

# Locomotion and body proportions of the Saint-Césaire 1 Châtelperronian Neandertal

(postcrania/biomechanics/early modern humans)

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**ABSTRACT** The initial Upper Paleolithic (Châtelperronian) of western Europe was associated with late European Neandertals, best known through the Saint-Césaire 1 partial skeleton. Biomechanical cross-sectional analysis of the Saint-Césaire 1 femoral diaphysis at the subtrochanteric and mid-shaft levels, given the plasticity of mammalian diaphyseal cortical bone, provides insights into the habitual levels and patterns of loading on the lower limbs from body mass, proportions, and locomotion. The overall robustnesses of the femoral diaphyses of European Neandertals and early modern humans are similar once contrasts in body proportions are incorporated into the body size scaling. Saint-Césaire 1 matches these samples only if it is provided with Neandertal-like hyperarctic body proportions. And the rounded proximal femoral diaphysis of Saint-Césaire 1 is similar to those of earlier Neandertals, likely also reflecting similar cold-adapted broad pelvic regions. However, although morphologically similar to those of archaic *Homo*, the Saint-Césaire 1 femoral midshaft exhibits the anteroposterior reinforcement characteristic of early modern humans. Consequently, Saint-Césaire 1 appears as a morphological Neandertal with hyperarctic body proportions who nonetheless had shifted locomotor patterns to more closely resemble those of other Upper Paleolithic humans.

In 1979, discovery of a fragmentary associated skeleton of an undoubted Neandertal securely associated with an initial Upper Paleolithic (Châtelperronian) assemblage at La Roche à Pierrot, Saint-Césaire, central-western France (1) and the subsequently identified fragmentary Neandertal remains associated with the Châtelperronian in the Grotte du Renne at Arcy-sur-Cure in northern France (2) led to reassessments of the relationships between late archaic humans (Neandertals), early modern humans, and the Middle-to-Upper Paleolithic transition in western Europe. In particular, these discoveries have promoted considerable debate regarding the phylogenetic (2–7) and culture–historical relationships (2, 8–10) between these late archaic humans, their Middle Paleolithic archaic human predecessors, and Upper Paleolithic early modern humans. Yet, even though there has been renewed interest in the behavioral implications of Châtelperronian archeological assemblages from western Europe (10–13), there has been little effort to discern possible behavioral shifts as reflected in the biologies of these Upper Paleolithic-associated late Neandertals.

With this point in mind, we have undertaken a diaphyseal cross-sectional analysis of the Saint-Césaire 1 remains. The Saint-Césaire 1 young adult partial skeleton retains significant portions of the diaphysis of at least one side for most of the long bones (humerus, radius, ulna, femur, and tibia), making

it amenable to such a functional morphological approach. In addition, mammalian diaphyseal cortical bone is highly responsive during development and adulthood to the levels and patterns of habitual biomechanical loads placed on it (14–17). As a result, one can use assessments of the quantity and distribution of cortical bone in diaphyseal cross-sections, appropriately scaled to body mass and beam length, as reflections of the actual loading regimes during the individual's life history.

All of the Saint-Césaire 1 long bones except those of its left forearm lack at least one epiphysis and a major portion of the diaphysis. Moreover, the upper limb remains are all from the left side, which [in contrast to the right arm (18, 19)] provides more of a baseline and shows little directional change between late archaic and early modern humans in Europe. We therefore have focused on the right femur of Saint-Césaire 1 (Fig. 1) because it is sufficiently intact to provide cross-sections for two biomechanically relevant levels (subtrochanteric and mid-shaft). Moreover, analysis of the femur provides insights into body proportions and locomotor loading patterns, both of which are of relevance to the adaptive evolution of Late Pleistocene hominids (19–24).

## MATERIALS AND METHODS

The analysis is based primarily on the Saint-Césaire 1 skeletal remains. To assess its morphofunctional affinities, it is compared with European later Pleistocene late archaic humans (from the sites of La Chapelle-aux-Saints, La Ferrassie, Fond-de-Forêt 1, Krapina, Neandertal, and Spy) and to earlier Upper Paleolithic (>20,000 years B.P.) early modern humans (from the sites of Cro-Magnon, Dolní Věstonice, Grotte des Enfants, Mladeč, Paglicci, Parabita, Paviland, Pavlov, and La Rochette). Additional data for body proportions derive from the destroyed Předmostí remains (25).

