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ANATOMICAL FORM AND BIOMECHANICAL FUNCTION INFERRED FROM THE
UPPER LIMB REMAINS FROM LIANG BUA CAVE, FLORES INDONESIA

A Thesis in

Kinesiology

by

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Abstract

The evolutionary status of human remains recovered from the Liang Bua cave on the tropical Indonesian island of Flores is disputed. While some posit that the remains represent a novel hominid species that descended in situ in isolation from *Homo erectus*, alternative explanations propose that the remains from the only relatively complete specimen, LB1, dated to approximately 18,000 years ago represent pathological modern *Homo sapiens*. This thesis presents new evidence from the reconstruction of upper limb phenotype of an extant female exhibiting an unknown pervasive developmental disorder, with comparisons to the recovered remains. There is significant correspondence between the extant human and the recovered remains in terms of clavicle and other upper limb bone morphology. Thus, it is suggested that the classification of species is inclusive of individuals outside a non-pathological range of variation in both phenotype and endophenotype.

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Introduction

Basis of Research and Review of the Relevant Literature

Scientific excitement was spurred by the 2004 publication of the initial findings of a “small-bodied hominin” recovered from a cave on the tropical Indonesian island of Flores dated to 18 thousand years ago(kyr) (Brown et al. 2004); the term hominin refers to what previously was referred to as hominid: humans and all their direct lineal antecedents that are not also ancestral to near relatives included in the genus *Pan* (Goodman et al. 1998). Described originally as an adult, estimated to be approximately 1.06 meter in height, with a cranial volume of 380 cubic centimeters, the skeleton was recovered in an “extremely fragile” state that was not fossilized, dated to 18 kyr. Based on the evaluation of an assortment of supposed novel and primitive characteristics, it was originally posited to be a descendant of *Homo erectus*. Since stone tools discovered previously elsewhere on Flores dated to 840 kyr had been attributed to *Homo erectus* based on their stylistic patterns, it was postulated that the population represented by the Liang Bua Cave skeletons had evolved in isolation on Flores over the same time period. However the time span from 18 kyr to present is within the time period for the existence of *Homo sapiens*.

Within that narrative, the specimen was given taxonomic status as a new species, *Homo floresiensis*, due to its supposed constellation of unique characteristics, including diminutive stature and brain size. The calculated stature of LB1, based on that of African pygmies, is significantly below the average for normal humans. The endocranial volume, based on seed measurement, was reported to be 380 cubic centimeters, which compares with average human volume of approximately 1,350 cubic centimeters, though worldwide the range for normal people is greater than 1,000 cubic centimeters and less than 2,000 cubic centimeters. This

estimate has been questioned and further study has revealed a significantly larger estimate of 418 cubic centimeters (Vannucci et al. 2011). Other features that according to Brown and colleagues contributed to the new species classification include a fissure separating the mastoid process from the petrous crest of the tympanic. The posterior portion of the cranium demonstrated plagiocephaly. Moreover, Brown and colleagues posit that there are numerous dental peculiarities, including increased tooth size and bilateral double mental foramina. There were features in the appendicular skeleton that Brown et al. advanced as being unique, including a pronounced lesser trochanter on the right femur. Since a normal human skeleton had never been recovered with this combination of characteristics dating to any period subsequent to about three million years ago, excitement in the scientific and popular press spurred wide interest given the supposed discovery of a diminutive new species (Brown et al. 2004; Lieberman 2005).

The hypothesis advanced by Brown and colleagues was that the peculiar features could be described as the result of insular dwarfism that caused allopatric speciation in isolation over the course of hundreds of thousands of years. However, as will be developed in detail later, from shortly after the announcement of the new species proposal, an alternative hypothesis was offered: that the key features of diminutive brain and body size were attributable to abnormal development (Henneberg and Thorne 2004). For example, the cranial volume is approximately one third the size of modern, non-pathological humans. If one considers small brain size as a sign of possible disease, there are hundreds of known causes of microcephaly, or abnormal smallness of the head, some genetic, some environmental and others idiopathic. For example, autosomal recessive primary microcephaly itself manifests as a clinically heterogeneous entity (Ashwal et al. 2009; Baxter et al. 2009; Jacob et al. 2006; Koyama et al. 2010; Mochida and Walsh 2001). Microcephaly itself is a sign associated with hundreds of diverse genetic disorders (Mochida

and Walsh 2001). This includes but not limited to Down Syndrome, Edward Syndrome, Cri-du-chat Syndrome, Cornelia de Lange Syndrome, Rett Syndrome and Smith-Lemli-Opitz Syndrome. However, these are relatively rare conditions, with at least one associated with advanced maternal age (Down Syndrome). Infectious causes, which prior to the introduction of chemotherapeutic and vaccination interventions, were endemic in many populations. Congenital infection with Cytomegalovirus, Rubella and Toxoplasmosis are associated with microcephaly. Many of the traits that Brown et al. referred to as unique exist in modern humans (Jacob et al. 2006). This is based on the assumption that LB1 is thus derived from a “normal” population (Martin et al. 2006).

Approximately a year later, there was a reevaluation of some of the original material, as well as description of newly discovered remains, assigned to a different subject (Morwood et al. 2005). Included there were revised estimates of the stature of a second skeleton, LB8. This was derived from coefficients based on tibial length of African Pygmies. Newer estimates based on the tibia indicate a stature of 109 cm. A newly discovered right tibia was described as small, with the shaft being laterally concave and oval in cross-section. The measured level of humeral torsion when analyzed with respect to select data sets was found to be 110° (which was later revised), is close to that which is found in *Hylobates*, and never found in normal humans. The use of several comparisons between indexes based on Africans and the recovered skeleton of the Liang Bua cave, which is located in South East Asia is quite peculiar; it is known that populations from different geographic regions have significantly different body proportions. (Wagner and Heyward 2000). Moreover, comparisons in limb proportions were made between LB1 and the *Homo erectus* skeleton KNM WT-15000, which is from 1.5 million years ago from the Turkana basin in Kenya, yet LB1 was dated to about 18 kyr, a quite anomalous method given the distant

time span (Morwood et al. 2005). Further comparisons were made between LB1 and AL 288-1, more commonly known as Lucy, which lived 3.2 million years ago in what is now Ethiopia. In fact Morwood and colleagues state: “Body proportions of LB1 are the same as AL288-1 *A. afarensis*, but differ from all other hominins for which there are reliable data, including *H. erectus*.” (Morwood et al. 2005). Morwood and colleagues dismissed the appropriateness of comparisons between LB1 and modern *Homo sapiens*, going to the extent of stating that a chimpanzee would be a good model for estimates of musculature and body mass.

Regardless of the explanations, the cranial volume of LB1 is substantially below that of modern humans. The size and shape of the cranium are highly sensitive and specific metrics for determining taxonomic status, yielding significant diagnostic information, and as such was the subject of numerous articles. Attempting to discredit those who assert a pathological etiology (inter alia: (Henneberg and Thorne 2004; Jacob et al. 2006), Falk et al. (2005) compared a virtual endocast of LB1 with a sample of great apes, *Homo erectus*, *Homo sapiens*, a sole human pygmy, a human who had microcephaly and earlier hominoid crania. As a result of an analysis of principal components, Falk and colleagues grouped the Flores cranium with *Homo erectus*, and separate from the single pygmy and *Homo sapiens* in the first axis of the principal component analysis. When compared with gorillas, chimpanzees, two early hominoids, and *Homo sapiens*, LB1 is grouped exclusively with *Homo sapiens* on the first principal component. Nonetheless, Falk concludes that the results “strongly suggests” a phylogenetic affinity between LB1 and *Homo erectus*, one that is “unknown small-bodied and small-brained”.

