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Faces of Homo floresiensis (LB1)

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Keywords

lb1, homo, faces, floresiensis, CAS

Disciplines

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Graphical abstract

Abstract

Since being excavated in 2003, the skull of LB1 (the holotype of *Homo floresiensis*) has been given many faces, though the details regarding how each was accomplished are typically few. Here we detail our application of known, and verified, relationships between the skull and soft tissues of anatomically modern humans to produce an evidence-based facial approximation of LB1. We then compare our results to nine pre-existing LB1 faces using geometric morphometrics. These analyses suggest our facial approximation differs in proportional facial width, upper lip height and nasal morphology. Some of these differences are likely due to a different interpretation of taphonomic and excavation damage, application of different 'forensic' methods and/or an idiosyncratic incorporation of aspects of non-human primate morphology. Other differences, and in particular upper lip height, are less justifiable in relation to the skeletal evidence.

Keywords:

Homo floresiensis, Liang Bua, Flores, Indonesia, Facial approximation, Facial reconstruction, Geometric morphometrics

1. Introduction

Since 2004 the partial skeleton of the holotype of *Homo floresiensis*, Liang Bua 1 (LB1) (P. Brown et al., 2004; M. J. Morwood et al., 2005), has been given a number of different faces using a method popularly referred to as ‘facial reconstruction’. We, along with others (e.g. George, 1987; Reichs & Craig, 1998; C. Stephan, 2005; R. G. Taylor & Angel, 1998), prefer the term ‘facial approximation’, both because it is a more accurate description of the results, and to distinguish the process from skull reconstruction following taphonomic and/or excavation damage, as is the case here. Regardless of nomenclature, however, this method of depicting facial appearance is (or at least can be) derived from known relations between the anatomically modern skull and its soft tissues. Not all of these relations have been verified scientifically, and those that are verified tend to be statistical averages, so the results can never be a definitive depiction of a unique face. Therefore, as the results are always approximate, it is only to be expected that facial appearances given to LB1 will differ – and they do.

Here we approximate the facial appearance of LB1 using 2D computer-graphic facial approximation techniques which have been previously applied to the archaeological remains of anatomically modern humans (Hayes, 2011; Hayes, Buckley, Bradley, Milne, & Dennison, 2012), and referring to the relevant findings following nearly a decade of research into this small bodied hominin. We then apply the geometric morphometric (shape) analysis tool, *morphologika2* (v2.5) (O'Higgins & Jones, 2006) to compare our results with pre-existing faces of LB1 from Europe (France, Holland, Spain), North America, Australia and Japan (with the images sourced from Anton, 2012; Balter, 2009; Carr, 2012; Davis & Deak, 2010; Daynès, 2008; Hall, 2010; Kemp, 2004; Roberts, 2011; Sawyer & Deak, 2007). The results of these analyses indicate that our facial approximation depicts a wider and shorter face, and a comparatively more modern human nasal morphology. This may be due to our use of facial approximation methods derived from anatomically modern humans, and/or that many of the faces given to LB1 include aspects of what appears to be a *Pan*-like facial morphology, particularly in regards to upper lip height, even though this is not strongly supported by the skeletal evidence.

2. Methods and Results

Our facial approximation is primarily based on verified, peer reviewed research regarding the relationship between the skull and its soft tissues. These relationships are derived from

studies of living and deceased modern humans, and are clearly limited in their application to archaic hominins. However, in the absence of any verified knowledge regarding the likely facial appearance of archaic hominins, our method does have a distinct advantage in being evidence-based, and therefore able to be subject to ongoing methodological development, informed critique and refinement.

The results of a facial approximation are a series of illustrations (see Figures 1 and 2). Therefore, we present the methods and results as a synthesis, and discuss where these methods are particular to the evidence provided by the LB1 mandible and cranium, and, where relevant, why we have chosen one particular method to approximate an aspect of the face over other published recommendations.

Fig. 1. Facial reconstruction and approximation of LB1 (a) right lateral STDs, profile outlines, feature location/morphology; (b) frontal STDs, feature location/morphology, reconstructed bone (shaded); (c) left lateral reconstruction (mandible only), STDs and CT slices for nasal projection.

