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Homo floresiensis and the evolution of the hominin shoulder

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Abstract

The holotype of *Homo floresiensis*, diminutive hominins with tiny brains living until 12,000 years ago on the island of Flores, is a partial skeleton (LB1) that includes a partial clavicle (LB1/5) and a nearly complete right humerus (LB1/50). Although the humerus appears fairly modern in most regards, it is remarkable in displaying only 110° of humeral torsion, well below modern human average values. Assuming a modern human shoulder configuration, such a low degree of humeral torsion would result in a lateral set to the elbow. Such an elbow joint would function more nearly in a frontal than in a sagittal plane, and this is certainly not what anyone would have predicted for a tool-making Pleistocene hominin. We argue that *Homo floresiensis* probably did not have a modern human shoulder configuration: the clavicle was relatively short, and we suggest that the scapula was more protracted, resulting in a glenoid fossa that faced anteriorly rather than laterally. A posteriorly directed humeral head was therefore appropriate for maintaining a normally functioning elbow joint. Similar morphology in the *Homo erectus* Nariokotome boy (KNM-WT 15000) suggests that this shoulder configuration may represent a transitional stage in pectoral girdle evolution in the human lineage.

Key words: Humeral torsion; Pectoral girdle; *Homo erectus*; *Homo floresiensis*; Flores hominins

Introduction

The 2004 announcement of the discovery of diminutive hominins with tiny brains living until 12,000 years ago on the island of Flores stunned the anthropological community (Brown et al., 2004). Initial claims that the holotype of *Homo floresiensis*, a partial skeleton (LB1), was an isolated pathological individual have been countered by the recovery of the remains from another eight individuals, some of even smaller stature that LB1 (Morwood et al., 2005), although skeptics remain (Weber et al., 2005; Jacob et al., 2006; Martin et al., 2006a, 2006b; Richards, 2006). Included in the LB1 holotype is a right humerus (LB1/50 – Fig. 1A) that is complete except for postmortem damage to both tubercles and some of the articular surface at the proximal end, and a missing lateral epicondyle and part of the capitulum at the distal end. The humerus is short (243 mm) and robust (midshaft diameters: ML 16.35 mm, AP 17.44 mm), but by far the most remarkable feature is the estimate of only 110° of humeral torsion (Morwood et al., 2005).

Humeral torsion refers to the orientation of the humeral head relative to the mediolateral axis of the distal humerus (most commonly, the distal articular surface). The presumed primitive condition for mammals is for the humeral head to be directed posteriorly so as to articulate with the ventral facing glenoid fossa of a scapula positioned on the lateral side of the rib cage. Humeral heads that are directed more medially are said to have a greater degree of humeral torsion.

Alteration of humeral torsion is most closely associated with the change from a dorsoventrally deep to a mediolaterally

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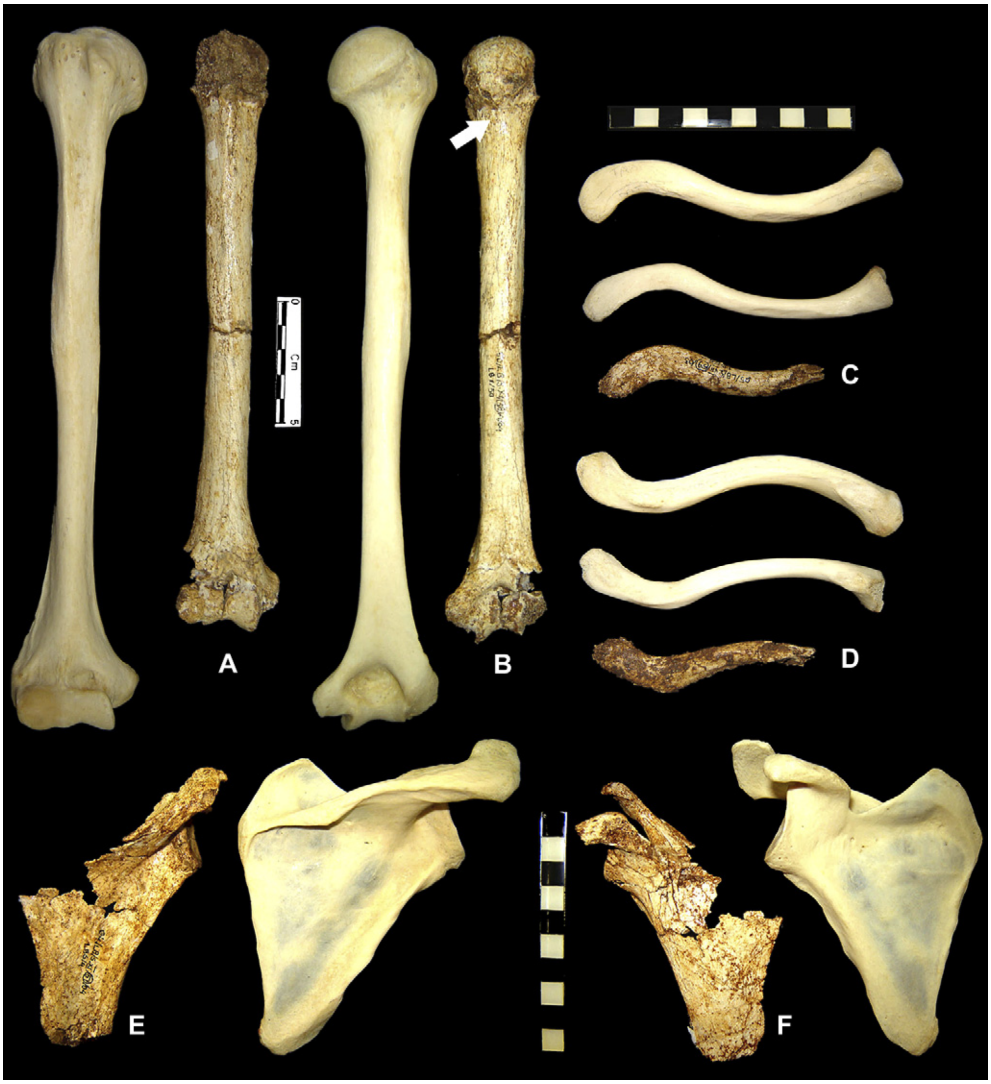

Fig. 1. *Homo floresiensis* pectoral girdle shoulder material. A. Anterior view of LB1/50 right humerus compared to modern Euro-American humerus. Both tubercles are missing due to postmortem damage. B. Posterior views of LB1/50 and modern humerus. White arrow indicates position of posterior buttress for the humeral head. C. Superior view of LB1/5 right clavicle compared to two modern Euro-American clavicles. LB1/5 is missing its medial end. D. Inferior views of LB1/5 and modern clavicles. Some matrix still covers the fossil. E. Dorsal view of LB6/4 right scapula compared to a modern Euro-American scapula. F. Ventral view of LB6/4 and modern scapula.

broad thorax in the course of hominoid evolution, and the concomitant dorsal repositioning of the scapula so the glenoid fossa faces more laterally than ventrally, and articulates with a medially directed humeral head. It should be emphasized, however, that change in the position and orientation of the glenoid only requires alteration of humeral torsion if it is necessary for the elbow to continue to operate in a sagittal plane (Inman et al., 1944). Hylobatids, for example, have dorsally placed scapulae and laterally facing glenoid fossae, but only limited humeral torsion (Evans and Krahl, 1945; Le Gros Clark and Thomas, 1951; Zapfe, 1960; Larson, 1988, 1996). As a consequence, their elbows have a lateral set; at rest the cubital fossa of their elbow faces more laterally than anteriorly (Larson, 1988). This morphology dramatically increases the range of external rotation at the shoulder and is advantageous during arm-swinging, but is purchased at the price of a reduced range of internal humeral rotation, hence the lateral set to the elbow. Such a non-sagittally operating elbow joint would seem disadvantageous for a tool-making hominin, which *H. floresiensis* clearly was, judging from the abundance of tools that have been recovered on Flores (Morwood, et al., 2004; Brumm et al., 2006; Moore and Brumm, 2007). Indeed, modern humans have high levels of humeral torsion (Fig. 4).