The diaphyseal cross-sections were reconstructed noninvasively by using polysiloxane putty (Optosil II, Unitek Corp., Monrovia, CA or Cuttersil Putty Plus, Heraeus Kulzer, South Bend, IN) to transcribe the oriented subperiosteal contour and, from parallax-corrected cortical thickness measurements from biplanar radiography, to provide the framework for the interpolated endosteal contours. The resultant cross-sections were digitized by using a PC version (26) of SLICE (27) to compute cross-sectional areas and second moments of area ( $I_x$ ). Second moments of area and the sum of any two perpendicular second moments (the polar moment of area) are of particular interest because they provide an indication of bending rigidity in the anatomical plane of orientation and in sum approximate torsional rigidity.



FIG. 1. Posterior view of the Saint-Césaire 1 right femoral proximal diaphysis. Scale in centimeters.

To assess the biomechanical significance of the Saint-Césaire 1 femoral diaphyseal cross-sections, it is necessary to scale the cross-sectional properties to body mass and beam length. Body mass is best approximated, avoiding circularity by using strictly femoral dimensions using sex-specific multiple regressions based on stature and living bi-iliac breadth (28) given ecogeographically patterned variance in body breadth (29), with male and female predicted values averaged for specimens of unknown sex. For this, stature was estimated by using the ecogeographically most appropriate modern human sex-specific regression formulae available (28). When the pelvis was not sufficiently preserved for direct measurement of bi-iliac breadth, pelvic breadth was estimated from femoral maximum length by using the average recent human slope between bi-iliac breadth and femoral maximum length (0.237) and the mean values for each measurement in the appropriate reference sample (in this case, Neandertals and European earlier Upper Paleolithic humans). These skeletal bi-iliac breadths (BIB) were converted to external (soft tissue) measurements, such that  $BIB_{ext} = (BIB_{skel} \times 1.17) - 3.0$  (in cm) (28). The beam length is reflected in the biomechanical length of the bone in question (in this case the femur) (20). Given the scaling relationships between second moments of area and body mass times beam length, second moments of area ( $I_i$ ) were converted to section moduli ( $Z_i$ ), such that  $Z_i = I_i^{3/4}$  (20).

The femoral length and bi-iliac breadth of Saint-Césaire 1 are unknown because of fossilization damage, and they have to be estimated from the one sufficiently intact long bone segment, that of the left forearm. At the same time, European

Neandertals had a hyperarctic body form with relatively short distal limbs and broad trunks, and European early modern humans possessed subtropical to warm temperate body forms (22, 23, 30). Consequently, by using least squares regressions based on the long bone lengths (and hence body proportions) of each of the European Late Pleistocene samples, the femoral biomechanical length of Saint-Césaire 1 was estimated at  $\approx 416.0$  mm by using the Neandertal reference sample ( $r^2 = 0.855, n = 4$ ) and  $\approx 386.0$  mm by using the early modern human reference sample ( $r^2 = 0.892, n = 5$ ). Subsequent estimation of the bi-iliac breadth of Saint-Césaire 1 resulted in skeletal bi-iliac breadths of  $\approx 310.5$  mm by using Neandertal proportions (based on La Chapelle-aux-Saints 1 and the Near Eastern Kebara 2 specimen) and ca.  $\approx 259.3$  mm by using earlier Upper Paleolithic proportions ( $n = 6$ ).

The variables of primary interest here are the perpendicular anteroposterior and mediolateral second moments of area at the subtrochanteric (80%) and midshaft (50%) diaphyseal levels, for which  $I_x$  and  $I_y$  are used at midshaft and the approximately mediolateral and anteroposterior  $I_{max}$  and  $I_{min}$  are used at the proximal location. Overall strength (quantified by 50%  $Z_p$ ) and the individual midshaft section moduli ( $Z_x$  and  $Z_y$ ) then were compared with the product of body mass and femoral biomechanical length. Because the body proportions of Saint-Césaire 1 are not known, in the section moduli to mass times length distributions, two values are provided for it, one based on Neandertal body proportions and the other using earlier Upper Paleolithic early modern human ones.