2.1 Skull Reconstruction

The LB1 mandible and cranium display a combination of antemortem asymmetry (Baab & McNulty, 2009; Y. Kaifu et al., 2009; Yousuke Kaifu et al., 2010; McNulty & Baab, 2010) and taphonomic distortions, with further inadvertent damage and distortion occurring both during and after excavation (Peter Brown, 2012; Peter Brown & Maeda, 2009; P. Brown et al., 2004; Falk et al., 2010; M J Morwood & van Oosterzee, 2007). A virtual reconstruction was undertaken to best approximate the original form of both the mandible and aspects of the cranium, but limited to only those areas of bone that could be justified through information present in preserved areas of the skull. Our reconstruction of the cranium, therefore, is predominantly the zygomatic and orbital bones, and does not include, for example, the fronto-glabella region, the nasal bones or the sub-nasal region of the maxilla (see Table 1 and Sections 2.2, 2.4.2 and 2.4.3 and regarding our approximation of the craniofacial landmarks

and the soft tissues relating to these areas). The reconstructed areas of bone are shown shaded in the frontal view displayed in Figure 1b, and described in 2.1.1 and 2.1.2 below.

Fig. 2. *Approximation of underlying anatomy and surface appearance (a) right lateral underlying anatomical features; (b) frontal underlying anatomy overlaid with surface features; (c) final result.*

2.1.1 Reconstruction of the mandible

Taphonomic processes contributed to the mandible being broken at the junction of the right second and third molars, right premolar, and left incisor/canine junction, and the left condyle is incomplete (Peter Brown & Maeda, 2009). In addition there is lateral twisting to the right mandibular corpus and ramus, which could be due to antemortem positional plagiocephaly (Y. Kaifu et al., 2009) rather than taphonomy. Either way, further damage was inflicted post-excavation, causing an increase in bigonial breadth and an increase in the lateral twisting of the right corpus and ramus, both of which result in the mandible being unable to be articulated with either the mandibular fossae or the patterns of dental occlusion (Peter Brown, 2012; Peter Brown & Maeda, 2009).

In order to locate each condyle within its corresponding fossa, CT scan data (1mm slices) of the LB1 cranium with the mandible articulated to best fit with the right condyle and right dental occlusion patterns, were uploaded into Amira 5.2.0, and the skull orientated to the right Frankfurt Horizontal Plane (FHP) using the right external auditory meatus and inferior orbital rim. Orthogonal images of the frontal and lateral views were captured, with distortion to the mandible resulting in the left condyle sitting approximately 10mm below the left mandibular fossa. A high resolution stereolithography cast of the LB1 cranium and mandible was articulated to best left premolar and molar occlusion when the left condylar process is orientated within its mandibular fossa, which is located more anteriorly than the right fossa by approximately 6mm. This articulation results in the left mandibular body sitting at an

elevation of 11° to the right FHP. Using Amira 5.2.0, the skull was re-orientated to this left mandibular elevation, and orthogonal images of the left lateral and frontal view of the mandible were captured. All images were uploaded into Adobe Photoshop CS4 (64bit), and scaled to life size. The frontal view of the elevated left mandible was extracted from the midline and relocated within the frontal view of the cranium orientated to the right FHP. Similarly, the elevated left mandible was extracted from the left lateral view and orientated within the left mandibular fossa, again with the cranium orientated to the right FHP (see Figure 1c). This results in a frontal view of the skull with both condylar processes of the mandible located within their mandibular fossa, and in reasonable accordance with both left and right dental occlusion (see Figure 1b).

Our reconstruction of the mandible is approximate. Although rearticulating the mandible by separating it at the midline allows for reasonable occlusion and condylar articulation within very differently orientated mandibular fossae, other reconstructions are possible. For example, it is not evident to what extent this articulation accords with the antemortem disharmonic occlusal relationship identified by Kaifu et al. (2009), and as this reconstruction results in the right and left gonion being symmetrically located despite the rami displaying clear morphological differences (refer Table 1 and Figure 1b). Therefore, it is likely that aspects of antemortem, as well as postmortem, mandibular asymmetry have been obscured.