The high degree of humeral torsion in modern humans has commonly been viewed as a shared derived feature of hominoids (Martin, 1986; Harrison, 1987). However, Larson (1996) estimated only modest levels of torsion in a set of early hominin humeri ranging from 111° to 130°, and concluded that the high torsion of modern humans is a more recently acquired characteristic. In fact, among hominoids, only African apes display as high a degree of torsion as modern humans. Larson (1988, 1996) argues that the marked degree of torsion in African apes is related to the necessity of a sagittally oriented elbow joint during quadrupedal postures, and the

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similarity in degree of humeral torsion between African apes and modern humans is due to convergence. However, if one views the close phylogenetic relationship between humans and chimpanzees as implying a knuckle-walking ancestry for early hominins (e.g, Richmond and Strait, 2000), the picture is somewhat more complicated. A knuckle-walking common ancestor would likely have had high torsion due to the functional relationship between humeral torsion and quadrupedal posture, which was then lost in early hominins but regained in later *Homo*. In either case, the similar high torsion in *Pan* and modern humans would be due to convergence.

When exactly a modern human shoulder configuration first appeared is unknown at present. In the absence of evidence to the contrary, the presumption has been that the hominin shoulder was essentially modern by at least the time of *Homo erectus*, possibly even as early as the appearance of *Homo* (e.g., Bramble and Lieberman, 2004). Although the ancestry of *H. floresiensis* is currently unknown, one interpretation is that it is derived from an early *H. erectus* ancestor, in which case its minimal degree of humeral torsion raises questions as to the actual course of hominin shoulder evolution during the early Pleistocene. In order to try and answer these questions, we have undertaken a functional analysis of the shoulder region of *H. floresiensis* and of the Nariokotome boy (KNM-WT 15000), the only currently known *H. erectus* skeleton (Leakey and Walker, 1989, 1993).

Materials and methods

The original fossil shoulder material from *H. floresiensis* consisting of a right humerus (LB1/50 – Fig. 1A,B) and an incomplete clavicle (LB1/5 – Fig. 1C,D) from the holotype skeleton, and a nearly complete right scapula of a different individual (LB6/4[1] – Fig. 1E,F), were examined at the Indonesian Centre for Archeology in Jakarta, Indonesia. Casts of the Nariokotome right clavicle (KNM-WT 15000 D), scapula (KNM-WT 15000 E), and humerus (KNM-WT 15000 F) were examined for this analysis.

Comparative data on clavicular and humeral length were collected for samples of gibbons, orangutans, gorillas, and chimpanzees, and for Euro-American humans, African Pygmies, and Andaman Islanders. Clavicular and humeral length data for African Nilotic and Kikuyu peoples were given to us by Chris Ruff, and Fred Grine and Louise Jacqui Friedling collected clavicular and humeral data for us on a sample of African Khoe-San. Comparative data on humeral torsion in early hominins are from Larson (1996). Torsion data for other human populations are taken from the literature (see below).

Since the LB1/5 clavicle is missing its medial end, we undertook an analysis of samples of modern human clavicles to determine whether it was possible to reconstruct total clavicular length from the preserved portion of LB1/5. We measured total clavicular length and length from the lateral end to the point of inflection of the medial curvature (incomplete clavicular length – Fig. 2) on a sample of 32 clavicles of average stature Euro-Americans, and 24 clavicles of small stature Andaman Islanders. The mean ratio of incomplete to complete clavicular length was derived, and dividing incomplete clavicular length by this ratio yielded a predicted clavicular length for the comparative samples and for LB1/5. Pearson correlation coefficients were found between predicted and actual clavicular length for the two modern samples, and mean absolute prediction error was calculated as (observed clavicular length – predicted clavicular length)/predicted clavicular length.

Clavicular length comparisons were made by regressing clavicular length against humeral length, and by comparing clavicular to humeral length ratios, which are commonly reported in the literature (e.g., Schultz, 1930, 1937; McCown and Keith, 1939; Martin and Saller, 1959; Marquer, 1972). Humeral length was chosen to establish relative clavicular length since Jungers (1994) has shown that humeral length has a conservative scaling relationship to body size with relative humeral length being virtually identical in different sized human populations as well as in African apes. Although initial reports suggested that LB1 had long upper limbs (Brown et al., 2004), a reanalysis of limb proportions by Jungers et al. (2006b) indicates that the humerus and radius of *H. floresiensis* are actually relatively short, although they approach those of small humans. It is the extremely short lower limbs of the Flores hominins that result in high intermembral or humerofemoral indices, thereby giving the false impression of long upper limbs. Therefore, humeral length is likely to give a very conservative estimate of *relative* clavicular length in LB1. The KMN-WT 15000F humerus is missing its proximal epiphysis, but Walker and Leakey (1993) estimate that its complete length would have been 319 mm, and that value was used here.

Humeral torsion refers to the orientation of the humeral head relative to the distal end of the humerus. The reference axis most commonly used is the axis of the distal articular surface (Evans and Krahl, 1945; Krahl and Evans, 1945; Krahl, 1947; Le Gros Clark and Thomas, 1951; Martin and Saller,

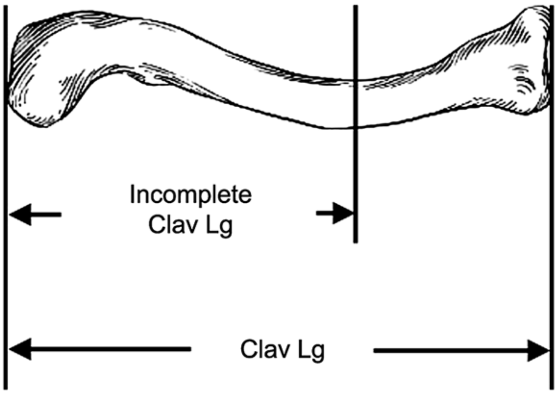

Fig. 2. Superior view of a human right clavicle. Total clavicular length was measured on an osteometric board as maximum length. Incomplete clavicular length was determined by aligning the most anterior points of the lateral end and the anterior surface of the medial curvature, and measuring the distance between the lateral end and the point of inflection of the medial curvature.

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[1] Associated with the LB6/4 scapula are a partial ulna (LB6/3), a complete radius (LB6/2), and a mandible (LB6/1).

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1959; Zapfe, 1960; Larson, 1988, 1996) in recognition of the fact that humeral torsion and elbow orientation are linked (Inman et al., 1944), and is the convention used for the measurement of torsion in this study (Fig. 3). However, some authors, such as van Dongen (1963) and Edelson (1999, 2000), use the anterior surface of the distal humerus as their reference axis, which will produce torsion angles that are somewhat lower than those derived using the distal articular axis (Fig. 3). There is also variation in the literature as to how humeral head position is expressed. In the anthropological literature, the presumed primitive condition for mammals with the humeral head facing posteriorly is considered to be the default position, and deviation of the humeral head from this orientation to facing more medially is referred to as increased torsion. If expressed directly relative to the axis of the humeral distal articular surface, the default value for humeral torsion is 90° (e.g., Martin, 1933; Le Gros Clark and Thomas, 1951; Martin and Saller, 1959; Zapfe, 1960; Larson, 1988, 1996). However, some authors (e.g., Evans and Krahl, 1945; Krahl and Evans, 1945; Krahl, 1947) refer to this default position as 0° of torsion. The former measuring convention is used in this study (Fig. 3). In the human clinical and sports literature (e.g., Kronberg et al., 1990; Pieper, 1998; Edelson, 1999; Crockett et al., 2002), humeral head orientation is referred to as humeral retroversion with a humeral head facing directly inward viewed as the default condition (0° retroversion), and increasing posterior deviation reported as greater retroversion. For those familiar with this literature, it is important to appreciate that retroversion is the inverse of torsion as used here: large retroversion angles correspond to small torsion angles, and vice versa (Fig. 3). In addition to how humeral head position is expressed, retroversion angles are often derived using different measuring conventions than traditional humeral torsion studies. For example, the retroversion angles reported by Kronberg et al. (1990) are based on radiographs of living subjects rather than skeletal material, and a line connecting the epicondyles was used as the distal axis, while head position was determined by a line across the anterior and posterior edges of the humeral articular surface at the humeral neck. Therefore, direct comparisons of humeral torsion and retroversion angles can be problematic.