The resultant values are provided in the form of bi-variate plots of section properties relative to each other or to body mass times femoral length. To assess degrees of similarity between the samples, the raw residuals from the reduced major axis regressions of the pooled Neandertal and early modern human sample are compared, and z-scores for Saint-Césaire 1 based on the sample residual distributions are provided relative to each reference sample. For the comparisons of section moduli to mass times length distributions, two sets of z-scores are provided for Saint-Césaire 1, given the two body shape reconstructions and associated body masses and femoral lengths.

## RESULTS

The preserved femoral diaphysis of Saint-Césaire 1 (Figs. 1 and 2) exhibits relatively rounded cross-sections. The subtrochanteric one has a distinct but not prominent lateral swelling with a large gluteal tuberosity. The midshaft one has a clear *linea aspera* but no evidence of a *pilaster* or elevation of the *linea aspera* above the convex diaphyseal contour. It possesses a very prominent posteromedial swelling, the medial buttress, which is common among archaic *Homo* femora and usually is reduced or absent on those of recent humans (31, 32). The Saint-

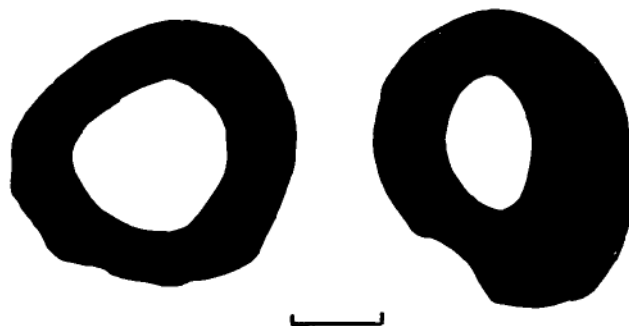


FIG. 2. Reconstructed cross-sections of the Saint-Césaire 1 femoral midshaft (50%) (Right) and subtrochanteric (80%) (Left) regions, viewed from the distal end. Anterior is above, and medial is to the right. (Scale = 1 cm.)

Césaire 1 femur, as with the rest of its morphology (1, 7), therefore is aligned with the European Neandertals and other archaic *Homo*. However, the degree of development and particularly dorsal extension of its medial buttress near mid-shaft are exceptional for an archaic human.

The plot of femoral midshaft polar section modulus to body mass times femoral length (Fig. 3) shows complete overlap of the two reference samples, which is reflected in the resultant high *P* value (Table 1). The Saint-Césaire 1 value based on a Neandertal body form is relatively high, although it is approached or exceeded by La Chapelle-aux-Saints 1 and La Ferrassie 2 and several early modern human specimens (especially Cro-Magnon 1 and Parabita 1). The resultant z-scores between 0.9 and 1.4 reflect this position. However, if an early modern human body form is used for Saint-Césaire 1, the data point position is exceptionally high, resulting in z-scores of 3.5 and 4.5.

Comparisons of diaphyseal cross-sectional shape (Fig. 4), in contrast, reveal highly significant separation of the two reference samples. In the midshaft comparison, only Neandertal 1 and Pavlov 1 overlap, and in the 80% comparison, the earlier Krapina 213 femur overlaps Dolní Věstonice 16. In these comparisons, Saint-Césaire 1 is securely with the Neandertals in the subtrochanteric comparison, but it falls with the early modern humans in the midshaft analysis. This result is reflected in z-scores  $\approx 3.0$  between Saint-Césaire 1 and Neandertals and between Saint-Césaire 1 and the early modern humans in the 50% and 80% comparisons, respectively (Table 1).

