Morphology, body proportions, and postcranial hypertrophy of a female Neandertal from the Sima de las Palomas, southeastern Spain

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Considerations of Neandertal geographical variation have been hampered by the dearth of remains from Mediterranean Europe and the absence there of sufficiently complete associated postcrania. The 2006 and 2007 excavation of an articulated partial skeleton of a small adult female Neandertal at the Sima de las Palomas, Murcia, southeastern Spain (Sima de las Palomas 96) provides substantial and secure information on body proportions among southern European Neandertals, as well as further documenting the nature of Neandertal biology in southern Iberia. The remains exhibit a suite of cranial, mandibular, dental, and postcranial features, of both Neandertals and archaic *Homo* generally, that distinguish them from contemporary and subsequent early modern humans. Its lower limbs exhibit the robustness of later Pleistocene *Homo* generally, and its upper limbs conform to the pattern of elevated robustness of the Neandertals. Its body proportions, including relative clavicular length, distal limb segment lengths, and body mass to stature indicators, conform to the "cold-adapted" pattern of more northern Neandertals. Palomas 96 therefore documents the presence of a suite of "Neandertal" characteristics in southern Iberia and, along with its small body size, the more "Arctic" body proportions of other European Neandertals despite the warmer climate of southern Iberia during marine isotope stage 3.

clavicle | femur | humerus | scapula | hamate

Considerations of the paleobiology of the Late Pleistocene European Neandertals have been focused principally on fossil remains from more northern portions of Europe given the presence of associated partial skeletons from Belgium, France, Germany, and Ukraine and their near absence in Mediterranean Europe. There are a variety of Neandertal remains from south of the Alps and Pyrenees, deriving principally from sites in central Italy and near the coasts of Iberia (1, 2). However, they are primarily craniofacial and dental with occasional incomplete postcranial elements. To date, the only associated postcranial remains are the fragmentary elements of Palomas 92, and it lacks indisputable cephalic elements (3). It is in this context that we describe an associated skeleton of an adolescent-to-young-adult female Neandertal, from the early last glacial levels of the Sima de las Palomas del Cabezo Gordo, Murcia, southeastern Spain.

Sima de las Palomas and Palomas 96

The Sima de las Palomas, Cabezo Gordo, Torre Pacheco, Murcia, Spain (37° 47′ 59′′ N, 0° 53′ 45′′ W) is a Late Pleistocene in-filling of an ~18-m vertical shaft in a hill of Permo-Triassic marble, which was largely emptied by late 19th century miners (4–7) (*SI Appendix*, Figs. S1 and S2). They left a vertical sediment column against one side of the shaft, which has been systematically excavated in the uppermost 3–4 m (the upper cutting) (7).

The upper cutting (*SI Appendix*, Fig. S2) consists principally of a cemented massive scree (conglomerate A), sloping down from the west side, overlain to the east by an infilling of softer sediment containing small angular stone clasts, within which there is a dark-gray lens, the upper gray layer. Both conglomerate A and the later finer sediment lie on an additional extensive gray horizon (the lower gray layer). This lower gray layer covers, in turn, another heavily cemented bone-bearing breccia (conglomerate B), which in turn covers a looser scree. All of these sedimentary deposits in the upper cutting contain abundant Middle Paleolithic (Mousterian) lithic and faunal remains and have yielded ~100 variously complete human fossils.

The Palomas 96 associated remains, discovered in 2006 and 2007, derive from conglomerate A along with the partial Palomas 92 skeleton (3) and the partial remains of a juvenile in anatomical connection (Palomas 97) (7). All three have been excavated from variably hard breccia. Some bones are badly compressed but others are in excellent condition and in anatomical connection; they are slowly being extracted from their encasing matrix. It is as yet unclear how the skeletal elements came to be entombed in conglomerate A, but current scenarios involve intentional burial, accidental burial in a rock collapse, and washing in from the adjacent slope (7). If the first scenario, it would be the only Neandertal burial known from Mediterranean Europe, but it would be unexceptional for Late Pleistocene Neandertals (8).

A combination of accelerator mass spectrometry (AMS) radiocarbon, laser ablation multicollector plasma mass spectrometry (LA-ICP-MS) uranium-series, optically stimulated luminescence (OSL), and paleoclimatic correlation dating places the upper gray layer to ≥40,000 calendar years before present (cal y BP) and those in conglomerate A to ~50,000–60,000 cal y BP [early marine isotope stage (MIS) 3] (6, 7). The deeper levels of the sediment column should extend back through much of the Late Pleistocene. Only Middle Paleolithic lithic remains have been found in situ.

