

Body size, body proportions, and encephalization in a Middle Pleistocene archaic human from northern China

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The unusual discovery of associated cranial and postcranial elements from a single Middle Pleistocene fossil human allows us to calculate body proportions and relative cranial capacity (encephalization quotient) for that individual rather than rely on estimates based on sample means from unassociated specimens. The individual analyzed here (Jinniushan) from northeastern China at 260,000 years ago is the largest female specimen yet known in the human fossil record and has body proportions (body height relative to body breadth and relative limb length) typical of cold-adapted populations elsewhere in the world. Her encephalization quotient of 4.15 is similar to estimates for late Middle Pleistocene humans that are based on mean body size and mean brain size from unassociated specimens.

climatic adaptation | paleoanthropology | Pleistocene

Individually associated cranial and postcranial human fossils from the Middle Pleistocene are extremely rare. Thus, evaluation of temporal changes during this period in important characteristics such as relative brain size (encephalization) have relied on either comparisons of group means for brain and body size (1) or indirect methods of evaluating body size from cranial dimensions, such as orbital size (2, 3). In addition, analyses of geographic or temporal variation during this period in aspects of body shape that are of adaptive and phylogenetic significance, such as body breadth relative to height or limb length (4, 5), have been hampered by a lack of individually associated elements from critical areas of the skeleton, again necessitating more indirect methods for evaluating these characteristics (6).

We present data here from a Middle Pleistocene human fossil skeleton from northeastern China, Jinniushan, dated to $\approx 260,000$ B.P. The specimen includes enough of the postcranial and cranial skeleton to allow estimation of both body mass and brain size in a single individual, as well as body height and body breadth. This is the only such specimen reported to date that falls chronologically between KNM-WT 15000 at ≈ 1.6 million years ago from East Africa (7) and Tabun 1 at $122,000 \pm 16,000$ years B.P. from the Levant (8). In fact, even these two specimens are not ideal for such an analysis: KNM-WT 15000 is a juvenile whose adult body mass must be derived through growth extrapolation (9), and Tabun 1 does not include a completely preserved pelvis, so no direct estimation of body breadth is possible. Thus, the Jinniushan specimen represents a nearly unique opportunity to assess key aspects of morphology in an important period of human evolution, when relative brain size appears to have been increasing rapidly (1, 2) and geographic variation in body shape was becoming pronounced (6, 10) as the geographic range of the human species expanded to cover most of the Old World.

Background and Dates

The Jinniushan specimen was discovered near the town of Yinkou in Liaoning Province in northeastern China (N 40° 34' 40'', E 122° 26' 38'') in an isolated karst prominence in a fissure of a collapsed limestone cave (11, 12). It was excavated in 1984

by a group from the Department of Archaeology at Beijing University directed by L.Z. The human specimen was discovered near the base of 15 m of deposit in the bottom of Layer 7, which also contained the remains of Pleistocene fauna, specifically *Macaca robustus*, *Trogontherium* sp., *Megaloceros pachyosteus*, *Dicerorhinus mercki*, and *Microtus brandtioides* (11, 13). Electron-spin resonance and uranium series dating of animal teeth from Layer 7 suggest a date of $\approx 260,000$ years ago, consistent with the faunal assemblage (13). Later dates had been previously reported for this specimen (14, 15), but they represented an average of dates taken from several stratigraphic levels of the site, including some levels that were higher in the section than the human remains. We are therefore comfortable with a date of $\approx 260,000$ years ago for the level containing the Jinniushan hominid specimen.

The Jinniushan site is high in latitude, north (and east) of Beijing, although the climate at 260,000 years ago may have been somewhat more temperate than today based on the presence of *M. robustus* and *D. mercki* as well as on sedimentological analysis.

The Jinniushan Specimen

The individual skeletal elements of the Jinniushan specimen were all found within an area of < 2 m² and consist of a cranium with most of the maxillary dentition, six vertebrae (one cervical and five thoracic), two left ribs, a complete left patella, a complete left ulna, numerous articulated bones of both hands and both feet, and a complete left os coxae (Fig. 1). There is no duplication of elements, and the joint surfaces of adjacent bones articulate comfortably, so there is no reason to think that more than one individual is represented.

The sex of the specimen is significant to our interpretation here for at least two reasons. First, estimations of stature and body mass are made by using sex-specific regression equations. Second, interpretation of those estimates must always take sex into account.