Further analysis of the midshaft proportions is possible by scaling each of the section moduli to body mass times femoral length (Fig. 5). In each case, the Saint-Césaire 1 data point using earlier Upper Paleolithic body proportions is highly divergent, providing z-scores that range between 3.0 and 5.0. In the anteroposterior ( $Z_x$ ) comparison, there is modest separation of the reference samples with the early modern humans having generally higher values. In this, the Neandertal-based Saint-Césaire 1 value falls among the more anteroposteriorly reinforced femora, close to the higher early modern human values, above all of the Neandertal values and approached among the Neandertals only by La Ferrassie 2. In contrast, in the mediolateral ( $Z_y$ ) comparison, the Neandertals have greater relative diaphyseal strength, and Saint-Césaire 1 is

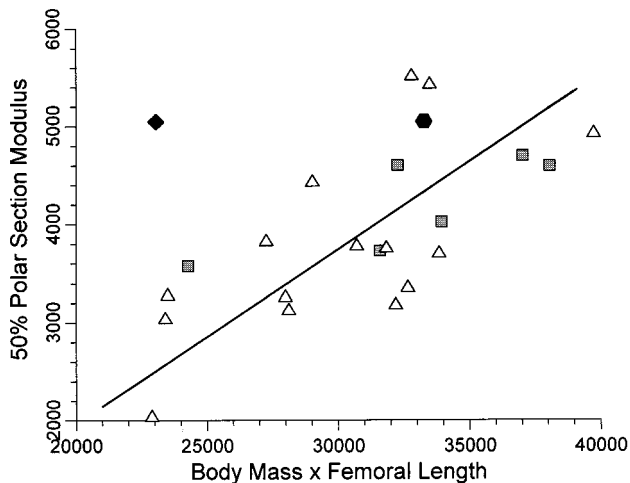


FIG. 3. Bivariate plots of femoral midshaft polar section moduli vs. body mass times femoral lengths. Solid hexagon, Saint-Césaire 1 with Neandertal-based body proportions; solid diamond, Saint-Césaire 1 with earlier Upper Paleolithic-based body proportions; gray squares, Middle Paleolithic Neandertals; open triangles, earlier Upper Paleolithic early modern humans. The reduced major axis line through the pooled reference samples is provided.

positioned among the Neandertals and above all of the early modern human femora except the small La Rochette 1.

## DISCUSSION

These femoral diaphyseal comparisons highlight two aspects of the Saint-Césaire 1 Neandertal remains, namely its probable ecogeographically relevant body proportions and its femoral (hence locomotor) loading patterns.

**Body Proportions.** Levels of femoral robustness (or appropriately scaled diaphyseal strength) are relatively uniform across Pleistocene members of the genus *Homo*, with only a slight decrease before the Holocene (19, 20). It is therefore reasonable to assume that the level of femoral robustness of Saint-Césaire 1 fell within the currently known range of variation of these otherwise relatively highly reinforced lower limbs. Given this, the comparisons of its femoral midshaft section moduli to body mass times femoral length using the more linear body proportions of European early modern humans appear unreasonable. Indeed, Saint-Césaire 1 would have to have been extraordinarily robust, even for a Neandertal or an earlier archaic *Homo* individual, to exhibit the implied level of femoral robustness. At the same time, the hyperarctic body proportions of the Neandertals, which are more extreme than those of the most cold-adapted living humans (24), provide Saint-Césaire 1 with body mass and femoral length estimates that still indicate a relatively robust femoral diaphysis, but one that falls within the known range for later Pleistocene *Homo*.

The inference that Saint-Césaire 1 maintained the body proportions of the Neandertals is supported further by the cross-sectional shape of its subtrochanteric region. Variation in pelvic proportions between males and females among modern humans (33) and among Early and early Middle Pleistocene *Homo* (22) is reflected most strongly in the proximal femoral diaphysis. The resemblance of Saint-Césaire 1 to the Neandertals in this region argues for similar pelvic and hip proportions, part of which (bi-iliac breadth) is an integral element of overall body proportions. The relatively broad femoral midshafts of the Neandertals and Saint-Césaire 1 probably also reflect (to a lesser extent) coronal plane contrasts in pelvic and hip proportions (22).