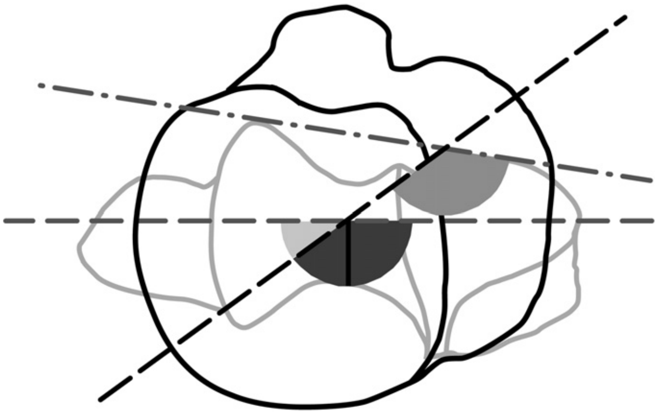

Fig. 3. Measurement of humeral torsion. In this schematic view of a right humerus, the humeral head (viewed from above with anterior toward the top of the page and medial toward the left) is transparent so the distal end of the humerus is visible. Humeral torsion is most commonly quantified as the angle between the axis of the humeral head (black dashed line) and the axis of the distal articular surface (gray dashed line) (darkest gray angle). The presumed primitive condition for mammals is for the humeral head to face posteriorly, (i.e., have the axis of the solid black line). This default condition is commonly assigned the value of 90° in order to express torsion as deviation directly from the reference axis, and is the practice used in the present study. However, some researchers prefer to give the default condition the value of 0°, in which case, torsion is expressed as only the acute portion of the darkest gray angle. The lightest shaded angle is the humeral retroversion angle commonly used in human clinical and sport related studies, and is the supplement of the humeral torsion angle. Different measurement protocols sometimes include use of different reference axes, which can affect reported torsion values. For example, a reference axis across the anterior face of the distal humeral articular surface (e.g., van Dongen, 1963; Edelson, 1999, 2000) (gray dot-dash line) can produce somewhat lower torsion angles (intermediate gray angle).

In modern humans there is recognized variation in humeral torsion between populations, between males and females within a population, and between right and left sides of an individual (Krahl and Evans, 1945; Edelson, 1999). Much of this variation is thought to be due to differences in habitual activities; (i.e., right vs. left arms, behavioral differences related to gender, differences between populations related to methods of resource procurement, etc.) (see Rhodes, 2006). In addition, Churchill (1994, 1996) has shown that variation in thoracic shape can influence humeral torsion, with the increased chest size as observed in cold-adapted populations (e.g., Neanderthals) corresponding to decreased torsion angles. Torsion increases with age and most of that increase occurs during the prenatal and childhood growth periods (Krahl, 1947). By adolescence the rate of change drops dramatically, and Krahl and Evans (1945) report no correlation between age and torsion or between humeral length and torsion among adults. Finally, different researchers using slightly different measuring techniques can also contribute to variability in reported torsion values (see Fig. 3).

Since the most proximal end of the LB1/50 humerus is damaged, it is possible that the published measurement of 110° of humeral torsion is inaccurate. In addition, the KNM-WT 15000F humerus is missing its proximal epiphysis and to date no attempt has been made to estimate its degree of torsion. We therefore measured torsion in KNM-WT 15000F and re-measured torsion in LB1/50 using two alternate landmarks for the orientation of the humeral head. One was a bisector of the intertubercular groove, which Larson (1996) has shown can be used as an indicator of humeral head position in other fossil humeri. The other was the position of a posterior buttress for the humeral head, which is aligned with the humeral head axis (Fig. 1).

The angle between the glenoid fossa and the ventral bar, a bony ridge near the axillary border on the costal surface of the scapula (Stern and Susman, 1983), and the angle between the base of the scapular spine and the axillary border (Larson, 1995) were measured on the LB6/4 and KNM-WT15000E scapulae. These characters have been shown to be distinctive in modern humans.

Statistical analyses were done using SPSS 11.0 for Windows.

Results

Using the bisector of the intertubercular groove as an alternative indicator of humeral head position (Larson, 1996) yielded torsion values of 119° for LB1/50 and 111.5° for KNM-WT 15000F. Torsion estimated from the position of the posterior buttress for the humeral head was 121° for LB1/50, and again 111.5° for KNM-WT 15000F. The average of the two new torsion measurements for LB1 is 120°, and while it is slightly higher that the published estimate (110°, Morwood et al., 2005), it confirms that humeral torsion in *H. floresiensis* was very low. Since 110° and 120° represent two independent attempts to measure torsion on a damaged humerus, it is not clear which is more correct and their average (115°) will be used to represent torsion in LB1/50. Both methods of estimating torsion in KNM-WT 15000F yielded the same value, but since the Nariokotome boy is believed to have died in his early adolescence (Smith, 1993; Dean et al., 2001), it is possible that his adult torsion value would have been somewhat higher. According to the human growth trajectory chart presented by Krahl (1947), humeral torsion in newborns is already 88% of the adult mean value, and torsion increase ceases at about 20 years of age. By the age of 10, an average human child displays approximately 92% of the average of adult torsion, and by 15 years of age the humerus would have reached about 98% of average adult torsion. Therefore, one could estimate an increase in humeral torsion of less than 8% had the Nariokotome boy reached maturity, which would have resulted in a maximum adult value of only about 120°, still well below modern human mean values (see Fig. 4).

Mean humeral torsion values for several modern human populations and fossil hominins are presented in Fig. 4. In order to compare LB1 and KNM-WT 15000F to as broad a comparative sample as possible, much of this data has been taken from the literature. Unfortunately, literature reports often include only mean values, or at most the mean and standard deviation. Therefore, to better reflect population variation, we have computed 95% confidence intervals (CIs) for each sample. For cases in which only the mean value was available (samples marked with an asterisk [*] in Fig. 4), we used the average standard deviation from the other human samples to compute an approximate CI. Although there is variation in mean values among the human samples, they hover near 140° (mean of means = 142.4°, sd = 6.95). LB1 and KNM-WT15000F fall outside the 95% CIs of most of the human