Palomas 96 retains portions of all skeletal units except the feet (*SI Appendix*, Table S1 and Fig. S3). The skull was badly crushed in situ with loss of the mandibular corpus and of the posterior, inferior, and most of the left neurocranium (Fig. 1 and *SI Appendix*, Figs. S4 and S5). The right facial elements, although broken and displaced, are undistorted. Twenty-two teeth remain, cemented into the facial skeleton. The axial skeleton is incomplete and consists principally of partial lower cervical, upper thoracic, and lumbar vertebrae; five sacral bodies; and six or more right ribs cemented to the right scapula and clavicle (*SI Appendix*, Figs. S6 and S15). The right scapula and clavicle are largely complete, as are all six upper limb long bones (*SI Appendix*, Fig. S6). The metacarpals and manual phalanges are mostly present and in anatomical position, permitting secure digit identification,

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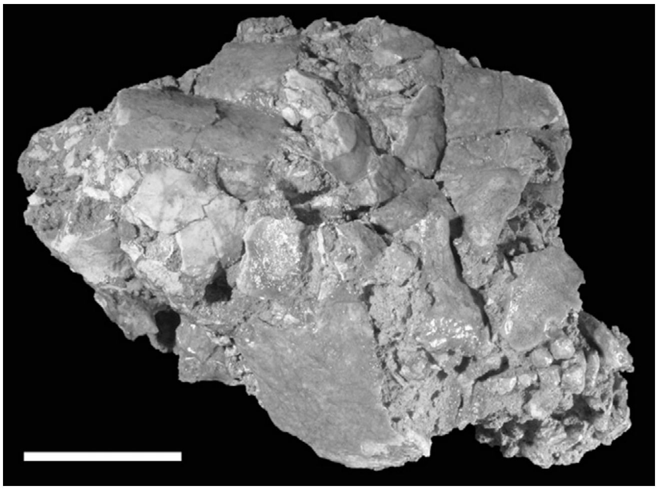

Fig. 1. Right lateral view of the Palomas 96 crushed skull. The squamous frontal bone and the parietal bone are evident in pieces, as are the right supraorbital torus, the lateral zygomatic bone, the mandibular ramus, the infraorbital region of the right maxilla, and a portion of the dentition. (Scale bar: 5 cm.)

but few carpals remain uneroded. All elements of the ossa coxae except the posterior ilium are present on at least one side, but broken, displaced, and cemented (*SI Appendix*, Fig. S7). The femora are almost complete, as is the left tibia.

Aspects of Palomas 96 will yield further data as processing continues, but the remains furnish sufficient morphometric and discrete data to provide insight into southern European Neandertal paleobiology. In particular, Palomas 96 is one of only two Neandertals (along with La Ferrassie 1) that provide reliable lengths of all four major limb segments, clavicular and scapular lengths, and weight-bearing articular dimensions.

The open left greater sciatic notch identifies Palomas 96 as female (*SI Appendix*, Fig. S8). On the basis of the full occlusal eruption of the left M^3 combined with ventrally unfused sacral bodies, unfused proximal clavicular epiphysis, and partially fused iliac crest, she has an estimated age at death of ≤20 y with a probable range of 16–20 y (9–12) (*SI Appendix*, Figs. S9–S12). All of the sufficiently preserved long bone and manual epiphyses are fused. Although Palomas 96 was not fully skeletally mature at death, it is unlikely that additional growth would have altered the morphological features or body size and proportions of this individual.

Palomas 96 Morphology

Affinities of Palomas 96. The Palomas 96 remains present a series of discrete characteristics that, in a European MIS 3 context, identify her as a Neandertal (13). Although some features are plesiomorphous (13) and some continue into Early/Mid-Upper Paleolithic (E/MUP) modern humans (14), these are aspects that are common among the Neandertals and rare or absent from geographically and chronologically adjacent samples of early modern humans, both Middle Paleolithic modern humans (MPMH) and E/MUP.

These elements for the cranium include a distinct lateral supraorbital torus and broad supratoral sulcus, a large frontozygomatic suture with a columnar frontal process of the zygomatic bone, little horizontal angulation of the anterolateral zygomatic bone, absence of a canine fossa, and a strongly bilevel nasal floor with a sharply angled inferior nasal aperture margin (15–18) (Fig. 1 and *SI Appendix*, Table S3 and Figs. S13 and S14). Its estimated nasal aperture breadth (30–32 mm) falls at the overlap zone between Neandertals and E/MUP modern humans (18, 19) (*SI Appendix*, Table S3). The right mandible exhibits a high coronoid process and a mandibular notch with the lowest point closer to the condyle, a prominent superior medial pterygoid tubercle on the ramus (17) (Fig. 1 and *SI Appendix*, Table S3 and Fig. S14), and the left one has a rounded gonial angle. The dentition possesses a strongly shoveled I^2 with marked labial convexity, a combination found predominantly among the Neandertals (20, 21).

There are also postcranial features that align her with the Neandertals, aspects that are apparently unrelated to skeletal hypertrophy and/or that appear early in development. The upper limb ones include the strong dorsal sulcus of the right scapula, a narrow medial humeral pillar, a medially oriented radial tuberosity, subequal pollical phalangeal lengths, and ulnar deviation of the pollical distal phalanx (22–26) (*SI Appendix*, Tables S2 and S4 and Fig. S15). She also has an elongated superior pubic ramus with a thinned ventral margin, the absence of pilasteric development on the femora, a rounded convex cross-section of the tibial diaphysis, and the absence of distinct fibular diaphyseal sulci (13, 27–29) (*SI Appendix*, Fig. S16).