2.1.2 Reconstruction of the zygomatic and orbital bones

Overall cranial distortion is more clearly visible when viewed in the transverse plane (i.e. above or below), forming what Kaifu et al. (2009) describe as horizontal parallelogram skewing, and which they consider to be symptomatic of antemortem posterior deformational plagiocephaly (PDP). This cranial asymmetry is still, however, within the normal range for modern humans, extant African apes, and aspects of asymmetrical skewing is a common taphonomic process borne by all hominin fossils (Baab & McNulty, 2009). Excavation damage to the cranium includes inadvertent removal of part of the bregma and left frontal bone, all of the left supraorbital rim, the glabella region, nasal bones and subnasal part of the maxilla, and all of the upper incisors. Taphonomic distortion to the right zygomatic arch includes being broken anteriorly and depressed medially, and while the left zygomatic is also broken, it has been reattached (P. Brown et al., 2004; Falk et al., 2010; Yousuke Kaifu et al., 2011).

Comparison of the superior view of the direction and shape of the undamaged section of the right zygomatic root with the left zygomatic root and arch suggests the most lateral point on the right zygomatic arch is on a par with the maximum protrusion of the inflated right supramastoid region. This zygomatic landmark (refer Table 1) and the morphology of the undamaged borders of the left zygomatic bone were used to orientate a reflected section of the left zygomatic, taken from the commencement of the angle of the left temporal margin. Best fit at the angle of the right temporal margin of the right zygomatic bone involved a 6° medial rotation. The left temporal margin of the left zygomatic bone was approximated using a reflected corresponding section of the right zygomatic bone, taken from 4mm superior to the commencement of the angle of the temporal margin of the right zygomatic bone. This segment needed to be rotated medially by 1.2° to fit with the undulation of the left marginal tubercle. Again, as with our reconstruction of the mandible, it is likely that this method reduces LB1's antemortem as well as postmortem bizygomatic facial asymmetry. However, as mentioned, LB1's overall cranial asymmetry is more clearly visible in transverse planes, and is far less apparent when the skull is viewed from the front (though see Section 2.6).

The left superior orbital rim is largely absent, although there is a small section of preserved bone evident on a 3D print produced from the original set of LB1 CT scans, which captured a somewhat less damaged skull (refer M J Morwood & van Oosterzee, 2007), and this appears to be a fragment of the left supraorbital notch. With the virtual skull orientated in the frontal view, a section of the right superior rim (from right supraorbital notch to the frontozygomatic suture) was extracted, reflected, and warped to best fit with the arc indicated by the remains of the superior orbital shape and the preserved bone fragment. This results in a reconstruction of the left orbit where the left superior orbital rim is 3.8mm lower than the right (see Figure 1b), which may be in keeping with the overall pattern of asymmetry displayed by the LB1 remains, and is clearly discernible when the skull is viewed from the front.

2.2 Soft Tissue Depths

The soft tissue depths (STDs) applied in this facial approximation are from Stephan and Simpson (2008) (refer Table 1 and Figures 1a-c). Over the past 130 years many STD studies have been undertaken and published using a variety of methods (e.g. cadaveric needle-punctures, radiographs, ultrasound, CT scans), typically with a focus on a particular population ('race') and sub-divided by sex, age, body mass and/or tissue depth range. Two of the more cited studies include Rhine and colleagues' African American (N=69) and European

(N=63) cadaveric needle-puncture “tissue thicknesses” (reproduced in K. T. Taylor, 2001), and Helmer’s adult, white European (N=124) ultrasound “tissue measurements” taken from living subjects (reproduced in Caroline Wilkinson, 2004). As Stephan and Simpson (2008) note, there are a few problems with STD data collection, including *ad hoc* assignments of population affinity, age and body mass; variation in landmarks, their definitions, actual identification and measurement; and, typographic errors in data set reproductions. Referring to previous studies, Stephan and Simpson report a typical STD measurement error rate of 10%, which, when combined with other influences (e.g. methods used, physical identification of landmarks), produces what they conservatively estimate to be a typical error rate in excess of 2mm. Stephan and Simpson analysed 25 commonly measured landmarks from 55 of the more reliable studies of adult STDs and found that differences arising from publication year, method of measurement, population affinity and sex had little practical value as these differences were consistently less than the conservative STD measurement error value. Therefore, Stephan and Simpson created a pooled STD data collection, comprising total weighted means for each landmark, and a subset of weighted means from the studies reporting standard deviations. The main advantages of the Stephan and Simpson data set is that it is more robust than individual studies, being derived from very large sample sizes (average 3250 individuals, range 545-6786), and is broadly applicable across both sex and population affinity.