The 2005 article by Falk et al. generated replies. For example, Weber et al. (2005) highlights the fact that Falk included a mere solitary cranium with microcephaly. Weber and colleagues analyzed 19 microcephalic crania, ranging in size from 280 to 591 cc (note that the volume of

LB1 is within this sample). One endocast with a capacity of 415 cc was found to have nearly identical diagnostic metrics as that of LB1. Moreover, it was noted that there is wide and deep heterogeneity in the observed phenotype called microcephaly. Falk et al. provide a technical rejoinder (Falk et al. 2005a). Martin and colleagues (2006) further critique Falk, and posits that LB1 is a pathological microcephalic dwarf specimen of *Homo sapiens*. This brief discussion on the discourse related to the cranium is emblematic of the controversy that LB1 has engendered, providing context for this paper.

The most comprehensive alternative hypothesis offered to date (i.e. alternative to the idea that the Liang Bua cave skeletons represent a new human species) was offered by Jacob et al. (2006). They presented evidence that LB1 represented a constellation of regional, geographic characteristics within the skeleton and dentition that are common to Australomelanesian populations, particularly those currently living on Flores, along with signs of abnormal development, including but not limited to microcephaly and marked skeletal asymmetry. Reasonable questions, including how members of a species with one third the brain size of *Homo sapiens* would be able to create and use advanced stone tools commonly found with late hominins, particularly when a simple alternate explanation would be that the tools were made by non-pathological members of an Australomelanesian population, went unanswered. It would appear that given the morphometric qualities of LB1, it does not fit conventional scaling equations for relationships between brain size, height and mass (Herschel 1972; Müller et al. 2011). Jacob and colleagues also questioned the frequent comparisons between African populations and Australomelanesians populations, given the known differences in standard morphology. In addition, Jacob and colleagues questioned the assumption that there was only one inward migration event 840 kyr to the Flores island. Most importantly, they posited that it

was grossly inappropriate to define a new species, *Homo floresiensis*, based merely on fragments of one skeleton that had a not insignificant probability of being from a pathological subject. The authors demonstrate that the more than one hundred proposed unique features of LB1 could be found within the wide range of variation of modern *Homo sapiens*, especially Australomelanesians (Eckhardt 2010). For example, the absence of a true chin was described as a distinguishing feature in both Brown et al. (2004) and Morwood et al. (2005). However, study of the local extant Rampasasa demonstrates the majority also share that supposed distinguishing feature. The cranium of LB1 was also found to be asymmetric to an extent outside the range of normal human variation (Eckhardt 2010).

The range of the reported unique features in LB1 extends to the upper appendicular skeleton. For example, the humerus was first asserted to have but 110° of humeral torsion, supposedly well below that of modern humans (Larson et al. 2007); this was later revised to 120° (Larson et al. 2009). For comparison, in a sample of humans with short stature from East Central Africa, it was found that females had a range of humeral torsion from $111^\circ - 140^\circ$, thus putting LB1 barely below the sample range. Further, the clavicle is short compared with modern humans. The claviculohumeral ratio was estimated to be 37.5%, which is below the mean range for modern humans of 43% to 49.1%. Larson and colleagues go on to dismiss the possibility that this condition could be caused by pathology, “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.” However, Larson and colleagues go on to note that the humeral torsion is within a 95% confidence interval of Australians, and that short clavicles have been described in a limited number of modern humans that do not exhibit any other abnormalities. These unusual upper limb features of LB1 are ascribed to a transitional stage in the pectoral

girdle evolution between hominids and modern humans (Larson, et al., 2007; Larson, et al., 2009).

Contrary to the hypothesis that LB1 represents a new species, the testable hypothesis that LB1 suffered from a developmental disorder of unknown etiology needs to be shown to be false for the claim of a new species to proceed. It is not possible to designate a specimen as a type specimen for a new species if it is pathological. Given the heterogeneous manifestation of and relatively rare occurrence of developmental abnormalities, it is difficult to find a so-called exact match. Nonetheless, one of the possible diseases is Laron Syndrome, a disease in which there is a mutation in the receptor for somatotropin, also known as growth hormone. Originally described in a consanguineous Yemenite Jewish family, Laron Syndrome has been found in hundreds of individuals, mainly in consanguineous groups. Born short, the afflicted children remain short and become obese, with notable hypogenitalism, protruding forehead, saddle nose, underdeveloped facial bones, delayed motor development and a high-pitched voice. Growth velocity is severely reduced, with stature 4 to 10 standard deviations below the median, with peak stature of between 116 and 142 cm in males. Other notable signs include late closure of bony epiphyses, thin bones with reduced bone density and highly variable psychological performance, ranging from relatively normal to complete mental disability (Laron 2004; Laron et al. 1993). Some of the similarities between subjects with Laron Syndrome and LB1 have been described, including reduced stature and cranial size, cranial and dental characteristics and axial skeleton congruence (Hershkovitz 2007). However, Falk and colleagues state that most of the claims made by Hershkovitz rely on previously unpublished data, and based only on qualitative description. Further, it is claimed that there are few if any major similarities in morphology of either the skeleton or cranium (Falk et al. 2009).

The purpose of the current study is to show a range of variation in modern humans that is consistent with that found in LB1. This thesis will focus on the upper appendicular skeleton. First, a discussion of published literature specifically relating to LB1, and associated claims, will be presented. Limited comment will also be provided on the humerus, forearm and carpals. As a comprehensive evaluation of all associated claims is outside the scope of this thesis, the clavicle will be the primary focus, with secondary attention to preliminary findings on the carpals.

Materials and Methods

A review of the anatomy in general and a qualitative description of the recovered remains follows. While this author has not conducted primary research on these bones, there is wide opportunity to test alternative hypotheses; many statements about the morphology of the LB1 skeletal remains are contradicted using previously published literature. A thorough description of the recovered upper limbs of LB1 was published in 2009 by Larson and colleagues. This paper postulated further unique features in LB1, especially in the appendicular skeleton, many of which have been refuted herein.

Biomechanics of the Clavicle

In the inferior view, the clavicle appears S-shaped with two curves, one convex and one concave. The rounded medial end articulates with the sternum. There is no marrow cavity in the clavicle and is composed exclusively of cancellous bone with an outer shell of compact bone. The wide lateral end, articulates with the acromion of the scapula (Marieb et al. 2011; Tortora and Grabowski 1996). The clavicle serves to hold the upper appendicular unit away from the midline, increasing the range of motion of the arm. Movement of the scapula along the thoracic wall is facilitated by the clavicle. Further, the clavicle helps to protect the neurovascular bundle that

supplies the upper limbs. The clavicle also serves to transmit forces from the upper limbs to the axial skeleton (Moore and Dalley 2010). The internal curvature of the clavicle acts as a crank that helps the pectoralis major during arm flexion, the effect of which is compounded by the sinusoidal nature of the clavicle. However, there is comparative weakness in flexion and torsion, thus leading to frequent fractures in the middle of the clavicle (Voison 2006).