It remains unclear whether the perpetuation of these Neandertal body proportions in a Châtelperronian Neandertal was more the result of phylogenetic baggage or continued anatomical adaptation to the thermal stresses of glacial Europe. There is developmental plasticity in mammalian body proportions as a result of thermal stress (30, 34). Yet, among at least recent human immigrant groups displaced to different environments, there is little change in body proportions, even over a number of millennia (23). Certainly, the archeological evidence for improved shelter (35, 36) and the technology to pierce and assemble objects (hence clothing) (13) imply greater protection from thermal stress among these Châtelperronian Neandertals than among their predecessors, supporting the phylogenetic baggage explanation for the probable hyperarctic body form of Saint-Césaire 1. This point is supported by the climatic interpretations of the archeological level at Saint-Césaire that yielded the Neandertal partial skeleton, which place it in a slightly warmer than full pleniglacial oscillation (37, 38).

**Locomotor Patterns.** At the same time, the degree of structural anteroposterior reinforcement of the femoral midshaft of at least recent humans parallels degrees of mobility, such that, on average, males exhibit greater midshaft anteroposterior reinforcement than females, including among Pleistocene *Homo* (33), and pre-industrial populations inhabiting more accentuated terrains exhibit an emphasis on anteroposterior femoral strength (39). The greater femoral midshaft anteroposterior strength in the early modern human sample

Table 1. Student's *t* *P* values between European Neandertals (Nean) and earlier Upper Paleolithic (EUP) samples, plus z-scores for Saint-Césaire 1 (SC1)

	Nean-EUP <i>P</i> value	SC1 vs. Neandertals	SC1 vs. EUP
50% $Z_p$ vs. $BM \times Length$ - Nean	0.780	1.349	0.944
50% $Z_p$ vs. $BM \times Length$ - EUP	0.780	4.542	3.455
50% $I_x$ vs. $I_y$	<0.001	3.071	0.572
80% $I_{max}$ vs. $I_{min}$	0.002	0.387	2.993
50% $Z_x$ vs. $BM \times Length$ - Nean	0.031	1.871	0.472
50% $Z_x$ vs. $BM \times Length$ - EUP	0.031	5.084	2.971
50% $Z_y$ vs. $BM \times Length$ - Nean	0.065	0.310	1.215
50% $Z_y$ vs. $BM \times Length$ - EUP	0.065	3.149	3.834

BM, body mass.

therefore suggests a higher average level of habitual mobility (contrasts in terrain *per se* are not relevant because the two reference groups occupied most of the same regions, and, if there are any differences in habitual terrain, it is more likely that the Neandertal sample experienced a steeper topography because many of the early modern human remains derive from the more open central European plains). With respect to this, Saint-Césaire 1 falls clearly with the early modern humans and separate from the Neandertals.

Of interest, this shift in femoral diaphyseal structural reinforcement occurred without the development of a pilaster (the modern human solution) but instead involved the hypertrophy

and dorsal expansion of the medial buttress (the archaic *Homo* solution).

### CONCLUSION

Biomechanical analysis of the preserved Saint-Césaire 1 femoral diaphysis therefore indicates the maintenance of the hyperarctic body proportions of the Middle Paleolithic Neandertals among the Châtelperronian Neandertals, probably more as a result of populational genetic continuity than a perpetuation of the anatomical adaptation to the thermal

