Neandertal clavicle length

Erik Trinkaus^{a,1}, Trenton W. Holliday^b, and Benjamin M. Auerbach^c

^aDepartment of Anthropology, Washington University, Saint Louis, MO 63130; ^bDepartment of Anthropology, Tulane University, New Orleans, LA 70118; and ^cDepartment of Anthropology, University of Tennessee, Knoxville, TN 37996

Contributed by Erik Trinkaus, February 7, 2014 (sent for review December 10, 2013)

The Late Pleistocene archaic humans from western Eurasia (the Neandertals) have been described for a century as exhibiting absolutely and relatively long clavicles. This aspect of their body proportions has been used to distinguish them from modern humans, invoked to account for other aspects of their anatomy and genetics, used in assessments of their phylogenetic polarities, and used as evidence for Late Pleistocene population relationships. However, it has been unclear whether the usual scaling of Neandertal clavicular lengths to their associated humeral lengths reflects long clavicles, short humeri, or both. Neandertal clavicle lengths, along with those of early modern humans and latitudinally diverse recent humans, were compared with both humeral lengths and estimated body masses (based on femoral head diameters). The Neandertal do have long clavicles relative their humeri, even though they fall within the ranges of variation of early and recent humans. However, when scaled to body masses, their humeral lengths are relatively short, and their clavicular lengths are indistinguishable from those of Late Pleistocene and recent modern humans. The few sufficiently complete Early Pleistocene *Homo* clavicles seem to have relative lengths also well within recent human variation. Therefore, appropriately scaled clavicular length seems to have varied little through the genus *Homo*, and it should not be used to account for other aspects of Neandertal biology or their phylogenetic status.

humerus | femur | pelvis | Sunghir

It was first noticed a century ago (1) that the La Ferrassie 1 Neandertal possessed absolutely long clavicles, ones that were especially long relative to his humeri (Fig. 1 and *SI Appendix*, Fig. S1). Since that time, descriptions of the sufficiently complete Neandertal clavicles in associated skeletons (2–5), as well as estimations of the lengths of additional ones (6, 7), have reinforced the impression that the Neandertals in Europe and southwest Asia possessed long clavicles—and hence broad shoulders and possibly deep chests—relative to modern humans (8–14). In contrast, Middle and Upper Paleolithic modern humans have clavicular proportions principally within the range of variation of recent humans (6, 15–19), the one exception being the very long clavicles of Sunghir 1 (20, 21). These long clavicles of the Neandertals and the dichotomy with recent humans in claviculohumeral length proportions have been invoked with respect to ecogeographic body proportion patterning in the Late Pleistocene (11, 22), Neandertal thoracic shape (10, 23), scapular positioning on the thorax (14, 24), shoulder biomechanics (24), contrasts in temporal labyrinthine morphology (25), Neandertal DNA sequences (26), later *Homo* trait polarities (27), and Late Pleistocene population dynamics (28).

In the majority of these assessments of Late Pleistocene clavicular length, clavicle length has been compared with humeral length, in most cases using the claviculohumeral index (29). However, it is not clear whether the patterns of these indices result from variance in the denominator (humeral length), the numerator (clavicle length), or both. Furthermore, claviculohumeral proportions have not seemed to follow ecogeographical patterning in recent humans (9, 11, 30).

Most claviculohumeral studies predate the development of reliable, independent measures of body size to separately scale humeral and clavicular lengths. In addition to the problems of

interpreting variance in ratios, humeral length is a poor proxy for body size within *Homo* [as opposed to across primates (14)]; it varies ecogeographically with respect to body core size in recent and Pleistocene humans (22) and may also reflect regional population history (31). Ideally, stature would be the independent measure of body size for assessing the relative sizes of humeri or clavicles (32). However, estimates of stature would rely on femoral and/or tibia length, and assumptions about body proportions (21, 33), which in turn limit the sufficiently intact fossil sample size. Improvements in body-mass estimation from the femoral head (34, 35) provide an alternative measure of body size, and they are used to assess whether the high claviculohumeral indices of the Neandertals were the products of long clavicles, short humeri, or a combination of the two.

Results

Neandertal Clavicle Length. The maximum clavicle lengths of the Neandertals cluster at or beyond the largest dimensions in the recent human samples, the highest value of which is 178 mm (Fig. 2A). All of the Neandertal values, except that of the small Palomas 96 female (~145 mm), are above the recent human sample means (*SI Appendix*, Tables S1 and S2). There is considerable overlap between the Neandertal and early modern human samples ($P = 0.063$), but they become significantly different if the exceptionally high value for the Upper Paleolithic Sunghir 1 (~194 mm) is ignored ($P = 0.039$).