Compared with the smooth superior surface, there are multiple ridges and grooves for muscle attachment on the inferior side. The deltoid tubercle is prominent on the superior side, providing an attachment point for the deltoid. On the proximal superior side, attachments for the sternocleidomastoid and pectoralis major muscles can be found. The attachment of the costoclavicular ligament on the sternal end of the inferior end connects the clavicle to the 1st rib. The sternohyoid muscle also attaches on the proximal inferior side. On the inferior, posterior surface proximal to the acromial end is the conoid tubercle, which serves as the attachment point of the medial part of the coracoclavicular ligament. The middle of the inferior surface serves as the attachment point for the subclavius muscle. Proximal to the acromial end is the lateral trapezoid line, to which the trapezoid attaches. Finally, proximal to the sternal facet on the inferior surface, the impression for the costoclavicular ligament can be found. Rarely, the rhomboid fossa can be found on the medial, inferior end of the bone, creating an irregular concavity (Kumar et al. 1988; Moore and Dalley 2010)

Remarkably, the clavicle is the first long bone to ossify, starting during the 5th embryonic week, from medial and lateral from condensed mesenchyme. Later cartilage forms and the sternal end fuses with the diaphysis between 18 and 25 years of age. Notably, this is also the last long bone to fuse (Moore and Dalley 2010).

There is a wide range of variation, both normal and pathological, that can be witnessed in the clavicle. Disorder can range from absence, to a bike handlebar shape, to malformations from congenital, maternally—inherited diseases including syphilis and rubella. Further, there is an assortment of potential fractures, with the majority occurring at the weakest point in the bone, the middle. Osteolysis and pseudoarthritis of the distal end is possible status post-trauma.

Infection with *Staphylococcus aureus* and septic arthritis can cause osteomyelitis. Moreover, the clavicle bone can be the site of neoplasm and metastasis, causing gross changes in morphology. Erosion of the bone is frequently seen in rheumatoid arthritis (Kumar et al. 1988).

There are numerous known genetic diseases for which altered clavicle morphology is a feature. For example, Lenz-Majewski hyperostotic dwarfism causes a broad and thick clavicle, along with progressive skeletal sclerosis, severe growth retardation and mental retardation (Robinow et al. 1977). Melnick-Needles syndrome, also known as Otopalatodigital syndrome spectrum disorders, can cause clavicular hypoplasia, curved long bones and flared metaphyses (Robertson 2006; Stevenson and Hall 2006). Oto-palato-digital syndrome type II presents with thin clavicles, microcephaly, cleft palate and overlapping fingers (Preis et al. 1994). Maroteaux type acromesomelic dysplasia causes a curved clavicle with pronounced disproportionate short stature (Bartels et al. 2004).

Clavicle of LB1

The right clavicle that was recovered is missing the medial/sternal end, with the fragment measuring 85.9 mm. In an earlier paper, Larson et al. reconstructed the total length of the clavicle to 91 mm, based on regressions between total clavicle length and length from the lateral

end to the point of inflection of the medial curvature on 32 average Euro-Americans and 24 clavicles of small statured Andaman Islanders (Larson et al. 2007). In the 2009 paper, the lateral end is described as “somewhat eroded and the articular facet for the acromion is not visible due to postmortem damage.” Larson makes the following claim, which will be tested in this thesis: “Voisin (2006) has reported that modern humans are distinct in displaying a single inferior curve of the clavicle in posterior view. His preliminary examination of LB1/5 (based on photographs only) indicates that it retains the primitive double curvature seen African apes and all hominins except modern humans (Voisin, pers. comm.)”.

The paper referenced is a study of clavicular morphology in extant hominoids and primates. Based on the work of Olivier (1951), a unit-free index of curvature to measure the four curvatures possible was used to compute standard measurements in a range of primates and humans. As shown in Figure 1, the external curvature is $e/h \times 100$; the internal curvature is $f/g \times 100$; the inferior curvature is $e'/h' \times 100$; the superior curvature is $f'/g' \times 100$. The index of curvatures will be used later in this thesis. However, notably, Voisin wrote: “Humans possess clavicles showing only the inferior curvature, which is less pronounced than that which exists in monkeys. Sometimes, some individuals show two curvatures in dorsal view, but these curvatures are slight in regard to the condition exhibited in the great apes” (Voisin 2006). This is in direct contradiction to the assertion made by Larson and others above.

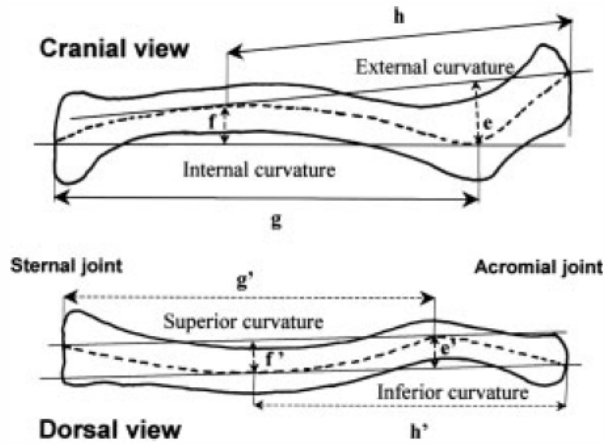


Figure 1 - Determination of the curvature of clavicles, shown on a right clavicle of *Pan troglodytes*, from (Olivier 1951)

Morphology of the Humerus

The humerus is the principal bone of the upper limbs, connecting the forearm to the skeleton.

The anatomical neck of the humerus is a groove that envelops the head and separates it from the tubercles. On the lateral proximal portion of the humerus, the greater tubercle is found. The lesser tubercle is found on the anterior proximal portion. These two structures are separated by the intertubercular groove. On the shaft of the humerus, the deltoid tuberosity is found laterally, providing a site of attachment for the deltoid muscle. On the posterior side, the radial groove provides a structure on which the radial nerve and deep artery of the arm lie. On the distal end of the humerus, the medial and lateral epicondyles are sites of numerous muscle attachment. The capitulum is the site of articulation with the head of the radius. The olecranon fossa envelops the ulna during full extension at the elbow (Moore and Dalley 2010).

Humerus of LB1

The humerus of LB1 is relatively complete, save for damage to both the greater and lesser tubercles and missing lateral epicondyle and capitulum. It is 243 mm in length. It is notable that Morwood and colleagues reported that it has but 110° of humeral torsion; however, this figure

was later revised upward to 120° (Larson et al. 2009; Morwood et al. 2005). Due to the absence of some of the standard points of measurement, humeral torsion had to be estimated. There are numerous rough areas visible where muscles attach, including the latissimus dorsi, triceps brachii and teres major. There is a fracture at the midpoint of the shaft, which has a round cross section.



Figure 2 - LB1 right humerus (Larson et al. 2009)

Ulnas of LB1

Fragments of both ulnas of LB1 were recovered. The fragment from the left side is 167 mm in length, is missing both ends, and is fractured in locations.

The right ulna is missing the distal head and shaft, and is 190 mm in length with two fractures. It is described as having a rounded contour, with an anteroposterior curve. On the proximal end, the portions of the trochlear notch are preserved, as are the coronoid process. The ulnar

tuberosity, which is the attachment site for the brachialis, is preserved. There are visible ridges for the attachment of muscles, including the brachialis, flexor carpi ulnaris and the anconeus.