The most reliable indicators of sex in humans are found on the pelvis, specifically the pubis. Examination of the traits that Phenice found to be best indicators of sex (16) provides the most convincing evidence that the Jinniushan specimen is female. Because of damage to the medial portion of the pubis, it is not possible to evaluate whether there was a ventral arc present. However, a subpubic concavity is present, and the medial aspect of the ischio-pubic ramus is ridged rather than flat. According to Phenice, these latter two features would classify the Jinniushan specimen as female. The sciatic notch, which is generally wider in females than in males in all human populations, is intermediate in breadth. Compared with the Kebara 2 Neandertal specimen (a male),

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Abbreviation: EQ, encephalization quotient.

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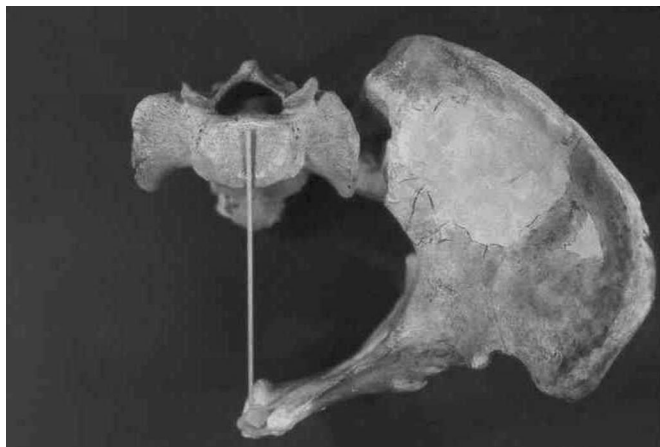


Fig. 2. The cast of the Jinniushan os coxae in position for measurement of total pelvic breadth (biiliac breadth) as described in the text. The sacrum is an unassociated modern human sacrum that allowed us to visually determine the position of the midline. Maximum perpendicular distance from the lateral edge of the iliac crest to the midline was taken and then doubled to estimate biiliac breadth. Note that, because of parallax and foreshortening in the photograph, exact dimensions cannot be measured on the figure.

this range by only a modest amount, to 325–363 mm. We consider these extreme values to be unlikely based on the overall morphology of the os coxae and the extremely narrow or wide sacra implied by them; however, they are used to bracket our best estimate of biiliac breadth in subsequent analyses of body shape and also body mass estimates that include this dimension.

Relative Limb Length

It has been shown that, like other geographically widespread mammalian species, humans conform to ecogeographic rules that relate body shape to climate so that surface area to mass is low in populations that come from cold climates and higher in populations that come from warm climates (10, 27–29). This pattern is manifested in both relative limb length (Allen's rule) and body breadth. In modern humans, populations from cold regions have relatively shorter limbs and wider bodies than those from warm regions. Fig. 3 shows the relationship between biiliac breadth and ulna length in equatorially adapted East Africans and Arctic-dwelling Inupiat and Aleuts. As expected, cold-adapted modern populations have relatively shorter ulnas for their trunk diameters than warm-adapted populations. Pre-Holocene humans from higher and lower latitudes follow the same pattern as modern humans. Six fossil individuals whose pelvic breadth and ulna length can be measured or estimated (see ref. 10 for details), including Jinniushan, are also plotted in Fig. 3. The four individuals from higher latitudes (the La Chapelle-aux-Saints 1 and Kebara 2 Neandertals and the Middle Pleistocene Atapuerca and Jinniushan specimens) all have very wide pelvic breadths relative to forearm lengths, near or beyond the upper limits for modern high-latitude humans. The Jinniushan specimen is particularly extreme, which may in part be due to its being female, because females have relatively shorter forearms than males (10, 29). The two pre-Holocene African specimens (WT 15000 and Sahaba 16) both have narrow bodies relative to ulna length, as predicted.

Body Mass

Body mass was estimated in two different ways: using a combination of estimated stature and biiliac breadth and using estimated femoral head diameter. The first approach can be termed “morphometric” (4), and the second can be termed “mechanical” (30). The stature/biiliac method is based on a geographi-