If clavicle length is compared with humeral length (Fig. 2B), as with the claviculohumeral index, the Neandertals all cluster at the top of the recent human ranges of variation. They are significantly different from the early modern humans ($P < 0.001$), and the only early modern human that overlaps the Neandertal variation is Sunghir 1.

However, it has been documented that Neandertals have humeri that are somewhat foreshortened relative to trunk length

Significance

Neandertal clavicle length, relative to that of modern humans, has long been considered distinctive. It has been invoked with respect to their ecogeographic body proportions, thoracic shape, scapular posture and biomechanics, temporal labyrinthine shape, and ancient DNA, as well as their trait polarities and phylogenetic status. Appropriate scaling of clavicle length to estimated body mass reveals that there is a consistent pattern of clavicle length to body mass proportions across early and recent modern humans, Neandertals, and probably most of the genus *Homo*. It is the relative abbreviation of Neandertal humeri, a reflection of ecogeographical body proportions and population history, that distinguishes the Neandertals from many modern humans. It is therefore inappropriate to use Neandertal clavicular length to assess their biology and evolutionary relationships.

Author contributions: E.T., T.W.H., and B.M.A. designed research; E.T., T.W.H., and B.M.A. performed research; E.T. analyzed data; and E.T., T.W.H., and B.M.A. wrote the paper.

The authors declare no conflict of interest.

¹To whom correspondence should be addressed. E-mail: trinkaus@artsci.wustl.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1402439111/-DCSupplemental.

Fig. 1. Right clavicles and humeri of the La Ferrassie 1 (Ferr1) and Regourdou 1 (Reg1) Neandertals in cranial (clavicles) and anterior (humeri) views. Both clavicles are complete from the sternal to the acromial ends with minimal damage.

(11, 22), and the same pattern applies when their humeral lengths are compared with estimated body masses (Fig. 3A). Their values overlap those of the modern humans, but most of them (all except Regourdou 1) are below the majority of the modern humans. Among the recent humans, there is an ecogeographical pattern, such that higher-latitude samples have relatively shorter humeri, and only the arctic sample is close to the Neandertals. The early modern humans fall among the lower-latitude samples. The two fossil samples remain significantly different ($P < 0.001$), despite low values for the early modern human Fanciulli 6, Mittlere Klaus 1, and Tianyuan 1 specimens.

In this context, there is little difference across the samples in clavicle lengths relative to estimated body masses (Fig. 3B). The Neandertal values are well within recent human ranges of variation, such that the highest Neandertal values, those of Kebara 2 and Regourdou 1 (*SI Appendix, Table S3*), are within 1 SD of the overall recent human mean (standardized residual < 1). The individual Neandertal values are thus similar to the recent human means, if slightly above those of the arctic sample. The Neandertal

relative clavicle lengths cluster among the higher early modern human values (the high outlier there being Sunghir 1), but the two fossil samples are not significantly different ($P = 0.117$).

At the same time, clavicle length does not seem to covary with the other skeletal indicator of body breadth, bi-iliac breadth (Fig. 4). Among recent humans, there is an ecogeographical pattern, with lower clavicle length to bi-iliac breadth proportions [reflecting absolutely wider pelves (36)] occurring among the higher-latitude samples. Matiegka (16) found a similar pattern, in that his low-latitude sample provided higher clavicle length to bi-iliac breadth indices, also reflecting ecogeographical variation in pelvic breadth. The early modern humans are again most similar in this body form to lower-latitude recent humans. The one Neandertal providing both clavicular and pelvic measures, Kebara 2, with its wide pelvis [even for a Neandertal (37, 38)], has a standardized residual (-0.600) most similar to the recent arctic sample (median: -0.505); it is within the early modern human interquartile range (-0.686 to 1.066) and overlaps all four recent human latitudinal sample ranges.

Given asymmetry in clavicular length (39), the same comparisons have also been made for right and left clavicles separately

Fig. 2. Box plots of the right-left average maximum clavicle length (A) and standardized residual of clavicle length versus humeral length (B) for Neandertals (Ne; $n = 7$ and 6), Middle and Upper Paleolithic early modern humans (EM; $n = 30$ and 29), and four latitudinal samples of recent humans (Arc, arctic, $n = 230$ and 230; CT, cold temperate, $n = 371$ and 366; Eq, equatorial, $n = 123$ and 121; WT, warm temperate, $n = 620$ and 598).