There are nonetheless aspects that are less common among the Neandertals. The dentition is markedly nontaurodont (*SI Appendix*, Fig. S9). The I^2 labial root length is unexceptional for Neandertals or early modern humans, but its I_1 root length is 3.1 SDs from a Neandertal mean (including Palomas 19 and 21) and at the lower limit of an E/MUP sample (*SI Appendix*, Table S5). The metacarpal 1 lacks an opponens pollicis flange. The manual terminal phalanges from digits 3 and 4 have apical tufts that lack the rounded curve of Neandertals (including Palomas 28) and present distinct ungual spines (*SI Appendix*, Fig. S15).

Palomas 96 therefore presents a suite of morphological aspects that align it with Late Pleistocene Neandertals, although there are a few aspects that are less common or previously unknown among

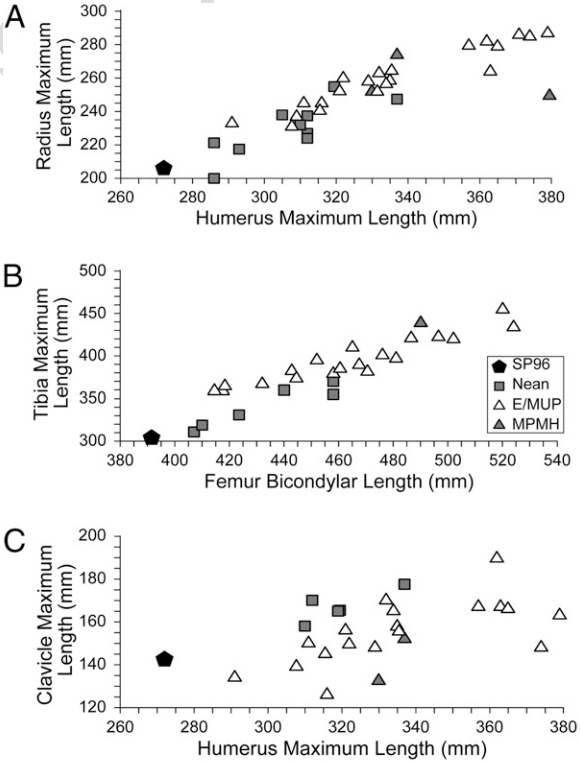

Fig. 2. (*A*–*C*) Bivariate plots of radius length versus humerus length (*A*), tibia length versus femur length [illegible] and clavicle length versus humerus length (*C*) (*SI Appendix*, Tables S2 and S7 for individual lengths and *SI Appendix*, Table S9 for residual comparisons). SP96, Palomas 96; Nean, MIS 5d-3 Neandertals; E/MUP, MIS 3 Early/Mid-Upper Paleolithic modern humans; MPMH, MIS 5c Middle Paleolithic modern humans.

these late archaic humans. In this pattern it is joined by other, more fragmentary, remains from Palomas (6, 7, 30).

Body Size. Her femoral and tibial lengths, as indications of stature (31), are among the smallest known for Neandertals (Fig. 2*B* and *SI Appendix*, Tables S6 and S7). Her estimated (from maximum trochanteric length given neck crushing) femoral bicondylar length, at ~391.5 mm, is below all reliable Neandertal lengths but approached by Palomas 92 (~394 mm). Her tibial maximum length of 304 mm is matched by the estimate for Shanidar 6 (~302 mm) but is below the remainder of the Neandertal values. Her femoral length can be found in the E/MUP sample, but not her short tibial length (Fig. 2*B*). Moreover, although small for a Neandertal, her body size is nonetheless approached by several other individuals from Palomas (3), as well as the southwest Asian Shanidar 6 and Tabun 1 individuals. Her upper limb segment lengths show a similar pattern (Fig. 2*A* and *SI Appendix*, Tables S2 and S8).

The best indicator of body mass, given the dearth of pre-MUP pelvises, is femoral head diameter (31). At 43.0 mm, Palomas 96 has the smallest one known (or estimated) for a Neandertal, being approached only by Palomas 92 and Tabun 1 (~44.2 and 44.5 mm) and to a lesser extent Palomas 77 (45.6 mm). It is matched by several E/MUP femora (Fig. 3*A* and *SI Appendix*, Table S7).

Body Proportions. Neandertals have been noted to contrast with E/MUP and Middle Paleolithic modern humans in their body breadths and distal limb relative lengths (32–34), and Palomas 96 can be directly evaluated for all except bi-iliac breadth.

There is only a modest difference in radiohumeral length proportions across the Late Pleistocene samples (Fig. 2*A*), despite strong ecogeographical patterning for brachial indexes among recent humans (32, 35). Palomas 96, despite its small size, falls within the other MIS 5d-3 remains but close to the Neandertal average. However, Neandertals exhibit relatively short distal leg segments, despite the estimated values for La Chapelle-aux-Saints 1 and La Ferrassie 1 (36, 37) falling close to the E/MUP distribution (Fig. 2*B*). Palomas 96 is among the Neandertals with short distal legs, who are highly significantly different from the early modern human samples (*SI Appendix*, Table S9).