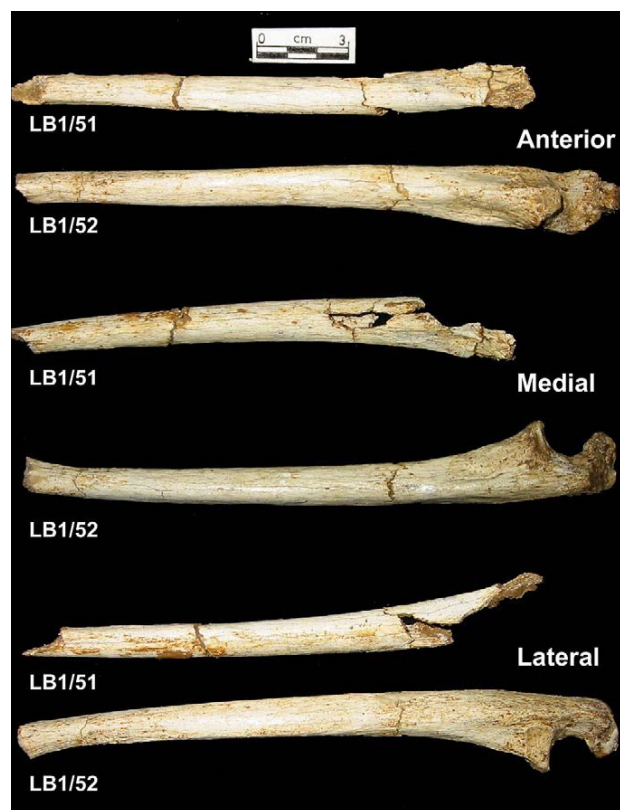


Figure 3 - LB1/51 left ulna and LB1/52 right ulna (Larson et al. 2009)

Carpals of LB1

The remains recovered include a scaphoid, capitate, hamate, trapezoid and lunate, all being from the left hand. For a thorough description of the bones, see Larson et al. (2009) and Orr et al. (2013)

There is minor damage to the tip of the tubercle of the scaphoid. It is described as having “well-preserved articular facets” which varies from both initial descriptions of the bones in addition to the state of other bones.

The head of the capitate is about the same width as the palmar aspect of the distal end. There is a knob-like process on the dorsoradial side. The hamate lacks the proximal half of the bone, in addition to the hamulus. The trapezoid is wedge-shaped, with six distinct surfaces noted. Finally, the lunate is missing 25% of the proximodorsal surface.

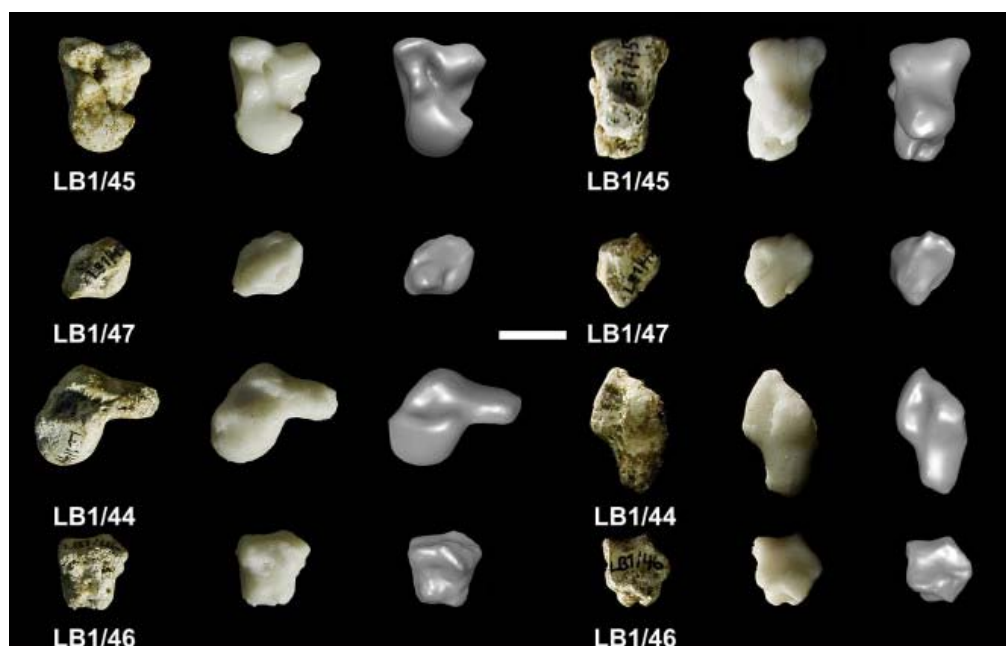


Figure 4 - The LB1/45 left capitate, LB1/47 left trapezoid, LB1/44 left scaphoid, and LB1/46 partial left hamate (scale bar = 1 cm). The 1st and 4th columns from the left show the original carpals; (Larson et al. 2009)

Comparative Human Materials

In an attempt to demonstrate a fraction of the described unique features of LB1, a female with a gross developmental disorder was recruited. This female self-described her syndrome on the internet, and was brought to Penn State Hershey Medical Center for a panoply of tests, including full body CT, MRI and quantitative and qualitative hematological and endocrinological study. This study was approved by the Human Subjects Institutional Review Board of the Pennsylvania State University on November 13, 2008 under approval number 28014, with renewal of authorizations for continuing study. While there is some uncertainty that this subject, who shall

henceforth be referred to as Subject A, has Laron Syndrome, also known as Primary Growth Hormone Insensitivity Syndrome, there is no molecular biological evidence type to confirm this. As such, Subject A will merely be described as having a disorder of physical growth and development – not otherwise specified.

After obtaining informed consent, Subject A was subjected to a full body, thin bone CT scan on a Siemens Sensation 40, 120 kv, 51 mAs, 1.000mm slice interval in the transverse plane. In addition, a thin bone CT scan was obtained of the wrist.

Isolation and segmentation of the relevant bones was accomplished using Mimics 14 (Materialise – Leuven Belgium). For further analysis, the models generated were analyzed using Geomagic Studio (Geomagic – Research Triangle Park, ND USA). Moreover, Geomagic was used to map differences in asymmetry. As deemed necessary, manual segmentation adjustment, smoothing and triangle reduction adjustments were executed. Images were generated to correspond with perspectives previously published, to facilitate easy comparison. Two dimensional projections were created, which were used as the basis for measurement. While there is some inherent degree of error, it was minimized. Further, given the high resolution of the scans, measurements should be just as accurate as if they were taken from the physical material.