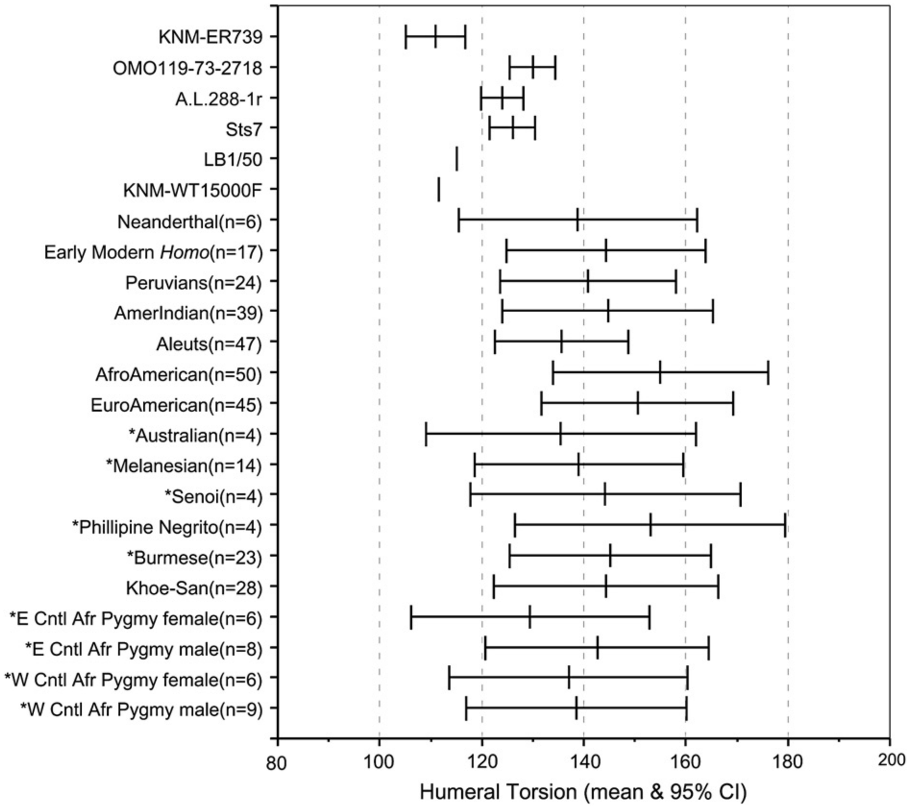

Fig. 4. Mean humeral torsion angles plus 95% confidence intervals for samples (CIs) from literature sources for different modern human and fossil hominin groups, and torsion measurements for individual fossils. Torsion estimates for early hominins are derived from regression analysis, and error bars represent possible ranges of torsion values based on mean absolute percent prediction errors (from Larson, 1996). Torsion data for Neanderthals (Lezetxiki 1, Régourdou 1, Neanderthal 1, La Chapelle 1, Tabūn C1, Kebara 2) and Early Modern *Homo* (Skhūl IV, Qafzeh 9, and humeri from 15 Early Upper Paleolithic sites) are from Churchill (1994), as are comparative data from Peruvians, Amerindians, Aleuts, Afro-Americans, and Euro-Americans. The torsion data for African pygmies are from Marquer (1972), and for Melanesians, Burmese, Philippine "Negritos", and Senoi (native people from Malay peninsula) are from Martin and Saller (1959). 95% CIs have been calculated using the reported standard deviation and sample size. An asterisk (*) indicates populations for which only the mean torsion value has been reported, and in those cases, the average standard deviation of the other modern populations was used to construct an approximate CI.

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samples, but they do overlap CIs of a few including African Pygmies.

The average value of the ratio of incomplete clavicular length to observed clavicular length was 0.65. Figure 5 displays a scatter plot of predicted vs. observed clavicular length for the two comparative samples of modern clavicles. The correlation between predicted and observed clavicular length for the sample of Euro-Americans was 0.78 ($p < 0.001$) and for the Andaman Islanders was 0.84 ($p < 0.001$). The average absolute predication error was 3.91%. The predicted total length for LB1/5 was 91.05 mm, with a range of 87.5 to 94.6 mm based on the prediction error value.

Figure 6 displays a scatter plot of mean clavicular length relative to mean humeral length in a variety of primates, modern humans (including populations of short and tall average statures), and fossil hominins. Regression analysis of the comparative primate data from Mivart (1868) reveals a linear relationship (r = 0.97) passing through the origin, which indicates an isometric scaling relationship between clavicular and humeral length (Mosimann, 1970; Jungers et al., 1995). To test how representative this relationship is, additional primate data taken from Schultz (1930) as well as ape data collected for the present study were added to the regression analysis, and the relationship remained isometric. The close adherence of most nonhuman taxa to this scaling relationship suggests that it may represent the primitive condition for primates. Among the outliers are baboons and *Ateles*, both of which fall well below the line. We suspect this could be due to reduced clavicular length in the former and elongation of the humerus in the latter, but we have not verified this speculation. However, even though the lesser apes also have elongated forelimbs, they appear to follow the isometric scaling relationship quite closely. Among great apes, chimpanzees fall slightly above the line while both bonobos and gorillas lie somewhat below. Orangutans, however, are highly divergent above the line indicating that they have very long clavicles relative to their humeri. All of the means for the modern human populations, including those of short stature, are also above the line, although the mean for native Australians falls only slightly above. Similarly, the means for samples of early modern *Homo* and Neanderthals are above the line. If the common isometric scaling relationship seen across nonhuman primates does indeed represent the primitive condition, then modern humans and recent fossil hominins all exhibit the derived condition of relative clavicular elongation. LB1 and KNM-WT 15000, however, fall very close to the line suggesting that they retain the putative primitive condition. As mentioned previously, contrary to the initial report by Brown et al. (2004), LB1 does not have long upper limbs but rather extremely short lowers limbs. The humerus of LB1 is actually relatively short, although it approaches that of small humans (Jungers et al., 2006b). Therefore, low relative clavicular length in LB1 is not due to an elongated humerus.

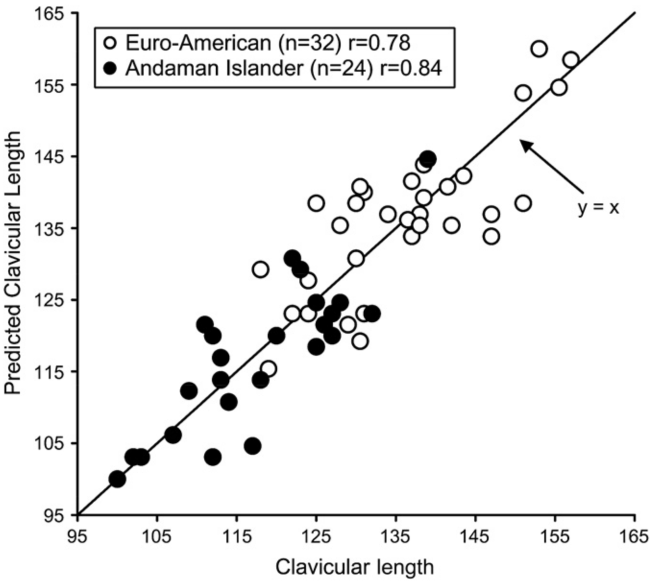

Fig. 5. Scatter plot of predicted clavicular length against measured clavicular length. Predicted length was calculated by dividing incomplete clavicular length (see Fig. 2) by the mean ratio of incomplete length/complete clavicular length (0.65) derived from a sample of average stature Euro-American clavicles (open circles), and small stature Andaman Islander clavicles (closed circles). Line represents equality between measured and predicted values. Absolute prediction error was 3.91%.

There is of course variation in relative clavicular length within populations, and Fig. 7 presents box and whisker plots of claviculohumeral ratios for the groups in Fig. 6 (except native Australians for which we do not have original data). Although there are differences between primate taxa, the general dissimilarity between nonhuman primates and hominins is readily apparent. With the exception of orangutans, all nonhuman primate groups have relatively short clavicles, although chimpanzees are surprisingly distinct from bonobos and gorillas. Modern humans and later fossil hominins all display relatively long clavicles, and variation in claviculohumeral ratios appears to be unrelated to overall stature. Among the modern human samples, the Khoe-San, who are of small to average stature, have the longest clavicles relative to humeral length, and the small-statured Andaman Islanders have the shortest. Both LB1 and KMN-WT 15000 are clearly more similar to the nonhuman primates. LB1 falls outside the ranges of nearly all of the modern human samples, and KMN-WT 15000 is at the lower fringes of modern humans. However, relative clavicular length for the Nariokotome boy is not as extreme as that of LB1, and the fact that both clavicular and humeral length change with age raises the question as to whether he would have had a more human-like claviculohumeral ratio as an adult. Jungers and Hartman (1988) report that humeral length displays isometric growth allometry in great apes and slight positive growth allometry in humans, while clavicular length displays negative growth allometry in all taxa. Therefore, no matter whether KNM-WT 15000 followed a great ape or human growth trajectory, if the Nariokotome boy had reached adulthood these scaling patterns would have resulted in an even shorter relative clavicular length, and the 40.9% claviculohumeral ratio reported in Fig. 7 is likely to be an *overestimate*.