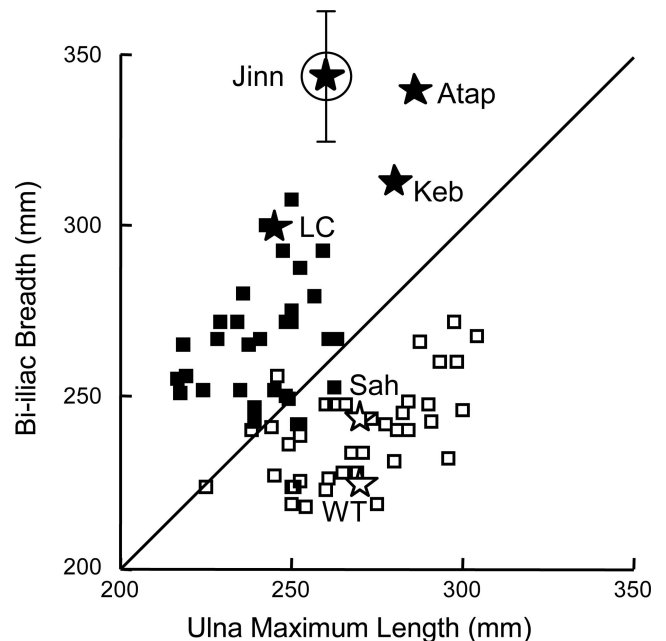


Fig. 3. The relationship between ulna length and biiliac breadth in modern humans. Open symbols represent modern East Africans, and filled symbols represent modern Inupiat/Aleuts. Open stars represent KNM-WT 15000 and Sahaba 16, and filled stars represent Atapuerca, Kebara, La Chapelle-aux-Saints 1, and Jinniushan (circled). The vertical bar shows the 95% confidence interval of the estimate of Jinniushan's biiliac breadth.

cally diverse sample of living humans (4) and has been tested and verified on a number of different living samples of known body mass, including athletic and “normal” mid-lower-latitude humans (31) and high-latitude populations with wide bodies (22). As recently modified (22), the regression equation for females is body mass = $0.504 \times \text{stature} + 1.804 \times \text{biiliac breadth} - 72.6$ ($r = 0.82$, $\text{SEE} = 4.0$) (with conversion of skeletal to living biiliac breadth as described in ref. 1). Using the estimates derived above for Jinniushan stature and biiliac breadth in this equation yields an estimated body mass for this specimen of 79.6 kg.

Our second method of estimation of body mass was from the diameter of the femoral head, a joint through which body weight must pass during locomotion and stance. No femur is preserved for the Jinniushan specimen, but we estimated femoral head diameter from the dimensions of the other side of the hip joint, namely acetabular height, using a regression equation based on 39 individuals from a recent archaeological sample: femoral head diameter = $0.9877 \times \text{acetabular height} - 8.39$ ($r = 0.95$, $\text{SEE} = 0.3$) (E. Trinkaus, personal communication). Acetabular height for the Jinniushan specimen is 59.3 mm, giving an estimated femoral head diameter of 50.2 mm, with a 95% confidence interval of 49.6–50.8 mm. We then used this measurement in two different published regression equations based on appropriate medium- to large-bodied modern populations (32, 33) (see ref. 30 for justification and further details) and obtained body masses of 77.4 and 78.0 kg, respectively (range using 95% confidence intervals for femoral head diameter, 76.0–79.3 kg). The average of these two estimates is 77.6 kg, which is within 2 kg, or $\approx 2.5\%$, of our best estimate from stature and biiliac breadth of 79.6 kg (see above). In what follows we have used the mean of these two estimates, 78.6 kg, as the estimated body weight for the Jinniushan specimen. (Note that the closeness of the two estimates also indirectly supports our reconstructed value for biiliac breadth.)

As shown in Table 1, the estimated body mass for Jinniushan is quite large compared with modern population means or other

Table 1. Body masses and encephalization quotients for modern and Pleistocene *Homo*

Sample	Temporal period, B.P.	Body mass, kg		EQ of pooled sex	
		Pooled sex, mean \pm SD (n)	Females, mean \pm SD (n)	Associated specimens, mean \pm SD (n)	Sample means
Modern, all	—	58.2 \pm 7.1* (51)	54.7 \pm 5.7* (23)	—	5.288
Modern, higher latitude	—	61.2 \pm 6.7* (24)	57.2 \pm 5.7* (13)	5.349 \pm 0.555 [†] (29)	—
Late Upper Palaeolithic	10–21,000	62.9 \pm 7.6 (71)	57.0 \pm 5.9 (23)	5.479 \pm 0.352 (18)	5.406
Early Upper Palaeolithic	21–35,000	66.6 \pm 7.5 (33)	59.6 \pm 6.4 (7)	5.467 \pm 0.449 (10)	5.352
Late archaic <i>Homo</i> sp.	36–75,000	76.0 \pm 5.8 (17)	67.2 \pm 0.4 (2)	4.984 \pm 0.467 (8)	4.781
Skhul-Qafzeh	90,000	66.6 \pm 7.0 (10)	58.4 \pm 4.4 (3)	5.369 \pm 0.166 (4)	5.293
Early Late Pleistocene	100–150,000	67.7 \pm 7.6 (10)	65.4 \pm 5.5 (6)	4.682 (1)	4.732
Late Middle Pleistocene	200–300,000	65.6 \pm 12.3 (6)	54.1 (1)	—	4.198
Jinniushan	260,000	—	78.6	4.150	—
Middle Middle Pleistocene	400–550,000	71.2 \pm 11.3 (11)	64.6 \pm 3.3 (2)	—	3.770
Late Early to early Middle Pleistocene	600–1,150,000	58.0 \pm 7.4 (3)	66.6 (1)	—	3.400
Early Pleistocene	1,200–1,800,000	61.8 \pm 8.9 (5)	—	3.064 (1)	3.458