RESULTS

Clavicle

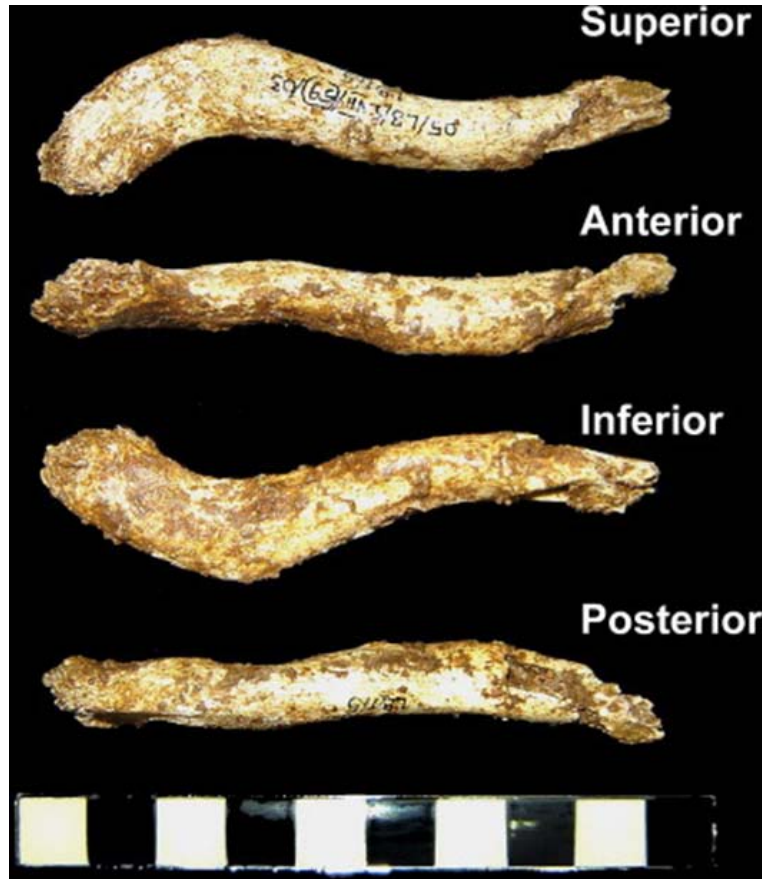


Figure 5 - Right Clavicle of LB1 (Larson et al., 2009)

Quantitative Analysis of the Clavicle of LB1

The method of Olivier for the quantifying the degree of curvature of the clavicle was applied to LB1. In this case, it is necessary to be acutely aware of the limitations of this method. As was previously stated, a significant piece of the sternal end of the clavicle is missing. This required that the total length be extrapolated, and consequently that some points of measurement be estimated. Furthermore, the only reference made available for this study was the composite picture from Larson et al. (2009) shown in Figure 5. This is not as desirable as having the CT

scan of the clavicle, but was the only option available due to the unavailability of the source materials or derivative representations.

As shown in Table 1, there are three measurements given for each curvature. This was based on the range of extrapolated total clavicle length given by Larson et al. (2009) The extrapolated length was assumed to all belong to the sternal end. As such, it did not affect measurements of the external and inferior curvatures.

Table 1- Measurements of Clavicle of LB1

	External	Internal	Inferior	Superior
Smallest	14.6	11.5	3.6	5.6
Medium	14.6	17.9	3.6	5.2
Largest	14.6	19.2	3.6	5.4

For the external curvature, LB1 is within 1 standard deviation of the mean of *Homo sapiens* of 16.1, according to the reference data of Voison (2006). For the internal curvature, LB1 is also within 1 SD of the mean of *Homo sapiens* of 12.6 if the smallest total length is taken. The inferior curvature of LB1 is within 1 SD of the mean of *Homo sapiens* of 5.1. LB1 is within 2 SD of the mean for *Homo sapiens* for the superior curvature, which has a mean of 2.9.

Clavicle of Subject A

The inferior view of the clavicle of Subject A is shown in Figure 7. Though it is difficult to appreciate, there are ridges in the inferior surface of the proximal third that serve as the binding site of the costoclavicular ligament. The costal tuberosity appears to be reduced in magnitude. The groove for the attachment of the subclavius is located more anterior and reduced in length.

The conoid tubercle is quite enhanced, yet the coracoid tuberosity is reduced and shifted medially.

In textbooks, it is noted that there is wide variation in the medial two thirds of the clavicle, with the normal presentation of a triangular prism, and is more cylindrical in “ill-defined specimens” (Morris 1942). The medial end is notably ovular.

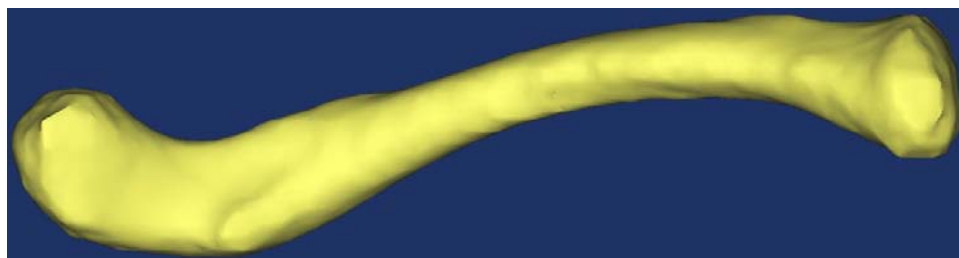


Figure 6 - Inferior View of Right Clavicle of Subject A, medial end at right

The superior view of Subject A is shown in Figure 8. Notably, the convex nature of the lateral end of the bone, the attachment site of the deltoid, is greater than a normal appearance, almost appearing between rounded and crescent. The deltoid tubercle is greatly reduced. There are two pronounced curves. The attachment site for the pectoralis major is rounded and smooth, and appears to be more indented. The attachment site for the trapezius is flattened.

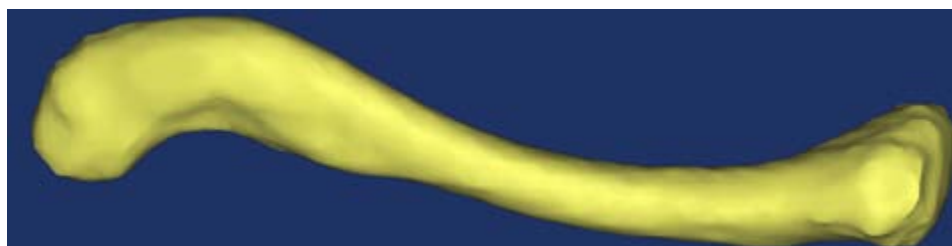


Figure 7 - Superior View of Right Clavicle of Subject A – medial end at right

Unfortunately, the anterior and posterior views of the clavicle are not well-described in the literature. There is a notable ridge for the attachment of the pectoralis major muscle. Also, in the

lateral third, the superior surface has a noted elliptical indentation for the attachment of the deltoid.