However, low humeral torsion and relatively short clavicles do not necessarily imply that early *H. erectus* and

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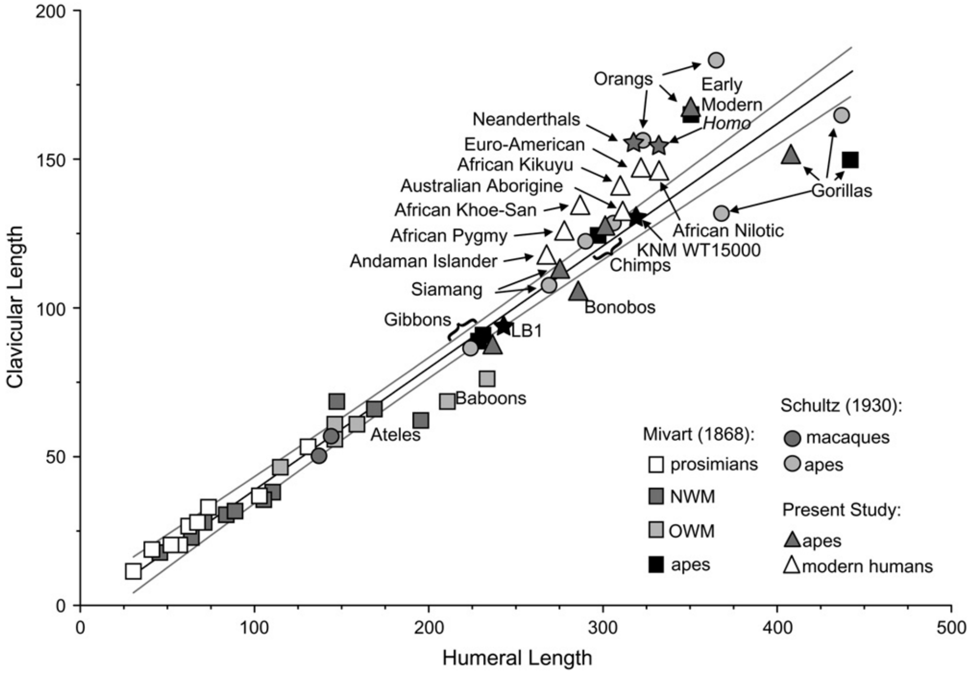

Fig. 6. Scatter plot of mean clavicular length against mean humeral length in nonhuman primates, a variety of modern human groups, samples of early modern *Homo* and Neanderthals, and LB1 and KNM-WT15000. Squares indicate data derived from Mivart (1868); circles indicate data from Schultz (1930); triangles represent data collected for the present study, except for that representing native Australians, which is from van Dongen (1963). Early modern *Homo* sample (grey star) includes: Abri Pataud 5 (Churchill, 1994), Jebel Sahaba, Wadi Kubbaniya (Angel and Kelley, 1986), Dolni Věstonice 13 & 15 (Sládek et al., 2000), and Skhūl IV & V (McCown and Keith, 1939). Neanderthal sample (grey star) includes: Kebara 2 (Churchill, 1994), Shanidar 1 & 3, Régourdou 1, Tabūn C1, La Ferrassie 1 (Trinkaus, 1983), and Neanderthal (McCown and Keith, 1939). Black stars indicate LB1 and KNM-WT15000. Regression line (with 95% confidence intervals) is for nonhuman primates only and has a correlation coefficient of 0.95. Since it passes through the origin, it indicates an isometric scaling relationship across primate species. See text for further discussion.

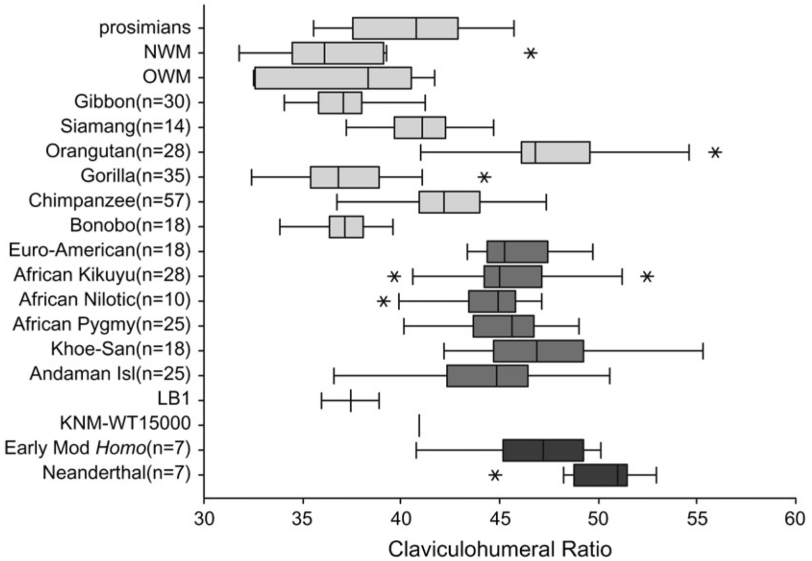

Fig. 7. Box and whisker plots of claviculohumeral length ratios for comparative samples and fossils. Error bars for LB1, *H. floresiensis*, were constructed using the mean absolute percent prediction error (3.91%) for the predicted length estimate of 91 mm for the LB1/5 incomplete clavicle. Prosimian, New World monkey, and Old World monkey samples were constructed from the mean values for clavicular and humeral length from Mivart (1868). Early modern *Homo* sample includes: Abri Pataud 5 (Churchill, 1994), Jebel Sahaba, Wadi Kubbaniya (Angel and Kelley, 1986), Dolni Věstonice 13 & 15 (Sládek et al., 2000), and Skhūl IV & V (McCown and Keith, 1939). Neanderthal sample includes: Kebara 2 (Churchill, 1994), Shanidar 1 & 3, Régourdou 1, Tabūn C1, La Ferrassie 1 (Trinkaus, 1983), and Neanderthal (McCown and Keith, 1939). Of the samples of modern humans, Euro-Americans are of average stature, African Nilotics and Kikuyu have a tall, linear build, Khoe-San are small to average in stature, and African Pygmies and Andaman Islanders are both of small stature. However, all have very similar claviculohumeral ratios, which are consistently higher than those of nonhuman primates except for orangutans. Both LB1 and KNM-WT 15000 have relative clavicular lengths more similar to nonhuman primates than modern humans. Neanderthals appear to have the longest clavicles among hominins.

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H. floresiensis simply retain the primitive condition for pectoral girdle/shoulder morphology. Both the LB6/4 and Nariokotome scapulae are similar to modern humans in scapular spine orientation (Fig. 8A), a feature that Larson (1995) reports sets humans apart from most other primates. In addition, both have bar-glenoid angles that actually exceed the average of modern humans (Fig. 8B), clearly indicating that they did not have cranially directed glenoid fossae, unlike apes and early hominins such as *Australopithecus afarensis* (Stern and Susman, 1983). The pectoral girdle/shoulder morphology of early *H. erectus* and *H. floresiensis* are also unlike later fossil hominins. Neanderthals are described as having low humeral torsion (Vandermeersch and Trinkaus, 1995), but Churchill (1994, 1996) has related this to increased chest size as an adaptation to the cold. While nothing is currently known about thoracic shape in *H. floresiensis*, Ruff and Walker (1993) and Ruff (1994) have described the skeleton of the Nariokotome boy as being very linear and more like topical-adapted people, making it unlikely that his low torsion could be related to large chest size. Neanderthals also have very long clavicles, which may be another correlate of chest size, that is, enlargement of the chest cavity results in greater separation of the shoulders that must be bridged by longer clavicles. In any event, their long clavicles make them very unlike either KMN-WT 15000 or LB1, and any similarity in humeral torsion is likely to be due to different reasons. Early Modern *Homo* fossils closely resemble modern human populations in degree of humeral torsion and relative clavicular length, and are therefore also quite unlike the Nariokotome boy and the Flores hominins.