Data are from ref. 1, except for Jinniushan and additional body masses for Atapuerca specimens (Atapuerca specimens also moved to middle Middle Pleistocene period; see text). Body mass for Atapuerca Pelvis 1 was derived as the mean of the mean estimate given in ref. 35 based on estimated stature and iliac breadth (94.2 kg) and that derived from acetabular breadth by using the same technique described in the text for Jinniushan (78.7 kg), i.e., 86.4 kg. Body masses for five other Atapuerca specimens are based on published acetabular breadths (35): AT-800, 75.1 kg; AT-835, 77.5 kg; AT-2350, 75.1 kg; Coxal I, 66.9 kg; AT-1004, 62.2 kg. The first four specimens were judged to be males, and the second two were judged to be females (35).

*Means and SDs of sex/population means, not individuals (see ref. 4).

[†]Pecos Pueblo (see ref. 1).

Pleistocene *Homo* specimens. Data in Table 1 were previously derived (1) using similar methods, except for six new body mass estimates derived for the late Middle Pleistocene Sima de los Huesos Atapuerca specimens (see Table 1). In addition, based on new dates for this site (34), Atapuerca specimens have been placed into the earlier, middle Middle Pleistocene sample, slightly increasing the average body size for this temporal period. Several male Pleistocene specimens, including “Pelvis 1” from Atapuerca (35), significantly exceed Jinniushan in estimated body mass. However, Jinniushan is the largest female yet reported in the pre-Holocene record; the next largest female in our sample is Grotte du Prince, from the early Late Pleistocene (100,000 years B.P.), with an estimated body mass of 74.0 kg. Body size in *Homo* appears to peak in the Middle Pleistocene with specimens such as Boxgrove and the Atapuerca sample (1, 10), and Jinniushan is consistent with this pattern. Her large estimated body mass is also again consistent with ecogeographic principles (Bergmann’s rule), i.e., a tendency among geographically widespread species to increase in body size in higher latitudes, probably as an adaptation to decrease surface area to body mass in colder climates (4, 28). It is also consistent with the observation that Middle Pleistocene humans, who were presumably less culturally buffered from the environment by such technological adaptations as insulating clothing and fire, may have had a steeper clinal distribution of body proportions than more recent humans (6).

Encephalization

Finally, because the Jinniushan specimen preserves both postcranial remains and a fairly complete skull, we have the unusual, if not unique, opportunity to examine the relationship between body size and cranial capacity in this Middle Pleistocene individual. Most estimates of relative brain size have been carried out by using brain size estimates and body size estimates from different specimens or have used body size estimates derived from cranial dimensions, which are less accurate and subject to possible circular reasoning. Jinniushan provides an opportunity

to compare an individually derived encephalization quotient (EQ) with previous estimates based on sample means for brain and body size.

To determine EQ in Jinniushan, we used 1,330 cm³, the midpoint of the various estimates of its cranial capacity. We then calculated brain mass following ref. 1, whose equation based on data from 27 primate species is brain mass = 1.147 \times cranial capacity^{0.976} and found a brain mass for Jinniushan of 1,284 g. Using the estimated body mass of 78.6 kg and the equation published by Martin (21) for mammals, EQ = brain mass/11.22 \times body mass^{0.76}, we determined an EQ of 4.150 for Jinniushan. This is remarkably close to an estimate based on sample means for body mass and brain mass for the late Middle Pleistocene: 4.198 (Table 1). The latter is derived from the mean brain mass of 13 specimens (1,132 cm³; from ref. 1 but not including the three Atapuerca crania or Jinniushan) and the mean body mass of six specimens (1). The mean estimated EQ for the preceding middle Middle Pleistocene, based on sample mean data, is 3.770, a slight reduction from our earlier estimates (1) because of the inclusion of the Atapuerca specimens. These results further document the rapid increase in encephalization among Middle Pleistocene *Homo* (1).

Summary

Jinniushan’s geographic location in the far north of China suggests a cold-adapted population. We see this reflected in her large body size, wide trunk, and relatively short limb length. She thus adds to the growing body of evidence for ecogeographic clines in body size and shape among Early and Middle as well as Late Pleistocene *Homo* (4, 9, 10, 29). Her brain size relative to body size is very similar to that predicted from sample mean data for the late Middle Pleistocene and provides an important data point in verifying the hypothesized increase in encephalization characteristic of this time period.

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