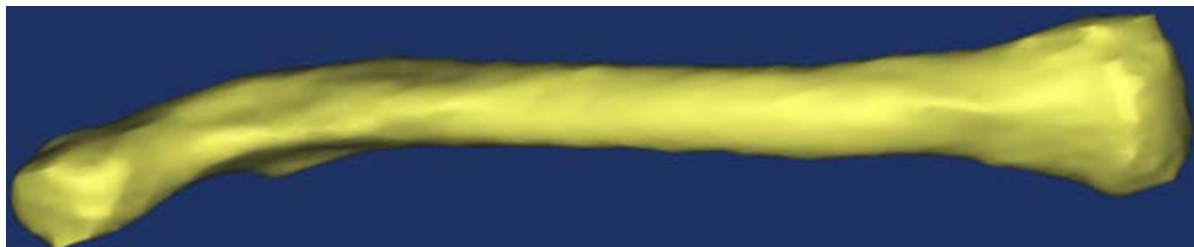


Figure 8 - Anterior View of Right Clavicle of Subject A – medial end at right

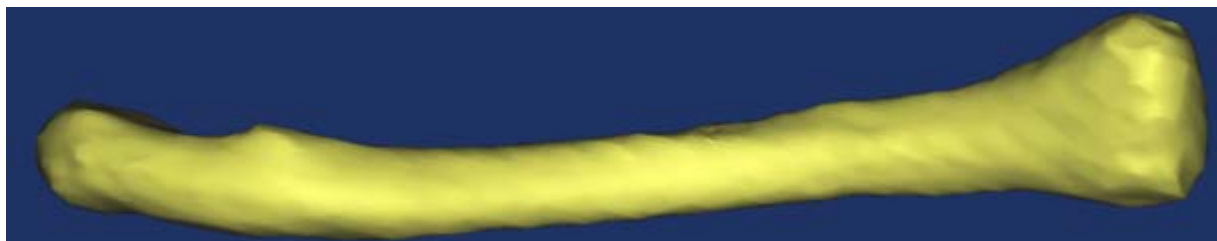


Figure 9 - Posterior View of Right Clavicle of Subject A – note superior aspect is facing down, medial end at right

Qualitative Analysis of Subject A's Clavicle

Voison states that some individuals have two curvatures visible in the posterior view. As is clearly visible in figure 10, which is equivalent to what Voison refers to as the dorsal view, a minor superior curvature proximal to the sternal end and an inferior curvature proximal to the acromial end are visible. By this very fact, which is supported by the work of Voison it is no longer possible to claim that the presence of two curves in the posterior view of a clavicle is a diagnostic criterion for *not* being a *Homo sapiens*. Subject A, who has a serious developmental disorder, is testament to this fact. As such, the presence of this characteristic must now be included within the range of variation when considering the analytical construction of a new species.

As described by Voison, when the gross morphology of the clavicle in the inferior view is considered, there are three possible major groupings, shown in . If Figure 7 is compared with Figure 11, it is clear that Subject A best fits into group 3a, which includes the genus *Homo*.




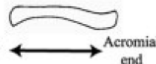
	Group 1	Group 2	Group 3	
Clavicle characteristics	Clavicle with: - a pronounced external curvature - a slight, or absent internal curvature	Clavicle with: - a pronounced internal curvature - a slight, or absent, external curvature	Clavicle with: - an internal curvature - an external curvature	
Diagram				
Primate species	- <i>Gorilla</i> - <i>Papio</i>	- <i>Hylobates</i> - <i>Ateles</i>	- <i>Homo</i> - <i>Pan</i> - <i>Pongo</i>	- <i>Procolobus</i> - <i>Colobus</i>

Figure 10 - Diagram of the characteristics of each clavicle group in cranial view. From Voison 2006

In the anterior view of the clavicle, there is greater interspecies variation. Voison describes four different groups as shown in Figure 12. From a glance, it would appear that Subject A most closely approximates a *Gorilla gorilla*. This highlights the flaw with using normal, non-pathological specimens as the diagnostic criteria for the definition of a new species. Given that a non-zero number of entities within a population will have a pathological morphology, failure to include these outliers will lead to spurious conclusions.

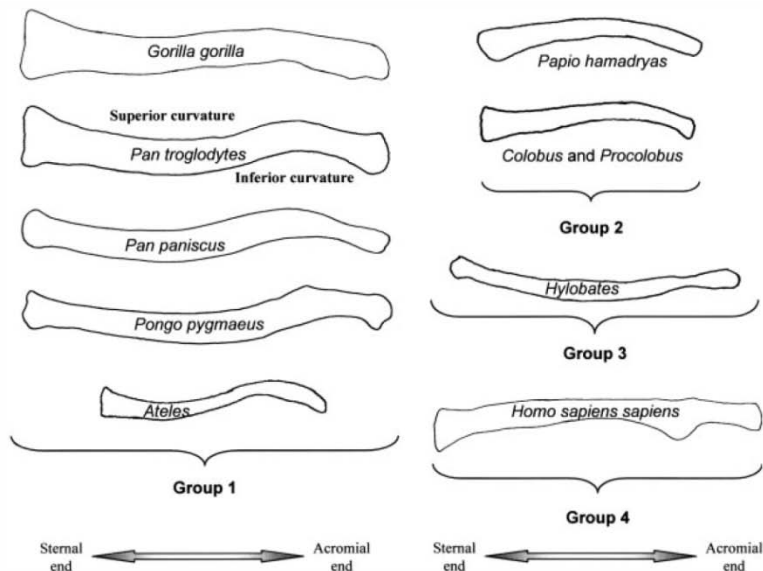


Fig. 9. Right clavicle in dorsal view (scale not respected).

Figure 11 - Right clavicles in dorsal view from Voison 2006

Quantitative Analysis of Subject A's Clavicle

It is tempting, yet erroneous to use quantitative metrics to define a species. If a modern human is defined as having an adult cranium between 1000 cc and 2000 cc, those with microcephaly would be excluded. If the same procedure were used for clavicle analysis here, equivalent incorrect conclusions would be reached. If the method described by Olivier is combined with reference data provided by Voison, some peculiar conclusions about Subject A would have to be drawn. For example, in the measurement of the external curvature in Figure 7, Subject A is 2.7 standard deviations from the mean of non-pathological *Homo sapiens*, putting Subject A below the 1st percentile. However, she is near the 50th percentile for *Pongo pygmaeus*, or the Bornean orangutan. Continuing, if Subject A's internal curvature were used as a diagnostic criterion, she would be closest to *Colobus*, or monkey (data not shown). This further highlights the errors that will result when potential pathology is not included within the range of variation for a species.

In terms of the superior and inferior curvatures, Subject A is in the 90th percentile for the superior curvature and 97th curvature for the inferior curvature. Nonetheless, she is within two standard deviations of the mean, and confirms that Subject A lies at the extremes of human variation for clavicular morphology.

Table 2 - Quantitative Characteristics of Subject A's Clavicle

	Subject A	Sample Mean	Sample SD	N	T	Percentile
Superior						
<i>Homo sapiens</i>	4.89	2.9	1.5	33	1.33	90.3
<i>Pan troglodytes</i>	4.89	7.9	3.2	26	-0.94	17.8
<i>Pongo pygmaeus</i>	4.89	5.6	2.5	19	-0.28	39.0
Inferior						
<i>Homo sapiens</i>	9.45	5.1	2.3	33	1.89	96.6
<i>Pan troglodytes</i>	9.45	10.7	3.3	26	-0.38	35.4
<i>Pongo pygmaeus</i>	9.45	9.2	1.9	19	0.13	55.2
External						
<i>Homo sapiens</i>	8.82	16.1	2.7	33	-2.70	0.6
<i>Pan troglodytes</i>	8.82	15.4	3	26	-2.19	1.9
<i>Pongo pygmaeus</i>	8.82	9.1	2.3	19	-0.12	45.2
Internal						
<i>Homo sapiens</i>	4.76	12.6	2.5	33	-3.14	0.2
<i>Pan troglodytes</i>	4.76	8.1	2.8	26	-1.19	12.2
<i>Pongo pygmaeus</i>	4.76	5.8	2.1	19	-0.50	31.3

Humerus of LB1

The right humerus of LB1 was recovered relatively intact, with the mid-shaft broken post-mortem. As previously mentioned, humeral torsion is an important descriptive metric of the humerus, and as such has been the subject of contention and revision. The humerus was originally reported to be approximately 110°, significantly less than modern humans (141–178°) (Morwood et al. 2005). However, due to damage to the proximal end of the humerus, traditional methods may not be most appropriate. Using alternative measures, previously detailed by Larson (1996), revealed an estimate of 119° and 121°; it was concluded that the degree of humeral

torsion is “well below human averages” (Larson et al. 2009). As a side note, in early papers, ranges of variation were used to describe the degree of humeral torsion, and in later papers, there was an inexplicable switch to providing averages. While it is not possible to know the etiology of this change, it seems reasonable to assume that the use of averages fits better within their narrative of not including samples at the extremes of variation.