With the exception of the right zygomatic (refer Section 2.1.2) and the subnasale (refer Table 1), each STD applied to LB1 arises from preserved bone. As mentioned in Section 2.1 we have not reconstructed the fronto-glabella region, the nasal bones or the sub-nasal region of the maxilla, all of which were inadvertently removed during excavation. Our choices were, therefore, to (i) guess the amount of bone removed, (ii) predict projection on the basis of a possible evolutionary affinity with a different hominin (e.g. Yousuke Kaifu et al., 2011), or, (iii) as we have done, default to the remains of preserved bone, fully aware that this will underestimate, to an unknown degree, the depth of the flesh covering the glabella, nasion, subnasale, mid-philtrum and prosthion. However, as all of the underestimated STDs are located on the cranial midline, the actual depths at these underestimated landmarks are not apparent in a frontal 2D facial approximation (refer Figures 2b and 2c).

Table 1: Craniometric points, definitions and soft tissue depths (STD), from Stephan and Simpson 2008. Note that the STD less one standard deviation (-1s) are calculated from a subset supplied by the authors. Refer Figure 1 for location of points and angles of STD.

	Definition	STD (mm) Weighted Mean	STD (mm) -1s from s Studies	Additional notes regarding identification for LB1
Median Points				Median points were taken primarily from the right lateral, unless otherwise indicated
Vertex	Highest midline ectocranial point	5	4	Highest point on the undamaged cranium corresponding with the midline
Glabella	Most anterior midline point on the frontal bone	5.5	4.5	According to Kaifu et al. (2011) this projects beyond the preserved mid-supraorbital margin by 0-2mm, following other adult <i>Homo</i> individuals from the Pleistocene. We locate this at the maximum lateral projection of the preserved bone (i.e. 0mm)
Nasion	Midline point on the naso-frontal suture	6.5	4.5	Using a midsagittal CT scan Kaifu et al. (2011) identify this as approximately the same height as the right anterior frontomale. In the lateral view we locate this at the most anterior section of the preserved medial border of the left orbit
Rhinion	Midline point at the inferior free end of the internasal suture	3 (not applied)	2 (not applied)	We take this to be correspondent with the most anterior fragment of the superior nasal aperture where the perpendicular plate of the ethmoid bone articulates with the nasal bones in the frontal view, which is lower than that suggested by Kaifu et al. (2011). This location also agrees with the average nasal aperture shape for black and white South Africans (McDowell, et al. 2012). Only the frontal point is approximated, and this is only used for partial calculation of nasal projection (rhinion-subnasale 26.8mm)
Subnasale	Midline point just below the anterior nasal spine	12.5	9.5	Slightly superior (1.5mm) to the preserved section of the right central incisor fossa. As this point cannot be located on preserved bone it is based on an observed relationship between the incisor fossa and the inferior border of the anterior nasal spine in anatomically modern humans, and which has not been verified.
Midphiltrum	Midline point midway between the base of the nasal spine and prosthion on the anterior edge of the maxillae	11	8.5	In lateral view, midway point on the most anterior section of preserved maxillary bone
Prosthion	Midline point at the most anterior edge of the superior alveolar ridge of maxillae	11.5	8.5	Following Kaifu et al. (2011) we locate this as 1mm superior to the preserved central incisor alveolar ridge, which also corresponds to their nasion-prosthion distance of 54mm
Lower lip	Midline point at the most anterior edge of on the inferior alveolar ridge of the mandible	13	10.5	In lateral view, at most anterior point of preserved alveolar ridge
Labiomental	Deepest midline point in the groove superior to the mental eminence	11	9	In lateral view, deepest midline point beneath the alveolar ridge of the mandible
Pogonion	Most anterior midline point on the mental eminence of the mandible	11	8.5	In lateral view, most anterior projection of the mandible beneath the alveolar ridge of the mandible

	Definition	STD (mm) Weighted Mean	STD (mm) -1s from s Studies	Additional notes regarding identification for LB1
Gnathion	Midline point halfway between the pogonion and menton	8.5	5.5	
Menton	Most inferior midline point at the mental symphysis of the mandible	7	4.5	
Bilateral Points				
Gonion	Point on the lateral aspect of the border of mandibular angle where a tangent bisects the angle formed by the posterior ramus border and the inferior corpus border	10	4	Our rearticulation of the left mandible to fit with the left mandibular fossa and molar occlusion results in the right and left gonion being symmetrical in location although the rami differ morphologically
Zygomatic	Most lateral extent of the lateral surface of the zygomatic arch	6	5	See our explanation of our reconstruction of right zygomatic (Section 2.1.2)
Midramus	Point at the centre of the mandibular ramus	17.5	13.5	Morphological difference between the rami results in the left midramus point being slightly lower (0.6mm) than the right

