neanderthals*, eds. Stringer, C. B. & Findlayson, J. C. (Oxbow Books, Oxford), in press.
- Svoboda, J., Ložek, V. & Vlček, E. (1996) *Hunters Between East and West* (Plenum, New York).
- Aldhouse-Green, S. & Pettitt, P. B. (1998) *Antiquity* **72**, 756–772.
- Giacobini, G. (1999) *Congr. Prehist. France* **24**, 29–39.
- Zilhão, J. (1991) *Etud. Rech. Archeol. Univ. Liege* **42**, 485–501.
- Moorrees, C. F. A., Fanning, E. A. & Hunt, E. E. (1963) *J. Dent. Res.* **42**, 1490–1502.
- Smith, B. H. (1991) in *Advances in Dental Anthropology*, eds. Kelley, M. A. & Larsen, C. S. (Wiley, New York), pp. 143–168.
- Anderson, M., Messner, M. B. & Green, W. T. (1964) *J. Bone Joint Surg. Am.* **46**, 1197–1202.
- Brabant, H. & Twisselmann, F. (1967) *Bull. Group. Int. Rech. Sci. Stomatol.* **10**, 5–180.
- Tompkins, R. L. & Trinkaus, E. (1987) *Am. J. Phys. Anthropol.* **73**, 233–239.
- Mallegni, F. & Trinkaus, E. (1997) *J. Hum. Evol.* **33**, 651–668.
- Tillier, A. M. (1987) in *Préhistoire de Poitou-Charentes*, ed. Vandermeersch, B. (Comité des Travaux Historiques et Scientifiques, Paris), pp. 201–206.
- Matiegka, J. (1934) *Homo Předmostensis, Fossilní Člověk z Předmostí na Moravě I* (České Akad. Věd a Umění, Prague).
- McCown, T. D. & Keith, A. (1939) *The Stone Age of Mount Carmel II* (Clarendon, Oxford).
- Tillier, A. M. (1981) *C. R. Acad. Sci. Ser. II* **293**, 725–727.
- Schutkowski, H. (1993) *Am. J. Phys. Anthropol.* **90**, 199–205.
- Stefan, V. H. & Trinkaus, E. (1999) *Bull. Mém. Soc. Anthropol. Paris*, **10**, 87–118.
- Stefan, V. H. & Trinkaus, E. (1998) *J. Hum. Evol.* **34**, 443–468.
- Houston, C. S. & Zaleski, W. A. (1967) *Radiology* **89**, 59–66.
- Trinkaus, E. & Ruff, C. B. (1996) *J. Hum. Evol.* **30**, 299–314.
- Tardieu, C. & Trinkaus, E. (1994) *Am. J. Phys. Anthropol.* **95**, 183–195.
- Anderson, J. Y. & Trinkaus, E. (1998) *J. Anat.* **192**, 279–285.
- Trinkaus, E. (1984) *Curr. Anthropol.* **25**, 509–514.
- Holliday, T. W. (1997) *J. Hum. Evol.* **32**, 423–447.
- Schultz, A. H. (1923) *Am. J. Phys. Anthropol.* **4**, 389–399.
- y'Edynak, G. (1978) *Am. J. Phys. Anthropol.* **45**, 569–574.
- Vlček, E. (1973) *J. Hum. Evol.* **2**, 537–544.
- Madre-Dupouy, M. (1992) *L'Enfant du Roc de Marsal* (Centre National de la Recherche Scientifique, Paris).
- Golovanova, L. V., Hoffecker, J. F., Kharitonov, V. M. & Romanova, G. P. (1999) *Curr. Anthropol.* **40**, 77–86.
- Ruff, C. B. (1994) *Yearb. Phys. Anthropol.* **37**, 65–107.
- Trinkaus, E. (1983) *The Shanidar Neandertals* (Academic, New York).
- Trinkaus, E. (1997) *Proc. Natl. Acad. Sci. USA* **94**, 13367–13373.
- Trinkaus, E., Ruff, C. B., Churchill, S. E. & Vandermeersch, B. (1998) *Proc. Natl. Acad. Sci. USA* **95**, 5836–5840.
- Trinkaus, E., Stringer, C. B., Ruff, C. B., Hennessy, R. J., Roberts, M. B. & Parfitt, S. A. (1999) *J. Hum. Evol.*, in press.
- Trinkaus, E. & Ruff, C. B. (1999) *J. Archaeol. Sci.*, in press.
- Ruff, C. B., Walker, A. & Trinkaus, E. (1994) *Am. J. Phys. Anthropol.* **93**, 35–54.
- Trinkaus, E. & Rhoads, M. L. (1999) *J. Hum. Evol.* in press.
- Trinkaus, E. (1999) in *Gibraltar and the Neanderthals*, eds. Stringer, C. B. & Findlayson, J. C. (Oxbow, Oxford), in press.
- Matiegka, J. (1938) *Homo Předmostensis, Fossilní Člověk z Předmostí na Moravě II* (České Akad. Věd a Umění, Prague).
- Churchill, S. E. (1994) Ph. D. Thesis (Univ. New Mexico, Albuquerque, NM).
- Heim, J. L. (1982) *Les Enfants Néandertaliens de La Ferrassie* (Masson, Paris).
- Holliday, T. W. (1997) *Am. J. Phys. Anthropol.* **104**, 245–258.
- Mengel, R. M. (1971) *J. Mammal.* **52**, 316–336.
- Nagel, U. (1973) *Folia Primatol.* **19**, 104–165.
- Markarjan, D. S., Isakov, E. P. & Kondalov, G. I. (1974) *J. Hum. Evol.* **3**, 247–255.
- Cheverud, J. M., Jacobs, S. C. & Moore, A. J. (1993) *Am. J. Primatol.* **31**, 23–39.
- Peres, C. A., Patton, J. L. & da Silva, N. F. (1996) *Folia Primatol.* **67**, 113–124.
- Bräuer, G. (1984) in *The Origins of Modern Humans*, eds. Smith, F. H. & Spencer, F. (Liss, New York), pp. 327–410.
- Smith, F. H. & Trinkaus, E. (1991) in *Aux Origines d'Homo sapiens*, eds. Hublin, J. J. & Tillier, A. M. (Presses Univ. France, Paris), pp. 251–290.
- Hublin, J. J., Spoor, F., Braun, M., Zonneveld, F. & Condemi, S. (1996) *Nature (London)* **381**, 224–226.
- Krings, M., Stone, A., Schmitz, R. W., Krainitzid, H., Stoneking, M. & Pääbo, S. (1997) *Cell* **90**, 1–20.
- Stringer, C. B. & Andrews, P. (1988) *Science* **239**, 1263–1268.
- Vigilant, L., Stoneking, M., Harpending, H., Hawkes, K. & Wilson, A. C. (1991) *Science* **253**, 1503–1507.
- Harpending, H. C., Batzer, M. A., Gurven, M., Jorde, L. B., Rogers, A. R. & Sherry, S. T. (1998) *Proc. Natl. Acad. Sci. USA* **95**, 1961–1967.
- Cavalli-Sforza, L. L. (1998) *Proc. Natl. Acad. Sci. USA* **95**, 11501–11503.