As was highlighted by Jacob and colleagues, there are phylogenetic, developmental and environmental components to the determination of humeral torsion. Between and within ethnic group degree of humeral retroversion is quite large. In a sample of bones from skeletons from various populations in the Americas and Asia, retroversion was found to vary between -8° and 74° . In a sample of fetal skeletons, the mean was 78° , indicating significant reduction in the level of humeral retroversion during normal life history. Overall, greater levels of retroversion were found in males and in the right humerus (Edelson 1999). For example, there is a significant intrasubject difference in humeral torsion in handball players, with a mean difference of 9.4° , and maximum difference of 29° (Pieper 1998). Compared with normal controls, subjects with recurrent anterior dislocation of the shoulder had a significantly reduced mean retroversion, or increased humeral torsion (Symeonides et al. 1995). In fact, one article cautions against population-based analysis, instead focusing on individual variation (Rhodes 2005; Taylor et al. 2009).

Carpals of LB1

Tocheri and colleagues conducted a detail examination of the recovered wrist bones of LB1. They note that the three recovered bones display no features of modern human or Neanderthal carpal (Tocheri et al. 2007). They state that difference in carpal shape in primates can be traced to production of carpal mesenchyme during embryonic development. Cursorily, they state “In

modern humans, the trapezoid, capitate, and trapezium arise in the mesenchyme in essentially their adult form by the 11th week of development, long before the processes of chondrification and ossification are complete...” However, it is known that the pisiform has not completed ossification till approximately week 13 (Hita-Contreras et al. 2012). Differences in developmental timing can cause malformations in initial carpal shape, but are localized and transient, according to Tocheri. Moreover, it is stated “The genes that result in dysplasias, however, do not normally become expressed until after normal shape formation of the carpal mesenchyme.”

Hypoplasias of isolated carpal and phalangeal elements are rare, but have been described (Davison 1962; van Goor and Houpt 1989). The interaction of numerous genes at specific locations and times is critically necessary for proper growth and patterning of limb elements. Mutations in the *Hox* genes, specifically *hoxd-12* and *hoxd-13* produce viable mice with malformations of the distal carpal bones (Davis and Capecchi 1996). Triple *Hox11aacdd* mutants have reduced carpal mesenchyme, with poorly defined, misshapen elements, with involution and fusion of several elements (Koyarma et al. 2010). Mutations in *Hox* genes, or interference in expression thereof, affects bone formation and patterning (Villavicencia et al. 2010). It is known that a downstream effector of growth hormone, IGFBP-1 interacts with *Hox* genes (Daftary and Taylor 2006). Ergo, it would be plausible that if LB1 did have Laron Syndrome or some other developmental disorder, significant variation in carpal bones would be expected.

As seen in Figure 13 to Figure 15, there is significant variation in the morphology of representative carpal bones of various hominoids. Contra Tocheri, it is grossly inappropriate to visually represent a solitary bone as representative of an entire species. A careful analysis of the

images shows that for many perspectives, Subject A appears to be a more close match to LB1 than that of the figure of modern *Homo sapiens*. This is especially visible in the scaphoid and capitates. Moreover, the colorings shown in the figures represents the presumed surfaces of articulation, which is then used in further statistical analysis; the method for the computation of these surfaces was very poorly described in the literature.

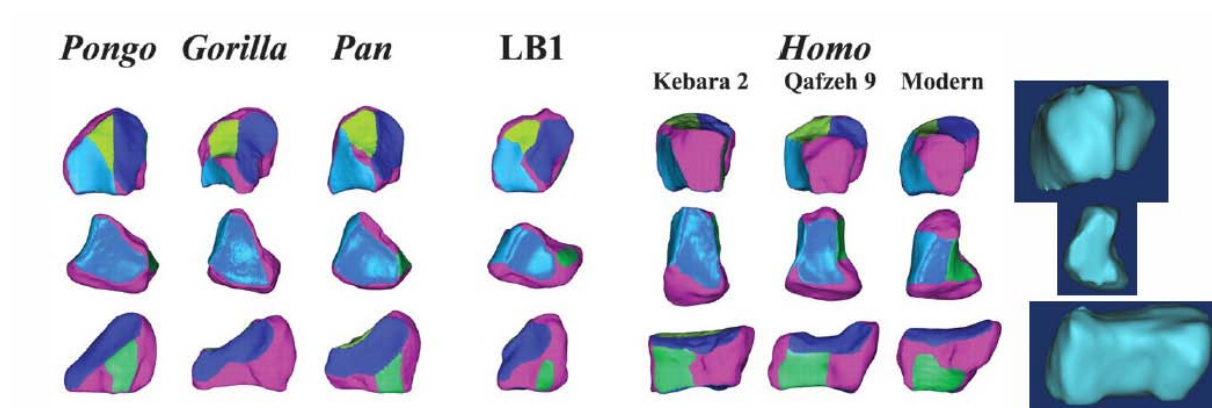


Figure 12 - Trapezoid - palmar, proximal and ulnar views, Subject A on right, not to scale (Tocheri 2007)

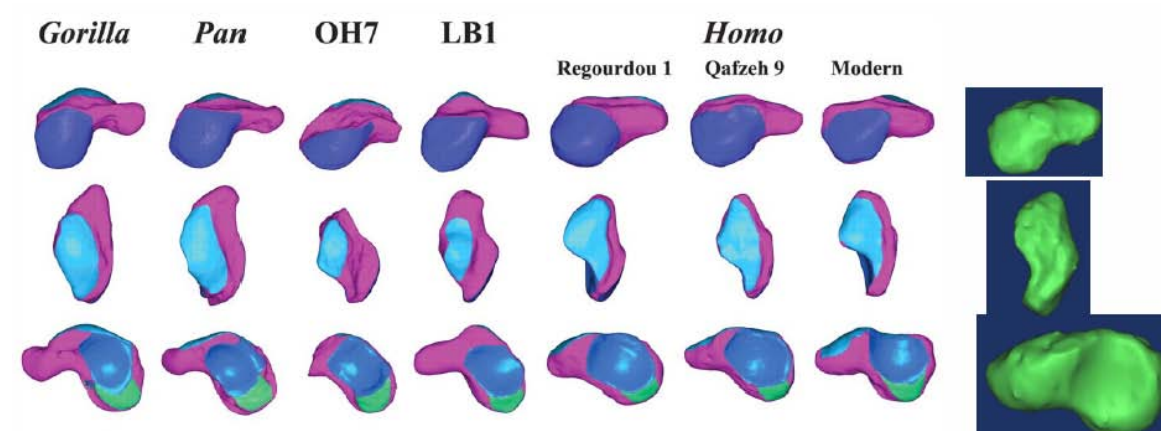


Figure 13 - Scaphoid - radial, distal and ulnar views, Subject A on right, not to scale (Tocheri 2007)