As can be seen, each STD displays two depths (Figures 1a-1c). The greater STDs refer to Stephan and Simpson's (2008) total weighted means, while the lesser depths are their subset of weighted means, minus one standard deviation (s). We chose STD(-1s) to approximate LB1's facial appearance because she is a small-bodied hominin, estimated to be only 106cm in height (P. Brown et al., 2004). This does, however, assume an unverified positive correlation between adult stature and STD¹. Both depths are illustrated, and the difference in facial outline is shown in the right lateral view (Figure 1a). As can be seen, both of the right lateral facial outlines appear to suggest LB1 has an underbite. As this is very likely an artefact of our decision to default to STD underestimation, this characteristic is also not emphasised in the frontal facial appearances (Figures 2b and 2c).

2.3 Underlying Anatomy

The lateral and frontal build up of the virtual facial muscles and parotid glands (see Figures 2a and 2b) are based on those initially developed and described for a computer graphic facial approximation of early Maori remains (Hayes et al., 2012), which was achieved in collaboration with two experienced anatomists, and subsequently applied to other

anatomically modern humans. Every application of this suite of virtual anatomy involves warping each muscle and gland to best fit with the particular morphology of a particular skull, and (where present) the indications of muscle attachments. For this approximation of LB1 the depressor labii inferioris has been further modified to form a better agreement with the descriptions provided by Standring (2008). However, and as noted in Standring, the presence, size and shape of many of these anatomical features vary considerably between individuals, and our observation is that both anatomical descriptions and anatomical depictions can also differ between publications, with the latter depending on the degree of stylisation, the dissector and/or the individuals dissected (e.g. Grant, 1943; Paff, 1973; Romanes, 1986).

2.4 Facial Features

Approximation of the location, size and shape of the facial features (eyes, nose, mouth, ears) and overall head shape are illustrated in Figures 1a and 1b, and again broadly follow the computer graphic methods previously applied to anatomically modern humans (Hayes, 2011; Hayes et al., 2012). There are a number of published recommendations for approximating facial features from the skull. Many of these recommendations, however, are one or all of the following: predominantly experience-based and/or published for a popular audience (e.g. Gerasimov, 1971; Prag & Neave, 1997); lack the evidence from which they were derived (e.g. Fedosyutkin & Nainys, 1993; Gerasimov, 1955); refer to artistic canons and heuristics that anthropometric studies (e.g. Leslie G. Farkas, 1994; Leslie G Farkas & Munro, 1987) largely discount; and/or have since proven to be somewhat less than accurate (e.g. Krogman & Iscan, 1986). Therefore we provide some explanation, where relevant, of our methodological choices for approximating the facial appearance LB1, acknowledging that many of these verified skull-soft tissue relationships are derived from predominantly 'white' or 'European' population affinities, and that application of these relationships is still subject to some degree of interpretation – both of the skull and of the methods themselves.

2.4.1 Eyes

According to Wolff (1948) the average human eyeball is 23.5mm horizontally and 23mm in height, whereas a recent CT scan study involving 375 individuals (204M and 171F, mean age 52.2 years) shows these average distances to be 24.3mm and 24.6mm respectively (Guyomarc'h, Dutailly, Couture, & Coqueugniot, 2012). This approximation uses an average diameter of 24mm, which is greater than Wolff's recommendation, yet less than the

unverified recommendations of 26mm (Prag & Neave, 1997) and 25mm (K. T. Taylor, 2001; Caroline Wilkinson, 2004). A long-standing forensic recommendation is to locate the eyeball centrally within the orbit (Gatliff & Snow, 1979; Krogman & Iscan, 1986). However, two cadaveric studies (C. Stephan & Davidson, 2008; C. N. Stephan, Huang, & Davidson, 2009) support earlier anatomical claims that the human eyeball is displaced from the orbital centre (e.g. Wolff, 1948). The combined results of these cadaveric studies are that, on average, the eyeball is displaced 1.4 mm superiorly and 2.3 mm laterally (C. N. Stephan et al., 2009), with these results being further verified by the CT scan study referred to above (Guyomarc'h et al., 2012).