Discussion

H. floresiensis and the Nariokotome skeleton are from very different times and places, with largely independent evolutionary histories, and there is much that is different about them, the most obvious of which, of course, is overall stature. Yet they are similar in displaying a relatively short clavicle and low humeral torsion in combination with a more modern

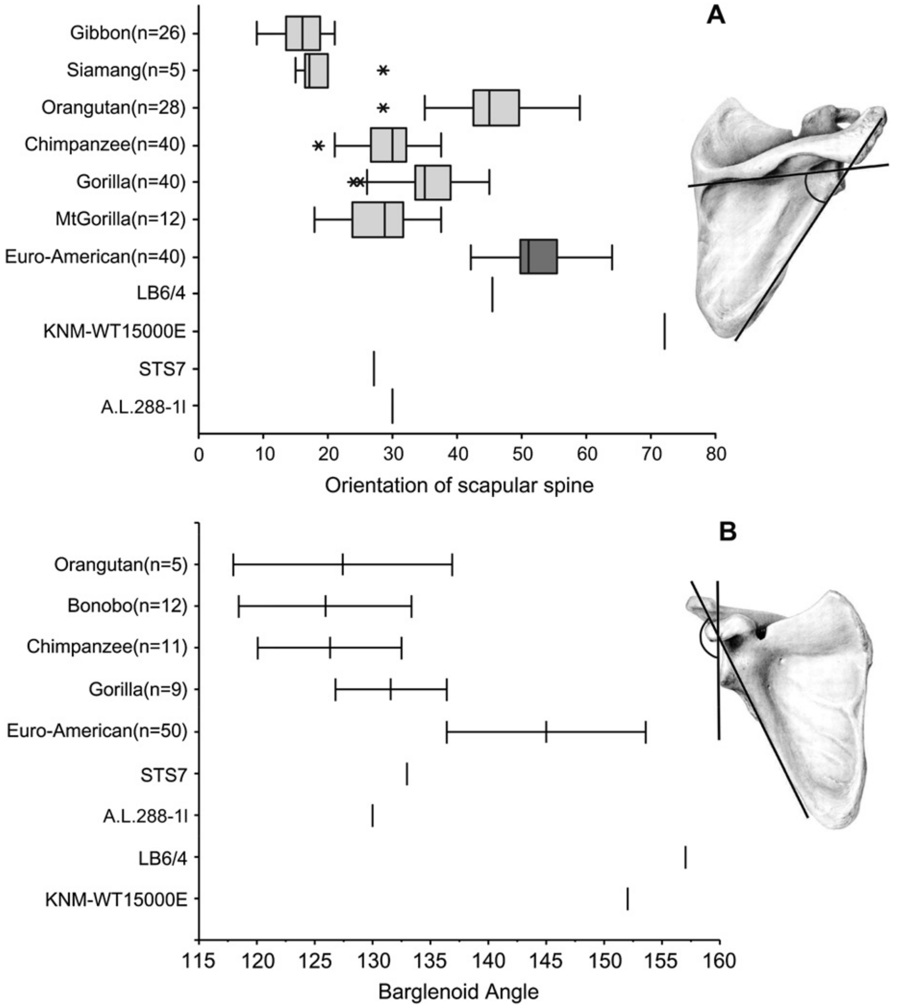

Fig. 8. A. Box and whisker plots for scapular spine angles for comparative samples and fossils. Comparative data is from Larson (1995). LB6/4, *H. floresiensis*, and KNM-WT15000E are like modern humans in having scapular spines that are oriented horizontally, unlike earlier hominins and apes with the exception of orangutans. B. Bar-glenoid angles for comparative samples and fossils. Since comparative data is from the literature (Stern and Susman, 1983), we could not construct box and whisker plots, and have instead calculated 95% confidence intervals for each sample. Both LB6/4 and KNM-WT15000E are "hyperhuman" in having large bar-glenoid angles indicating that their glenoid fossae do not face cranially as they do in earlier hominins MtGorilla = Mountain Gorillas.

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looking scapula. We believe that this unexpected combination of primitive and derived characteristics of *H. floresiensis* and early *H. erectus* shoulder material is indicative of a transitional stage in pectoral girdle evolution between the earliest hominins and modern humans. However, we recognize that there is controversy surrounding the Flores fossils, and therefore before describing our interpretation of this material, we will consider alternative views that have been offered.

Alternative interpretations of LB1

Although most debate regarding the validity of *H. floresiensis* as a new species has focused on brain size and configuration (e.g., Falk et al., 2005a,b, 2006, 2007; Weber et al., 2005; Martin et al., 2006a,b), two recent reviews of the LB1 skeleton have concluded that it was not a member of a distinct species of hominin, but rather was an atypical modern human. Richards (2006) argues that Flores hominins represent a *H. sapiens* group that became dwarfed in an island environment through changes to genes controlling the growth hormone – insulin-like growth factor I axis — and in addition, if LB1 is indeed representative of the population, underwent mutations in the genes controlling brain size (e.g., microcephlin/ASPM). According to Richards' scenario, disruptions to the normal developmental pathways are responsible for the distinctive features of LB1, and "Morphological features of the skeleton (wide pelvis, long arms relative to legs, tibial cross-sectional shape, etc.) that are said to link *H. floresiensis* with early hominids are also found in modern human pygmy populations" (2006: 14). In support of the latter contention, he reports that modern pygmies in general have low humeral torsion angles citing a mean torsion value of 129.5° from Marquer (1972) for a sample of six female Eastern Central African pygmies, with a range of 111° – 140°. However, the difference between this female mean and that of male Eastern Central African pygmies is in the opposite direction and exceeds in magnitude the typically observed differences between males and females of populations (see Edelson, 1999). With such a small sample it is possible that the low mean that Marquer (1972) reports for female Eastern Central African pygmies has been unduly influenced by an outlier who had unusually low humeral torsion. Unfortunately, we know nothing about this individual, and it should be kept in mind that a variety of factors can influence the degree of humeral torsion (see above). Since a sample of six is unlikely to be representative of variation within a population, we reconstructed an approximate 95% CI for humeral torsion in female Eastern Central African pygmies (see Fig. 4), and this broader range does indeed encompass LB1/50. It also includes KNM-WT 15000F. Can one therefore use the small stature of LB1 to explain its low humeral torsion? Male Eastern Central African pygmies, as well as both male and female Western Central African pygmies all have mean torsion values that are comparable to those of average stature peoples (Fig. 4). In addition, our sample of Khoe-San humeri, which are comparable in length to our sample of African pygmy humeri, also display a degree of humeral torsion similar to that of average stature peoples. Unfortunately, we do not have humeral torsion data for Andaman Islanders who have the shortest humeri among the populations sampled here. Nonetheless, we believe the evidence does not support Richards' (2006) claim that pygmy peoples in general have a low degree of humeral torsion. In addition, contrary to Richards' assertion that LB1's limb proportions are found in modern pygmy populations, Donlon et al. (2006) and Jungers et al. (2006b) have shown that limb proportions for LB1 are most similar to australopithecines and unlike any modern human populations. Finally, our sample of African pygmies do not display the low claviculohumeral ratios seen in LB1 and KNM-WT 15000 (Figs. 6, 7), and the similarity in humeral torsion *and* relative clavicular length in these two fossils that are widely separated in time and space suggests to us that these features are part of a functional complex that characterized a transitional stage in hominin pectoral girdle/shoulder evolution.

Jacob et al. (2006)[2] have also presented an analysis of the Flores fossil material and conclude that LB1 was derived from an Australomelanesian *H. sapiens* population and manifested microcephaly accompanied by other developmental abnormalities. While discussion of all of the supposed pathological traits of LB1 is outside of the scope of this paper, we can report that despite extensive search, we have not been able to identify a single syndrome manifesting microcephaly and short stature that refers to abnormalities in the proximal humerus or unusually short clavicles. In fact, one of the best known of these conditions, microcephalic osteodysplastic primordial dwarfism (MOPD) is often associated with relatively long, straight clavicles (e.g., Majewski et al., 1982; Hall et al., 2004), quite unlike LB1. Similarly, Argue et al. (2006) have recently analyzed the cranial and postcranial morphology of LB1, including comparisons to individuals suffering from MOPD II, and conclude that LB1 is unlikely to be a microcephalic human, and is distinct from any known hominin species.