The only body breadth measure that is available for Palomas 96 is clavicular length, although preliminary assessment suggests a broad bi-iliac breadth. The five Neandertals with sufficiently intact clavicles all have long claviculohumeral proportions, significantly different from the small E/MUP and MPMH samples (*SI Appendix*, Table S9). The estimated range for Palomas 96 (140–145 mm, given its absent proximal epiphysis) places it among those Neandertals and distinct from the variable E/MUP and MPMH samples (Fig. 2*C*).

It is also possible to assess relative body core mass by comparing femoral head diameter (as reflecting mass) to femoral length (reflecting stature); the Neandertals (especially the European ones) cluster along the "stockier" edge of the E/MUP distribution, distinct from the "linear" MPMH sample, and Palomas 96 is among those more northern Neandertals at the edge of the E/MUP distribution (Fig. 3*A* and *SI Appendix*, Table S10). Indications of a broad trunk are also apparent in the relatively broad femoral diaphyses of the Neandertals (Fig. 3*B*), in the context of scaled anteroposterior rigidity stasis through the Late Pleistocene (38); Palomas 96 again extends the Neandertal line to a smaller size range and is significantly different from the E/MUP sample (*SI Appendix*, Table S10).

Palomas 96 therefore suggests that southern European Neandertals shared the "hyperpolar" (35) body proportions of the latter.

Appendicular Hypertrophy. Recent reassessments (39) have documented little change in lower limb robustness through the Late Pleistocene, in the context of reductions in shoulder, arm, and hand hypertrophy with the establishment of early modern humans. In the former, Palomas 96 falls among the other Late Pleistocene humans in relative femoral rigidity (Fig. 4), who are not significantly different from each other (*SI Appendix*, Table S11). In the latter, the Palomas 96 estimated scapular breadth, reflecting both rotator cuff hypertrophy and scapular rotation moments, is among the similarly enlarged Neandertals (Fig. 5*A*). Related muscular hypertrophy is evident in pectoralis major tuberosity breadths scaled to humeral length (Fig. 5*B*); there is little archaic–modern overlap, and Palomas 96 clusters with La Ferrassie 2 and Tabun 1.

The right radius has a medially oriented tuberosity, in a position to maximize the biceps brachii moment arm through supination; this orientation is the dominant position among the Neandertals, is absent from the MPMH, and rare among E/MUP humans (39) (*SI Appendix*, Table S4). Manually, Neandertals exhibit, among other aspects (25), large palmar carpal tuberosities (including hamuli) and broad apical tufts (39) indicating large distal digital pads (42). Comparing the summed hamuli dimensions to hamate length places Palomas 96 among the other Neandertals and above the early modern humans (Fig. 6*A*). Scaling the average for the three middle phalanges (given distal phalangeal digit uncertainty for many specimens, but not Palomas 96) to humeral length (given the relatively shorter distal phalanges of modern humans) separates the modern humans from the Neandertals (Fig. 6*B*). The average of the Palomas 96 third and fourth ray distal breadths

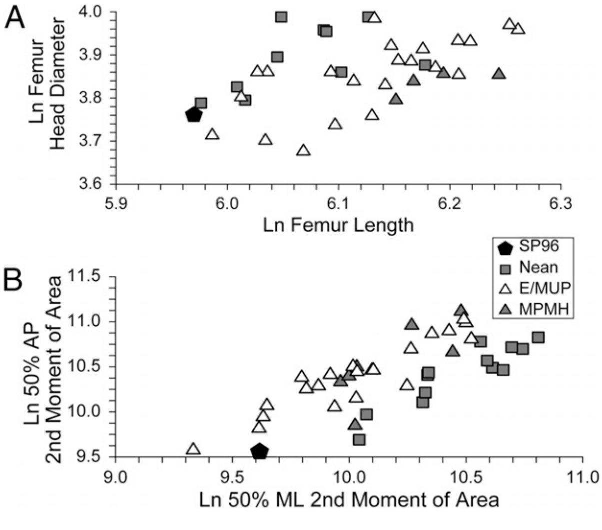

Fig. 3. Femoral reflections of relative body breadth. (*A*) femur head diameter versus femur bicondylar length. (*B*) Femur midshaft (50%) anteroposterior versus mediolateral second moments of area. Abbreviations are as in Fig. 2. The relatively small Neandertal femoral head diameters are from southwest Asian remains. See *SI Appendix*, Table S10 for residual comparisons.