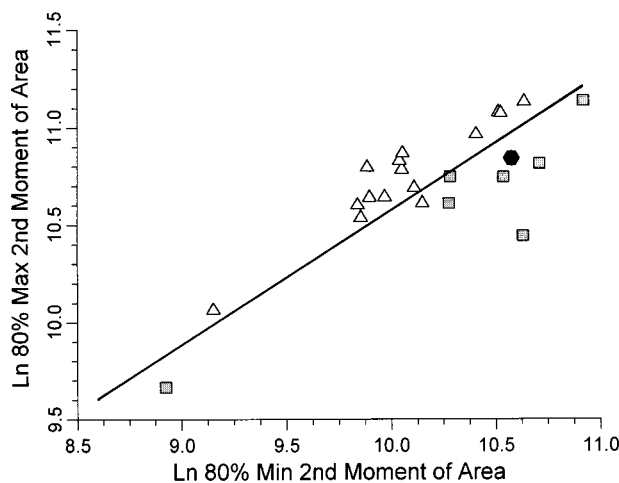
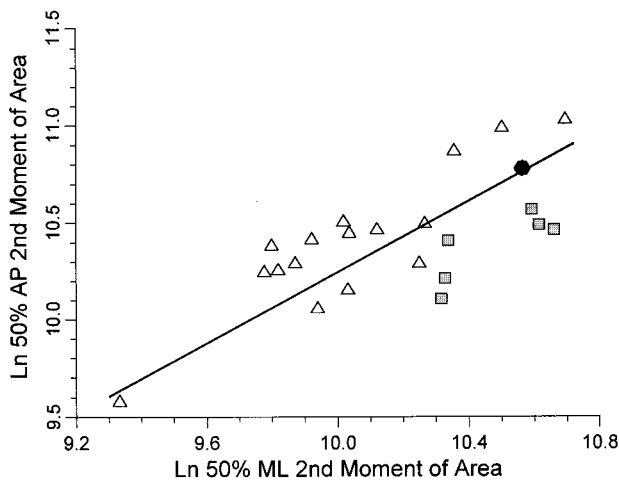


FIG. 4. Bivariate plots of midshaft (*Upper*) and subtrochanteric (*Lower*) perpendicular second moments of area. Symbols as in Fig. 3.

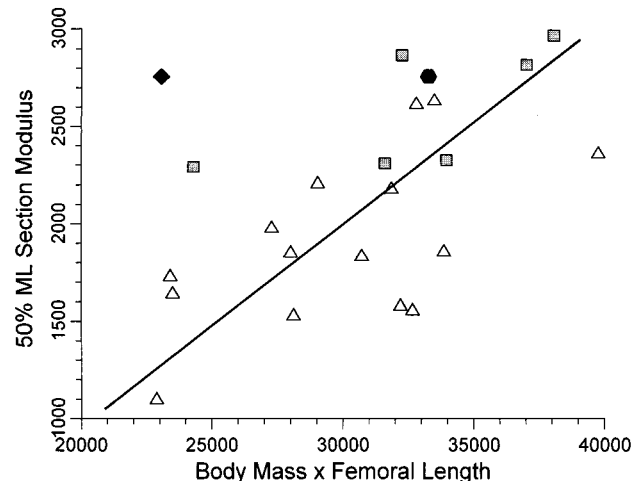
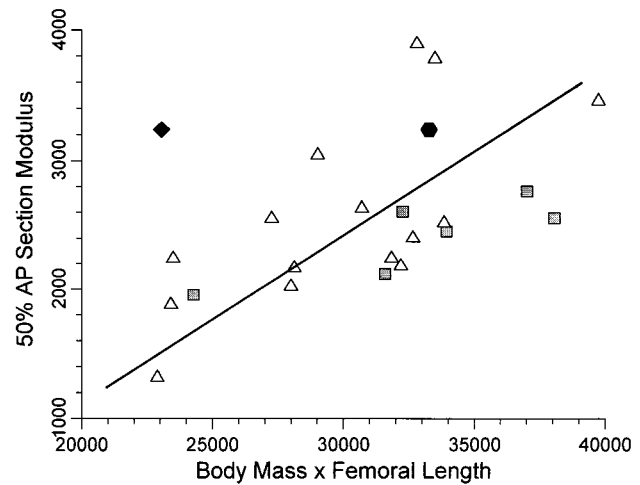


FIG. 5. Bivariate plots of midshaft anteroposterior section moduli (*Upper*) and mediolateral section moduli (*Lower*) vs. body mass times femoral lengths. Symbols as in Fig. 3.

stress that originally promoted its evolution. At the same time, there is evidence of a shift in locomotor patterns, with the presence of the femoral anteroposterior reinforcement associated with increased mobility and seen more frequently among early modern humans than among the Neandertals. The impression is of a late Neandertal, in the context of significant cultural change, reflecting in its otherwise fully Neandertal biology the emergence of an early modern human behavioral pattern.

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