To explore the degree to which LB1 displays traits characteristic of Australomelanesians, we have included in our analysis all humeral torsion and relative clavicular length data we could identify for samples of Australomelanesian peoples. We were able to locate humeral torsion values for Melanesians, Senoi, Phillipine Negrito, Burmese and native Australians (Martin and Saller, 1959), and relative clavicular length values for Andaman Islanders, and native Australians (Ray 1959; van Dongen, 1963[3]) (Fig. 6). Contrary to the notion of characteristic Australomelanesian traits, these populations are quite

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[2] In their review of the LB1 skeleton, Jacob et al. (2006) indicate that both clavicles are preserved. Although one of the specimens of LB1-associated material still partially in matrix was initially identified as a partial left clavicle, our recent reexamination of that material indicates that this specimen is probably a rib element.

[3] In addition to clavicular and humeral length data, van Dongen (1963) also measured humeral torsion for a group of native Australians. However, since he uses of the anterior face of the distal humeral articular surface as his reference axis, his torsion measurements are not comparable to those reported here (see Fig. 3).

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heterogeneous in regard to degree of humeral torsion (Fig. 4) and relative clavicular length (Fig. 6). Although the value for humeral torsion in LB1/50 just falls within the 95% CI of Australians, it should be recalled that this is only an approximate CI based on the average standard deviation of other populations, and is quite broad since the original sample is small. Australian aborigines, and to a lesser degree Andaman Islanders, also approach LB1 in claviculohumeral ratios. We suspect that the relatively short clavicles in these populations may be related to a body form adapted to the tropics. Abbie (1957, 1961) describes Australian aborigines as long-legged with a linear form including *narrow shoulders, chest and hips* (emphasis added), which would logically include a relatively short clavicle just as the large chest size of Neanderthals is associated with long clavicles. Although the two African tropically-adapted populations included in this study (Nilotics and Kikuyu) do not also display relatively short clavicles, the physical adaptations to latitude and temperature in these Asian and African populations are presumably independent and would not be expected to be identical in all respects. If a short clavicle and low humeral torsion are indeed functionally linked as we believe they are (see below), this association may partially explain the low claviculohumeral ratio and modest torsion in Australians, although we found no correlation between these two variables *within* our sample of Khoe-San. In any event, the heterogeneity observed among the Australomelanesian groups, and their lack of overlap with LB1 in most cases indicates to us that the short clavicle and low humeral torsion in LB1 (and mirrored in KNM-WT 15000) cannot be explained away simply as traits characteristic of Australomelanesian populations.

In regard to the explanation offered by Jacob et al. (2006) for low humeral torsion in LB1/50, they claim that because the muscle attachments sites on the humerus are not prominent, LB1 had weak muscles, and without the effect of muscles acting across the shoulder, there was little development of humeral torsion. Both cause and effect in this explanation are problematic. Recent work has shown that there is no simple relationship between size or complexity of muscle markings on bones and the size or strength of muscles (Bryant and Seymour, 1990; Robb, 1998; Wilczak, 1998; Zumwalt, 2006). In addition, contrary to the claims of Jacob et al. (2006), the long bones of LB1 have normal cortical bone thickness, well within modern ranges, and do not show enlarged medullary cavities (Jungers et al., 2006a; Larson et al., 2007). Thus, there is little evidence supporting the assertion that LB1 had weak muscles. As to the effect of muscular force on torsion development, one of the papers that Jacob et al. (2006) cite in support of the proposal that torsion is brought about by muscles acting across the shoulder also shows that most of the humeral torsion seen in modern humans develops prenatally (Krahl, 1947). According to the data presented by Krahl (1947), ‘‘primary’’ or inherited torsion is that which is seen in an early fetus before the development of muscular force acting across the shoulder, and accounts for nearly 60% of degree of torsion observed in adults. This would correspond to a torsion value of about 85° for an average modern human (using the mean of means value of 142.4°). Humeral torsion in a human newborn reflects both this primary torsion and some secondary torsion (due to contraction of shoulder muscles *in utero*) and is equal to approximately 88% of the average value for adults, which would correspond to 125° of torsion. So, if somehow LB1 did have a paralyzed upper limb, it should have displayed only primary torsion, and therefore its 115° of torsion is too high. However, it is unclear what sort of syndrome could produce prenatal upper limb paralysis and still result in an adult with fully formed upper limb bones. On the other hand, if LB1 was not paralyzed and had a modern human shoulder configuration, it should have had a much higher degree of torsion even at birth. As we describe below, we believe that *H. floresiensis* did not have a modern human shoulder configuration.

LB1 and KNM-WT 15000 and hominin shoulder evolution

The unexpected combination of primitive and derived characteristics of *H. floresiensis* and early *H. erectus* shoulder material highlights our ignorance regarding the course of transformation of the hominin pectoral girdle and shoulder from a more ape-like ancestral condition to the morphology of modern humans. In light of the morphological configuration observed in *H. floresiensis* and early *H. erectus*, we propose the following scenario for evolutionary transformation of the hominin shoulder: Fig. 9A represents the hypothetical ancestral hominin condition with dorsally placed scapulae, cranially directed glenoids (Fig. 8B), and low to modest humeral torsion (Fig. 4). Although at least two nearly complete early hominin clavicles exist (OH 48 [Leakey, 1960] and AL333x-6/9 [Lovejoy et al., 1982]), nothing is currently known about early hominin relative clavicular length, and on the basis of the condition in LB1 and KNM-WT15000, we propose that early hominins had relatively short clavicles. Because of the cranially directed glenoid fossae, the clavicles would have been oriented obliquely resulting in a ‘‘shrugged-shoulder’’ appearance (Fig. 9A, anterior view). Low to modest humeral torsion, judging from the estimates for early hominins by Larson (1996), was apparently sufficient for elbow functioning. In response to growing dependence on tool-making and tool-using, it would seem likely that an important change from this initial configuration would have been a drop in the position of the scapula on the thorax and loss of the cranial orientation to the glenoid fossa, especially as reliance on use of the forelimb in overhead supporting postures decreased along with the frequency of arboreality. Glenoid reorientation had clearly occurred in early *H. erectus* and *H. floresiensis*, and presumably the downward shift of the scapula had as well. Although such a change in glenoid orientation would have involved morphological transformation of the scapula, if we imagine this reorientation and shift in scapular position as if they were brought about by a ‘‘glenoid-down’’ rotation of the scapula, one can imagine how a relatively short clavicle could have constrained these changes and resulted in a forward shift in the position of the scapula so that it came to sit more laterally on the thorax

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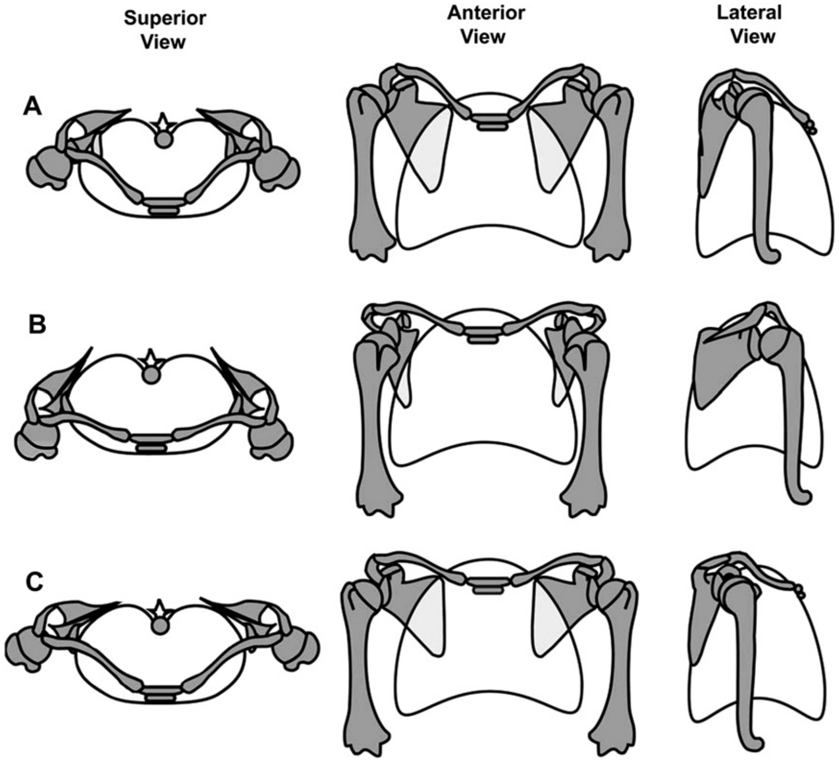