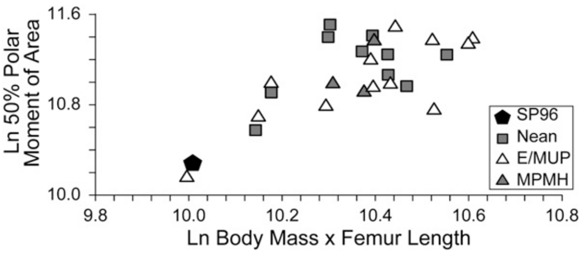

Fig. 4. Locomotor robustness as reflected in femoral midshaft (50%) diaphyseal rigidity versus femoral biomechanical length times estimated body mass. Body mass was estimated from femoral head diameters using the average of sex-specific (as applicable) formulas (40, 41). Abbreviations are as in Fig. 2. See *SI Appendix*, Table S11 for residual comparisons.

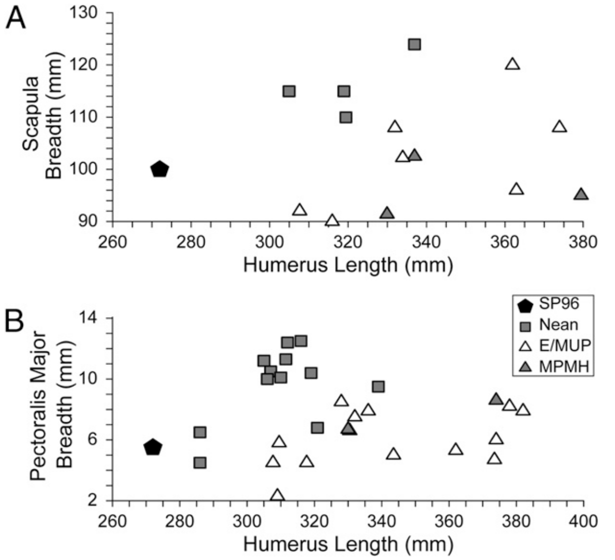

Fig. 5. (*A* and *B*) Scapular and thoracohumeral robustness, as reflected in scapular breadth (*A*) and pectoralis major tuberosity breadth (*B*) versus humeral length. Abbreviations are as in Fig. 2.

(8.2 and 7.8 mm) places her distinctly with the Neandertals (*SI Appendix*, Table S11).

It is therefore apparent that despite her small size and the diminutive dimensions of several reflections of her robustness, Palomas 96 conforms to the Neandertal pattern of elevated upper limb hypertrophy but no difference in locomotor resistance relative to early modern humans.

Discussion

The Palomas 96 associated partial skeleton provides a unique window onto the body proportions and appropriately scaled appendicular hypertrophy of a European Mediterranean Neandertal (*SI Appendix*, Fig. S1). Once her diminutive dimensions are taken into account, there is little in the Palomas 96 remains to distinguish her paleobiological reflections from those of either the more northern European Neandertals or those from southwest Asia. This result has been implied by previous analyses of incomplete postcrania from Palomas (3) and two other Iberian sites (24, 43), but it is only with Palomas 96 that is has been possible to confirm this pattern.

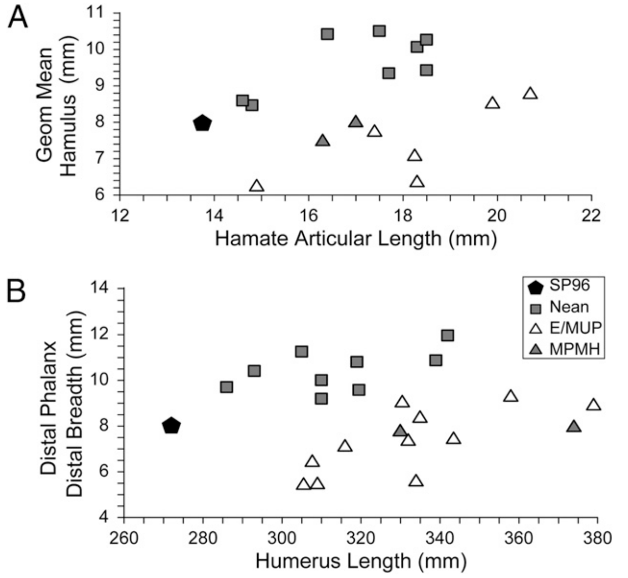

Fig. 6. (*A* and *B*) Manual robustness reflected in relative hamulus size (*A*) and distal phalanx tuberosity breadth (*B*). Hamulus size was quantified as the geometric mean of the proximodistal, radioulnar, and dorsopalmar maximum dimensions of the hamulus. Distal tuberosity dimensions are the average of the dimensions from digits 2–4 as available by individual. Abbreviations are as in Fig. 2. See *SI Appendix*, Table S11 for phalangeal residual comparisons.

Of greatest interest is the presence of the hyperpolar body proportions, characteristic of other European Neandertals, in the relatively mild climate of southeastern Iberia, even through the colder phases of MIS 3 (44, 45). Given the presence of sophisticated pyrotechnology among the Neandertals (46), including in Iberia (47), and the probable presence of clothing among them (48), the Palomas Neandertals were unlikely to have experienced the level of thermal stress commonly associated with the Neandertals.