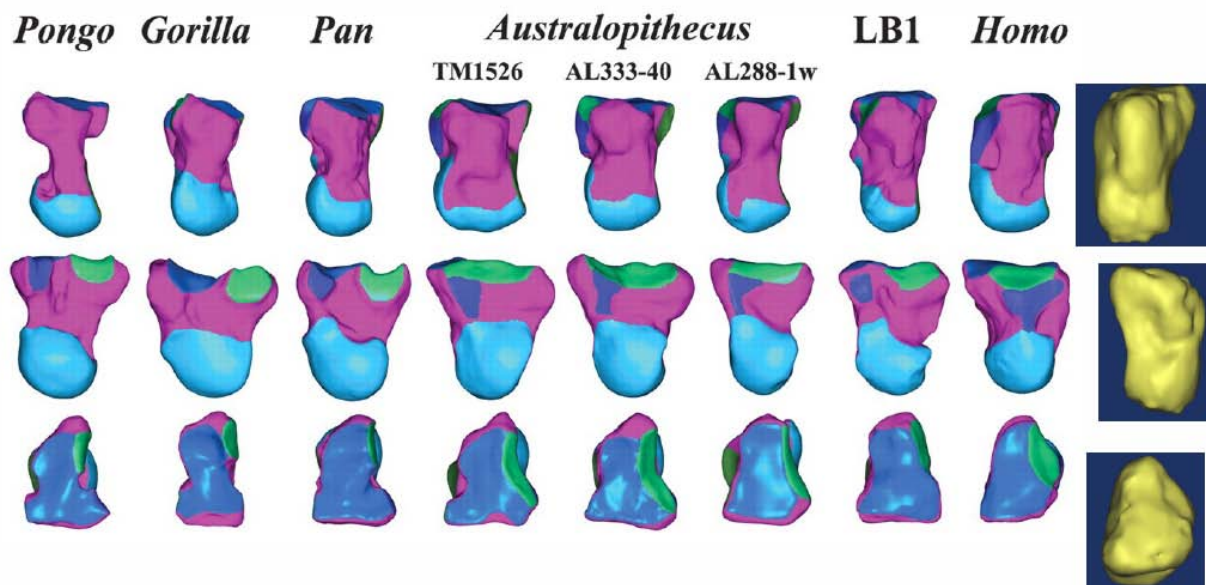


Figure 14 - Capitate - palmar, radial and distal views, Subject A on right, not to scale (Tocheri 2007)

Results

In the literature advocating for naming LB1 as a new species, there are frequent assertions that LB1 did not have a gross pathology, or otherwise afflicted with a syndrome adversely affecting development. For LB1 to be the type specimen for a new species, it cannot be shown, or perceived as being pathological, thus perpetuating the need to dismiss claims to the contrary. The manifestation of this is the failure to test systematically, the hypothesis that LB1 was diseased, and to encumber those who attempt. This has extended to the evaluations presented in this thesis. Numerous researchers have ignored requests for materials, including copies of CT scans of LB1.

In the literature, the carpals are represented as being relatively uniform in morphology, with very little, if any, allowance for variation, whether normal or pathological. As is clearly visible from the cartoon models above, *Homo* is presented as just one form, with no allowances for variation, as if just normal. This is not to mention the wide and deep forms of variation that are possible

with developmental disorders. While it would not be possible to evaluate the range of variation within a population, it is disingenuous to give the appearance that one cartoon model is representative of an entire species.

Variation comes in numerous forms. There is a very strong correlation between the size of a developing embryo and the volume of carpal cartilaginous structure (Durand et al. 2006).

Moreover, the os centrale is frequently found in primates, save African apes and humans, presenting as an accessory bone between the scaphoid, trapezoid and capitate. It develops in the embryo until the 8th week, when it fuses with the scaphoid. However, cases have been documented where it has failed to fuse (Greenspan and Gerscovich 1993). In patients who have hypoplasia of the thumb, a significant number also present with radial hypoplasia or absence of the trapezium and scaphoid. It is suggested that this could be caused by an “environmental insult” between weeks three and eight of embryological development (James et al. 1996).

Trisomy 21, also known as Down Syndrome, can produce an assortment of disease. There is some thought that disorders of chromosome non-disjunction and translocation can present with features that are atavistic (Opitz and Gilbert-Barnes 2005). This is well-documented in the extensor digitorum profundus muscle in the hand in human subjects with aneuploidy (Aziz and Dunlap 1986; Garcia-Mata and Hidalgo-Ovejero 2009). Therefore, it would be conceivable to misdiagnose traits that are from a subject as Down Syndrome as being from an earlier species. Moreover, there is a range of variation in patients with Down Syndrome that exceeds that found in normal subjects in various qualities, including height, hand measurements and bone age (Opitz and Gilbert-Barnes 2005). For example, only a portion of patients with Down Syndrome have clinodactyly of the 5th finger or the diagnostic single palmer crease (Korenberg et al. 1994). Just as there are no morphological necessary conditions to being diagnosed with Down Syndrome, it

follows that patients will present with a constellation of symptoms that tend to cluster together, yet are not equal.

More than thirty mutations including deletions, nonsense, frameshift, missense and splice mutations have been described in the literature that can cause Laron Syndrome. Exon deletions in the extracellular domain of GH-R, with most being in exons 2-7, in addition to mutations in the transmembrane domain and cytoplasmic domain have been elucidated (Zhou et al. 1997). A murine model for Laron Syndrome has been created in vivo. Regardless of the etiology, all result in the failure of the transmission of the growth hormone signal (Zhou et al. 1997) and the instantiation of a phenotype that while not uniform, is more closely related to other subjects with Laron Syndrome than patients without Laron Syndrome.

It is evident that there are differences between the presented bones of Subject A and LB1. Nonetheless, the clavicle shows a class of variation that was stated not to exist in humans. The clavicle also shows a quantifiable deviation from the expected values, a range that is equivalent to that found by both Subject A and LB1. Finally, the carpals share a moderate degree of gross morphological similarity. These results lend credence to the hypothesis that LB1 was afflicted with a growth disorder.

Conclusion

The discovery of this enigmatic specimen has generated a significant amount of public interest. While a majority accepts the conclusions that LB1 represents a holotype for a new species, there is strong evidence to suggest that it may have had a pathology. If true, it would preclude it from being accepted as the touchstone for the species. Those interested in seeing LB1 defined as a new species obviously have a strong interest in controlling access to the specimens and

derivatives, especially to those who may present an alternative conclusion. Given that LB1 lived well within the time span of modern *Homo sapiens*, not only would a strong case need to be demonstrated that it did not have a pathology, but that it is also not within the range of variation for modern humans, especially populations that reside in Southeast Asia.

Presented in this thesis is evidence that LB1 did have a pathology. Some of the supposed unique features of LB1 have been demonstrated to fall within an expanded range of variation for modern humans or is explicable through ecological evolutionary development theory. Whether it is the axial or appendicular skeleton, there is now sufficient evidence to question whether LB1 can be the type specimen for a novel species, let alone as to its taxonomic placement. This scientific discourse should generate a desire for careful introspection of the scientific process that has led to this gross misunderstanding.

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