Fig. 9. Proposed course of hominin pectoral girdle evolution. A. Superior, anterior, and lateral schematic views of thorax showing pectoral girdle and shoulder of a hypothetical ancestral hominin condition. Scapulae are dorsally positioned with cranially facing glenoids, and clavicles are short and oriented obliquely resulting in a "shrugged-shoulder" appearance. Humerus displays low to modest torsion. B. Proposed transitional stage in hominin pectoral girdle evolution in which change from a scapula positioned high on the thorax with a cranially oriented glenoid fossa has been brought about by a downward shift in position and morphological change analogous to a glenoid-down rotation of the scapula, constrained by a relatively short clavicle. Scapulae are more laterally positioned, and glenoid fossae face anteriorly. Sagittal functioning of the elbow joint is maintained without major increases in humeral torsion. Such a configuration would explain the low degree of humeral torsion and relatively short clavicles seen in early *H. erectus* (KNM-WT15000) and *H. floresiensis* (LB1). C. Pectoral girdle and shoulder of a modern human with elongated clavicles, dorsally positioned scapulae, and laterally facing glenoid fossae. The humerus displays marked torsion to maintain a sagittal plane for elbow function.

(Fig. 9B). A consequence of this shift in scapular position would be a glenoid fossa that faced anteriorly, and thus, a humeral head that faced posteriorly, that is, had low to modest torsion, would produce an elbow that functioned in a sagittal plane putting no restrictions on using the forelimbs for manipulation. We suggest that this pectoral girdle/shoulder configuration was characteristic of early *H. erectus*, and was retained in *H. floresiensis*.

Remarkably, an abnormality found occasionally in modern humans known as short or hypoplastic clavicle syndrome (Milgram, 1942; Guidera, et al., 1991; Beals, 2000; Beals and Sauser, 2006) appears to closely mimic this configuration. Individuals typically present with significant forward displacement of the shoulders due to laterally positioned scapulae and resulting anteriorly-directed glenoid fossae. The vertebral borders of the scapulae are widely separated and are often prominent posteriorly. Other than their shortened length, the clavicles are normal in appearance. In most cases there are no other abnormalities or upper extremity dysfunction, and the chief complaint is abnormal posture. In particular, there are no reports of individuals with short clavicle syndrome being of unusually short stature, nor are there any reported associations with microcephaly or any other physical disorders. Unfortunately, none of the studies describing short clavicle syndrome actually quantify clavicular length or report on the degree of humeral torsion in patients with this condition, although Guidera et al. (1991) notes that the humeri are located anteriorly on CT scans. However, given that humeral torsion is somewhat plastic developmentally (Krahl, 1947; Edelson, 1999, 2000), it would seem likely that these individuals have reduced humeral torsion to accommodate the anterior orientation of their glenoid fossae.

Indeed, the pronounced similarity between individuals displaying short clavicle syndrome and what we suggest here for the configuration of the early *H. erectus* and *H. floresiensis* pectoral girdle/shoulder leads one to wonder whether what we are seeing in these fossils are simply individuals with this syndrome. However, given that the two fossil forms included in this analysis are widely separated in time, place, and possible ancestry, it seems unlikely that both would just happen to display the same pathological condition. We suggest instead that this configuration was normal for early *H. erectus* and *H. floresiensis*, and the close similarity seen in individuals with short clavicle syndrome demonstrates the pronounced influence of a shortened clavicle on pectoral girdle/shoulder configuration.

If a more protracted scapula with an anteriorly-directed glenoid fossa and low humeral torsion is indeed an intermediate

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stage in the course of evolutionary change in hominin shoulder morphology, what might the stimulus have been for clavicular elongation to return the scapula to a more dorsal position so that the glenoid fossa faced laterally (Fig. 9C), concomitantly requiring an increase in humeral torsion such as occurred in later hominin evolution? Such a shift in scapular position would dramatically increase the range of upper limb motion, particularly in the posterior direction. One potential selective force favoring such an increase in shoulder mobility is throwing, which entails a significant component of posterior motion of the abducted arm during the cocking phase (e.g., Tullos and King, 1973; Atwater, 1979; Perry, 1983). As long as people have been attempting to explain the origins of upright posture and bipedalism, the throwing of objects for self-defense, hunting, etc., has been included as a significant factor contributing to the survival and success of the human lineage (e.g., Darlington, 1975; Bingham, 1999). Unfortunately, there is little physical evidence for when and where throwing skill might have evolved, but the discovery of 400,000-year-old throwing spears (Thieme, 1997) suggests that it had developed by at least the middle Pleistocene. The anterior position of the shoulder for early *H. erectus* postulated here would not have permitted the abducted arm posture that is an integral component of the form of overhand throwing with which we are familiar today. It is interesting to note in this context, that one incidental complaint of people with short clavicle syndrome is that they cannot throw well (Guidera et al., 1991; Beals, 2000). Effective throwing, therefore, could have been an important selective influence to transform the pectoral girdle/shoulder complex from the condition in *H. erectus* to that resembling modern humans.

A second potential selective force for clavicular elongation is running, which requires shoulder and upper body rotation to counteract the destabilizing torque created by the oppositely moving lower limbs. Although running ability to achieve higher speeds has obvious advantages, Carrier (1984) and more recently Bramble and Lieberman (2004) have argued that endurance running in particular has been instrumental in shaping hominin evolution, possibly contributing to the origins of the genus *Homo*. However, for the pectoral girdle to contribute to an effective upper body counter-rotation mechanism, the shoulders should be widely separated, and the analysis of the course of change in shoulder morphology presented here suggests that early *H. erectus* did not have particularly wide shoulders, and by inference, neither did earlier members of the genus. Although this would not have made running impossible for early *Homo*, the fact that their shoulders were narrow suggests that an effective upper body counter-rotation mechanism was not yet an important selective factor. As Bramble and Lieberman (2004) note, several of the changes in lower limb morphology seen in early *Homo* could also be explained as adaptations to long distance walking. However, running, whether for speed or endurance, could well have been an impetus for clavicular elongation at a somewhat later stage of human evolution to spread the shoulders apart in order to enhance the upper body counter-rotation mechanism.

Conclusions

Debate continues regarding the proper interpretation of the Flores hominins (e.g., Eckhardt et al., 2007 vs. Larson et al., 2007). Although the controversy may continue until additional material, especially new skulls, are found, studies looking beyond brain size such as Argue et al. (2006), Tocheri (2007), or the present study have observed unexpected morphology that defies simple explanations. Whatever the ultimate taxonomic attribution of the Liang Bua hominins, their unique morphology suggests unforeseen diversity in the human family. In regard to the present study, while LB1 and the Nariokotome skeleton differ in many ways and are known from very different times and places, they are similarly distinct in displaying a relatively short clavicle and low humeral torsion. We believe these are not chance similarities, but part of a previously unrecognized functional complex that characterized early *H. erectus* and was retained in *H. floresiensis*. The recently discovered early *H. erectus* postcranial material from Dmanisi (Fischman, 2005; Rightmire, et al., 2006) should provide an important test of this hypothesized transitional stage in pectoral girdle/shoulder evolution.

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