Fig. 3. Box plots of the standardized residuals of the right-left average humerus length (A) and clavicle length (B) versus estimated body mass for Neandertals (Ne; $n = 9$ and 6), early modern humans (EM; $n = 34$ and 27), and the four latitudinal samples of recent humans (Arc, arctic, $n = 226$ and 225; CT, cold temperate, $n = 346$ and 347; Eq, equatorial, $n = 105$ and 103; WT, warm temperate, $n = 564$ and 580).

(SI Appendix, Figs. S2–S5). There are only minor differences when the sides are compared separately to humeral lengths (SI Appendix, Fig. S3), estimated body masses (SI Appendix, Fig. S4), and bi-iliac breadths (SI Appendix, Fig. S5).

Sunghir 1 Clavicle Length. In the Late Pleistocene paleontological comparisons, the one outlier is the earlier Upper Paleolithic Sunghir 1. Its absolute clavicle length of ~ 194 mm (SI Appendix, Fig. S6) is 4.40 SDs from the pooled recent human mean (142.0 ± 11.8 mm, $n = 1,344$), 2.74 SDs from the early modern human mean (145.8 ± 17.6 mm, $n = 29$), and well above the next-highest early modern human length (Dolní Věstonice 16: ~ 170.0 mm). Its clavicle to humeral length proportion is 2.29 SDs from the recent human mean ($n = 1,315$), and its clavicle length to body mass proportion is 2.32 SDs from the recent human mean ($n = 1,255$) [2.26 and 3.29 SDs from the respective early modern human means ($n = 28$ and 26)]. There are no known recent or Late Pleistocene humans with clavicles as absolutely long as those of Sunghir 1, and only 10 recent human individuals ($<1\%$) in each

of the scaling comparisons have clavicles as relatively long as those of Sunghir 1.

Early Pleistocene Clavicle Lengths. There are three Early Pleistocene *Homo* clavicles that provide lengths: ATD6-50, OH-48, and KNM-WT 15000 (SI Appendix, Table S1). The late Early Pleistocene ATD6-50 length of 161.5 mm (40) is moderately high but unexceptional for a recent human, being 1.65 SDs from the pooled recent human mean and exceeded by 5.1% of that sample. If its length is scaled against earlier Middle Pleistocene estimated body masses ($n = 11$, from ref. 35), given that the dimensions of its diaphysis and of the associated ATD6 postcrania are similar to those of other Early and Middle Pleistocene archaic *Homo* (40, 41), its relative length is average for a recent human (mean standardized residual of -0.013 ; range: -0.944 – 1.970). The length of the less-complete and unassociated left clavicle from the Early Pleistocene of Olduvai, OH-48 (42, 43), was ~ 150 mm (44), well within Late Pleistocene and recent human variation. The apparently lower claviculohumeral proportions of the early adolescent Early Pleistocene KNM-WT 15000 (14, 45) probably reflect a combination of its equatorial body proportions (46) and immature status (47). However, estimated maximum clavicular length and body mass (refs. 45 and 48 and SI Appendix, Table S1) place it close to the recent human adult mean (standardized residual: -0.064).

Discussion

From these comparisons, it is evident that, relative to body size, the Neandertals did not have long clavicles; they had short humeri. All Neandertal clavicles except those of La Ferrassie 1 have absolute lengths that fall well within early and recent modern human ranges of variation. When scaled against estimated body masses, their relative clavicle lengths are among the majority of the early and recent modern humans, close to the overall recent human mean proportions. Their humeral lengths are most similar to the modern humans with relatively short humeri, especially those individuals from recent high-latitude populations. This pattern holds for both the higher- ($>40^\circ\text{N}$) and lower- ($<40^\circ\text{N}$) latitude Neandertals, from Europe and southwest Asia.

Fig. 4. Box plot of the standardized residuals of the right-left average clavicle length versus bi-iliac breadth for Neandertals (Ne; Kebara 2), early modern humans (EM; $n = 13$), and the four latitudinal samples of recent humans (Arc, arctic, $n = 172$; CT, cold temperate, $n = 301$; Eq, equatorial, $n = 74$; WT, warm temperate, $n = 356$).

In this context, there is little reason to invoke Neandertal clavicular length in the context of other possible contrasts between their biology and those of early and recent modern humans. Neandertal labyrinthine morphology (25, 49) may relate in part to their craniocervical proportions (25, 50), but it is unlikely to reflect particularly broad shoulders. It is possible that both the thoracic and the clavicular dimensions of the Neandertals are related to their body masses. However, the modest level of correlation between clavicular length and body mass in the pooled recent human sample ($r^2 = 0.256$; 0.279 also including the Pleistocene remains) suggests that the interrelationship is not strong. It is therefore not appropriate to make inferences concerning thoracic shape from clavicular length in the absence of sufficiently intact costal remains.