The other more "southern" Neandertal sample, the one from southwest Asia, differs from the more "northern" European ones only in the more modest femoral head dimensions relative to stature, evident in both those from the eastern Mediterranean littoral and the ones from the northern Zagros Mountains (25, 49). It has been possible to attribute the presence of largely similar body proportions among these southwest Asian Neandertals, particularly those from the southern part of the eastern Mediterranean littoral, to relatively frequent (in evolutionary time) dispersals from farther north in the region as part of an alternating use of the region with early modern humans dispersing from Africa during MIS 5 and 3 (34, 50). This interpretation would assume a relatively long-term (tens of thousands of years) stability in these body proportions (33) given their modest thermal advantage (51).

A similar model is less likely to apply to southern Iberia; Neandertals appear to have been long-term, consistent occupants of Mediterranean Europe (52–54), and the body proportions of Palomas 96 cannot therefore be attributed to a recent dispersal of Neandertals south into Iberia. It thus remains possible that the body proportions of Palomas 96, and other Neandertals, reflect more in their paleobiology than thermal regulation. Given the strong correlations between these body proportions and climatic indicators in recent humans (32, 33, 49), following general ecogeographical rules (55), Palomas 96 raises questions regarding both the long-term stability of such body proportions under changing climatic conditions (32, 33, 56) and what other factors might be influencing them (57).

Conclusion

Ongoing excavations at the Sima de las Palomas in southeastern Spain have yielded an associated partial skeleton of an adolescent-to-young-adult female Neandertal. Her Neandertal affinities are evident in a suite of craniofacial, dental, and appendicular discrete traits, and she provides the only current evidence for body proportions and appropriately scaled appendicular hypertrophy in southern European Neandertals. Her locomotor hypertrophy is similar to other Late Pleistocene humans, but her upper limbs conform to the Neandertal (and archaic *Homo*) pattern of elevated robustness. Her body proportions are indistinguishable from those of northern European Neandertals, in terms particularly of body breadth, distal leg foreshortening, and probable body mass to stature, and they contrast with those of Middle Paleolithic and earlier Upper Paleolithic modern humans. The Palomas 96 remains therefore raise the issue of the extent of ecogeographical patterning in body proportions among European Neandertals.

Materials and Methods

The Palomas 96 remains are compared principally to the available samples of Late Pleistocene (MIS 5d to 3) western Eurasian Neandertals and of pooled MIS 3 E/MUP modern humans. Additional data are provided for the southwest Asian MIS 5c MPMH. Data from other Palomas Neandertal specimens are included in comparative summary statistics, but are also mentioned individually. Comparative data are from primary published descriptions of remains supplemented by personal research. Right and left measurements, as available per individual, are averaged in sample statistics and data plots. For bivariate comparisons (Figs. 2–6) for which the regression slopes of the E/MUP sample are significantly different from zero (all but the scapular, pectoralis major, and hamate comparisons), the samples are compared using the distributions of the raw residuals from the reduced major axis line through the E/MUP sample (*SI Appendix*, Tables S9–S11).

Morphometric measurements follow Martin (58). Cross-sectional geometry parameters were generated using SLICE/SLCOMM (59, 60) and digitized from scaled fossilization breaks, and reconstructed cross-sections were generated using polysiloxane putty (CutterSil) and biplanar radiography projected and enlarged onto a Summagraphics 1812 tablet.