It is also unlikely that Neandertal clavicular lengths are related to the wide pelves of some Neandertals, given both the similarity of the Kebara 2 and modern human claviculopelvic proportions and the apparent variation in Neandertal pelvic breadths (38). Wide pelves may have been generally characteristic of archaic *Homo* (38, 51, 52), and they may have influenced body masses (35). However, it seems unlikely that pelvic breadth per se would have affected clavicular length, given that variance in recent human claviculopelvic proportions seems to be due principally to ecogeographic variation in pelvic breadth (36).

In the broader context of Pleistocene *Homo*, the few earlier Pleistocene specimens providing data indicate clavicle length to body mass proportions similar to those of recent humans (and the Neandertals). It therefore seems that clavicular length relative to body mass was established early in the genus *Homo* and that it remained similar through *Homo* evolution. The one Pleistocene outlier in this respect is the early modern human Sungir 1. Along with other unusual aspects of the Sungir human sample (21), his absolutely and relatively long clavicles may have implications for the population history of his social group, including their levels of isolation and/or inbreeding (53). It is unlikely, as suggested (28), that they relate to questions of Neandertal ancestry.

Conclusion

The relatively long clavicles of the Neandertals have been considered one of their hallmarks for more than a century, driven in part by the long clavicles of the La Ferrassie 1 skeleton. A reassessment of Neandertal clavicle length, appropriately scaled to body mass rather than to humeral length, indicates that their clavicular lengths, and hence shoulder breadths, are similar to those of early and recent modern humans (and probably most of

the genus *Homo*). The modestly longer lengths of some their clavicles most likely relate generally to their high, but not exceptional (21, 54), body masses, a feature they share with many Pleistocene *Homo* relative to recent humans.

Materials and Methods

The comparisons are based on clavicular and humeral lengths, along with estimates of body mass, for Late Pleistocene Middle and Upper Paleolithic humans (*SI Appendix*, Table S1). Only paleontological specimens for which at least two of these measures are available are included, and the Upper Paleolithic sample only includes remains ≥ 15 ka B.P. Similar data are used for diverse late Holocene (≤ 4 ka B.P.) samples ($n = 1,344$); they are pooled into four latitudinal samples at 20° intervals (*SI Appendix*, Table S2), given ecogeographic patterning of body proportions across recent humans (9, 22, 36). Only recent humans that provide clavicular length in addition to humeral length and/or femoral head diameter are included. All modern humans used in this study had fused medial clavicular epiphyses.

Skeletal dimensions were obtained using sliding calipers and osteometric boards; osteological measurements match those defined by Martin (29). Clavicle and humerus lengths were directly measured or estimated for specimens with minor epiphyseal damage (*SI Appendix*, Table S1). Body mass is used as the best indicator of body size for clavicle length scaling (14, 55), in the absence of independent measurements of stature. Body masses are estimated from femoral head diameters (FHDs). Following Auerbach and Ruff (34), for small individuals (FHD < 38 mm) the formula of McHenry (56) is used, for large individuals (FHD > 47 mm) an average of those of Ruff et al. (57) and Grine et al. (58) is used, and for those in between an average of all three formulae is used. Body mass estimates using bi-iliac breadth and estimated stature are available for many of these specimens, and such estimates correlate well with femoral head-based estimates among recent humans (33, 59). However, the dearth of sufficiently complete Late Pleistocene pelves (38) and difficulties in determining appropriate stature formulae for fossils (21) limit their utility here. The clavicle length to bi-iliac proportions of the one Neandertal providing both measures (Kebara 2) is nonetheless compared with early and recent modern humans.

For the bilateral measurements (lengths and FHDs), the right–left average or the more complete side is used, as available. However, given sometimes pronounced clavicular length asymmetry (39, 60), but more modest humeral length and femoral head asymmetry (61), relative clavicular length is also assessed separately for the right and left sides (*SI Appendix*).

Neandertal proportions are assessed against the samples of both early and recent modern humans. The proportions of the samples are compared using the standardized residuals from the reduced major axis lines through the pooled recent human sample (*SI Appendix*, Table S3). The degrees of similarity of the two Late Pleistocene samples are evaluated using nonparametric (Wilcoxon) tests on the standardized residuals. Given the large recent human pooled sample sizes (902–1,344), all of the resultant *P* values across them (using Kruskal–Wallis) are highly significant but biologically meaningless.

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