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1. Garralda MD (2006) Los Neandertales en la Península Ibérica [The Neandertals of the Iberian peninsula]. *Munibe* 57:289–314. Spanish.
2. Alciati G, Delfino VP, Vacca E (2005) Catalogue of Italian fossil human remains from the Palaeolithic to the Mesolithic. *J Anthropol Sci* 84S:1–184.
3. Walker MJ, Ortega J, López MV, Parmová K, Trinkaus E (2011) Neandertal postcranial remains from the Sima de las Palomas del Cabezo Gordo, Murcia, southeastern Spain. *Am J Phys Anthropol* 144:505–515.
4. Walker MJ (2001) Excavations at Cueva Negra del Estrecho del Río Quípar and Sima de las Palomas del Cabezo Gordo: Two sites in Murcia (south-east Spain) with Neanderthal skeletal remains, Mousterian assemblages and late Middle to early Upper Pleistocene fauna. *A Very Remote Period Indeed*, eds Milliken S, Cook J (Oxbow Books, Oxford), pp 153–159.
5. Walker MJ (2009) La Sima de las Palomas del Cabezo Gordo en Torre Pacheco y la Cueva Negra del Estrecho del Río Quípar en Caravaca de la Cruz: dos ventanas sobre la vida y la muerte del hombre fósil en Murcia [The Sima de las Palomas del Cabezo Gordo in Torre Pacheco and the Cueva Negra des Estrecho del Río Quípar in Caravaca de la Cruz: two sites regarding the life and death of fossil men in Murcia]. *Darwin y la Evolución Humana* [*Darwin and Human Evolution*], eds Verdú TF, Martínez FA (Caja Mediterráneo, Murcia, Spain), pp 71–96. Spanish.
6. Walker MJ, et al. (2008) Late Neandertals in southeastern Iberia: Sima de las Palomas del Cabezo Gordo, Murcia, Spain. *Proc Natl Acad Sci USA* 105:20631–20636.
7. Walker MJ, et al. (2011) The excavation of buried articulated Neandertal skeletons at Sima de las Palomas (Murcia, SE Spain). *Quat Int*, 10.1016/j.quaint.2011.03.034.
8. Maureille B, Vandermeersch B (2007) Les sépultures Néandertaliennes [Neandertal burials]. *Les Néandertaliens. Biologie et Cultures*, eds Vandermeersch B, Maureille B (Comité des Travaux Historiques et Scientifiques, Paris), pp 311–322. French.
9. Webb PAO, Suchey JM (1985) Epiphyseal union of the anterior iliac crest and medial clavicle in a modern multiracial sample of American males and females. *Am J Phys Anthropol* 68:457–466.
10. AlQahtani SJ, Hector MP, Liversidge HM (2010) Brief communication: The London atlas of human tooth development and eruption. *Am J Phys Anthropol* 142:481–490.
11. Wolpoff MH (1978) The Krapina dental remains. *Am J Phys Anthropol* 50:67–114.
12. Belcastro MG, Rastelli E, Mariotti V (2008) Variation of the degree of sacral vertebral body fusion in adulthood in two European modern skeletal collections. *Am J Phys Anthropol* 135:149–160.
13. Trinkaus E (2006) Modern human versus Neandertal evolutionary distinctiveness. *Curr Anthropol* 47:597–620.
14. Trinkaus E (2007) European early modern humans and the fate of the Neandertals. *Proc Natl Acad Sci USA* 104:7367–7372.
15. Sládek V, Trinkaus E, Šefčáková A, Halouzka R (2002) Morphological affinities of the Šal'a 1 frontal bone. *J Hum Evol* 43:787–815.
16. Smith FH, Ahern JCM (1994) Brief communication: Additional cranial remains from Vindija cave, Croatia. *Am J Phys Anthropol* 93:275–280.
17. Doboș A, Soficaru A, Trinkaus E (2010) The prehistory and paleontology of the Peștera Muierii, Romania. *Étud Rech Archéol Univ Liège* 124:1–124.
18. Franciscus RG (2003) Internal nasal floor configuration in *Homo* with special reference to the evolution of Neandertal facial form. *J Hum Evol* 44:701–729.
19. Wu X, Poirier FE (1995) *Human Evolution in China* (Oxford Univ Press, Oxford).
20. Bailey SE (2006) Beyond shovel-shaped incisors: Neandertal dental morphology in a comparative context. *Period Biol* 108:253–267.
21. Bailey SE, Weaver TD, Hublin JJ (2009) Who made the Aurignacian and other early Upper Paleolithic industries? *J Hum Evol* 57:11–26.
22. Trinkaus E, Churchill SE (1988) Neandertal radial tuberosity orientation. *Am J Phys Anthropol* 75:15–21.
23. Villemeur I (1994) *La Main des Néandertaliens* [*The Neandertal Hand*] (Centre National de la Recherche Scientifique, Paris). French.
24. Trinkaus E, Maki J, Zilhão J (2007) Middle Paleolithic human remains from the Gruta da Oliveira (Torres Novas), Portugal. *Am J Phys Anthropol* 134:263–273.
25. Trinkaus E (1983) *The Shanidar Neandertals* (Academic, New York).
26. Trinkaus E (2008) Kiik-Koba 2 and Neandertal axillary border ontogeny. *Anthropol Sci* 116:231–236.
27. Trinkaus E (1976) The morphology of European and Southwest Asian Neandertal pubic bones. *Am J Phys Anthropol* 44:95–103.
28. Rak Y (1991) The pelvis. *Le Squelette Moustérien de Kébara 2* [*The Kebara 2 Mousterian Skeleton*], eds Bar Yosef O, Vandermeersch B (Centre National de la Recherche Scientifique, Paris), pp 147–156. French.
29. Trinkaus E (1976) The evolution of the hominid femoral diaphysis during the upper pleistocene in Europe and the Near East. *Z Morphol Anthropol* 67:291–319.
30. Walker MJ, Lombardi AV, Zapata J, Trinkaus E (2010) Neandertal mandibles from the Sima de las Palomas del Cabezo Gordo, Murcia, southeastern Spain. *Am J Phys Anthropol* 142:261–272.
31. Auerbach BM, Ruff CB (2004) Human body mass estimation: A comparison of "morphometric" and "mechanical" methods. *Am J Phys Anthropol* 125:331–342.
32. Trinkaus E (1981) Neanderthal limb proportions and cold adaptation. *Aspects of Human Evolution*, ed Stringer CB (Taylor & Francis, London), pp 187–224.
33. Holliday TW (1997) Body proportions in Late Pleistocene Europe and modern human origins. *J Hum Evol* 32:423–448.
34. Holliday TW (2000) Evolution at the crossroads: Modern human emergence in western Asia. *Am Anthropol* 102:54–68.
35. Holliday TW (1997) Postcranial evidence of cold adaptation in European Neandertals. *Am J Phys Anthropol* 104:245–258.
36. Heim JL (1982) Les hommes fossiles de La Ferrassie II: Les squelettes adultes (squelettes des membres) [The fossil men of La Ferrassie II: The adult skeletons (limb skeletons)]. *Arch Inst Paléontol Hum*, 38:1–272. French.
37. Trinkaus E (2011) The postcranial dimensions of the La Chapelle-aux-Saints 1 Neandertal. *Am J Phys Anthropol*, 10.1002/ajpa.21528.
38. Trinkaus E (2011) The paleobiology of modern human emergence. *Origin of Modern Humans*, eds Smith FH, Ahern JCM (Wiley-Blackwell, New York), in press.
39. Shang H, Trinkaus E (2010) *The Early Modern Human from Tianyuan Cave, China* (Texas A&M Univ Press, College Station, TX).
40. Ruff CB, Scott WW, Liu AYC (1991) Articular and diaphyseal remodeling of the proximal femur with changes in body mass in adults. *Am J Phys Anthropol* 86:397–413.
41. Grine FE, Jungers WL, Tobias PV, Pearson OM (1995) Fossil *Homo* femur from Berg Aukas, northern Namibia. *Am J Phys Anthropol* 97:151–185.
42. Mittra ES, Smith HF, Lemelin P, Jungers WL (2007) Comparative morphometrics of the primate apical tuft. *Am J Phys Anthropol* 134:449–459.
43. Arsuaga JL, et al. (2007) New Neandertal remains from Cova Negra (Valencia, Spain). *J Hum Evol* 52:31–58.
44. Carrión JS, et al. (2003) Glacial refugia of temperate, Mediterranean and Ibero-North African flora in south-eastern Spain: New evidence from cave pollen at two Neanderthal man sites. *Glob Ecol Biogeogr* 12:119–129.
45. Barron E, van Andel TH, Pollard D (2003) Glacial environments II: Reconstructing the climate of Europe in the last glaciation. *Neanderthals and Modern Humans in the European Landscape during the Last Glaciation*, eds van Andel TH, Davies W (McDonald Institute for Archaeological Research, Cambridge, UK), pp 57–78.
46. Roebroeks W, Villa P (2011) On the earliest evidence for habitual use of fire in Europe. *Proc Natl Acad Sci USA*, 108:5209–5214. Portuguese.
47. Grupo para o Estudo do Paleolítico Português (1983) A Estação paleolítica de Vilas Ruivas (Ródão)-Campanha de 1979 [The Paleolithic site of Vilas Ruivas (Ródão) - 1979 season]. *O Arqueól Port Série IV* 1:15–38.
48. Sørensen B (2009) Energy use by Eem Neanderthals. *J Archaeol Sci* 36:2201–2205.
49. Ruff CB (1994) Morphological adaptation to climate in modern and fossil hominids. *Yearb Phys Anthropol* 37:65–107.
50. Stefan VH, Trinkaus E (1998) Discrete trait and dental morphometric affinities of the Tabun 2 mandible. *J Hum Evol* 34:443–468.
51. Aiello LC, Wheeler P (2003) Neanderthal thermoregulation and the glacial climate. *Neanderthals and Modern Humans in the European Landscape During the Last Glaciation*, eds van Andel TH, Davies W (McDonald Institute for Archaeological Research, Cambridge, UK), pp 147–166.
52. Arsuaga JL, Martínez I, Gracia A, Lorenzo C (1997) The Sima de los Huesos crania (Sierra de Atapuerca, Spain). A comparative study. *J Hum Evol* 33:219–281.
53. Rosas A (2001) Occurrence of Neanderthal features in mandibles from the Atapuerca-SH site. *Am J Phys Anthropol* 114:74–91.
54. Condemi S (1992) *Les Hommes Fossiles de Saccopastore et Leurs Relations Phylogénétiques* [*The Fossil Men of Saccopastore and Their Phylogenetic Relationships*] (Centre National de la Recherche Scientifique, Paris). French.
55. Mayr E (1963) *Animal Species and Evolution* (Belknap, Cambridge, MA).
56. Holliday TW (1995) Body size and proportions in the Late Pleistocene Western Old World and the origins of modern humans. PhD thesis (Univ of New Mexico, Albuquerque, NM).
57. Weaver TD, Steudel-Numbers K (2007) Does climate or mobility explain the differences in body proportions between Neandertals and their Upper Paleolithic successors? *Evol Anthropol* 14:218–223.
58. Bräuer G (1988) Osteometrie [Osteometry]. *Anthropologie I*, ed Knussman R (Fischer, Stuttgart), pp 160–232. French.
59. Eschman PN (1992) *SLCOMM Version 1.6* (Eschman Archeological Services, Albuquerque, NM).
60. Nagurka ML, Hayes WC (1980) An interactive graphics package for calculating cross-sectional properties of complex shapes. *J Biomech* 13:59–64.