Kaifu et al. (2011) comment that LB1 has a “unique, tall orbital shape”, and while are able to locate LB1’s eyeballs 1.4mm superior to their orbital centres, we found they could only be reasonably displaced 1mm laterally. It is possible that LB1 had a smaller than average eyeball diameter to better fit with the orbital widths, however there is an experience-based recommendation that orbital dimensions bear no relationship to eyeball size (Gerasimov, 1955), at least for anatomically modern humans.

With regards to eyeball projection, this has been traditionally located projecting to the maximum extent of the superior and inferior orbital rims (Krogman & Iscan, 1986). Two studies, however, show eyeball projection exceeds this point. One study (C. N. Stephan, 2002) reviewed published exophthalmometric measures, which included MRI measures (n=79), and reports that the modern human eyeball, on average, protrudes 3.7mm beyond the tangent formed by connecting the superior and inferior orbital rims. A related study (Caroline Wilkinson, Caroline, & Sophie, 2003), examined 39 MRI scans of mature European adults (11M, 28F, 60-90yrs), and found average eyeball protrusion to be very similar (3.8mm). For this approximation right lateral eyeball projection is approximately 3.75mm.

Our estimation of the location of LB1’s palpebral fissures is based on a line connecting the endocanthion and exocanthion. The malar tubercle is often cited as corresponding to the location of the lateral canthal tendon (e.g. Fedosyutkin & Nainys, 1993; Gerasimov, 1955), which Stephan and Davidson (2008) verify as a consistent finding. For LB1 the exocanthion (lateral canthus) is located at the marginal tubercle, which appears present for both orbits, while the endocanthion (medial canthus) is inserted into the remains of each lacrimal fossa 1mm below the exocanthion. Stephan and Davidson (2008) offer other orbital landmarks to

identify the average orientation of the endocanthion, however, as it has been observed, many of LB1's cranial sutures are difficult to identify even from CT scans (P. Brown et al., 2004; Yousuke Kaifu et al., 2011), and this includes the sutures required to identify the dacryon.

Other recommendations regarding eye morphology that have been applied in this approximation include: the average iris diameter is 10-12mm (Larrabee & Makielski, 1993), with 10mm being selected for the surface result (see Figure 2c); the location of the superior eyelid fold may correspond to the same height of the soft tissue nasion (George, 2007), the shape of the superior eyelid fold may be related to the shape of the superior orbital rim (Fedosyutkin & Nainys, 1993); and, dominant brow-ridges have been observed to display thicker soft tissues and a soft transition over the ridges (Gerasimov, 1955).

2.4.2 Nose

Overall, our approximation of LB1's nasal morphology is highly approximate. Although the skeletal remains still include the general lower shape and maximum width of the aperture, and the preserved remains of the ethmoid plate indicate approximate aperture height, excavation damage has removed all accurate locations for the nasion, rhinion and subnasale, and the anterior edge of the right lateral wall of the aperture. Therefore, other than nasal width and the general shape of the left nasal wing and nasal tip, different interpretations and evidence to approximate these missing aspects is both possible and justifiable.

Gerasimov's observation (1955, 1971) is the most well-known and applied skeletal method for estimating the location of the nasal tip. That is, the nasal tip will be found where a line continuing the general direction indicated by the nasal bones intersects with a line continuing the general direction indicated by the anterior nasal spine (e.g. Prag & Neave, 1997; K. T. Taylor, 2001; Caroline Wilkinson, 2004). Unfortunately, in addition to being experience, rather than evidence, based, this description of the method combines a misleading overgeneralisation with an unfortunate mistranslation. According to one of Gerasimov's students, 'nasal bones' more specifically refers to the most anterior undulation of the nasal bones at the rhinion, and nasal spine should instead refer to the right and left base of the nasal aperture, lateral to the nasal spine, and not the anterior nasal spine itself (Ullrich & Stephan, 2011).

Our approximation uses a subset of the regression equations developed by Rynn et al. (2010) and derived from 79 North American CT scans and 60 European cephalograms (N=139) of the adult (< 50 years) head and face and, as the authors note, ‘white’ ancestry dominates the data (n=110). The results of this study also include some verification of Gerasimov’s other observations regarding the relationship between aspects of the nasal aperture and the soft tissues of the nose.

To estimate profile nasal dimensions, Rynn et al. (2010) use up to three cranial measures involving the nasion, acanthion, rhinion and subspinale landmarks (see Table 1, and note that subspinale is referred to here as subnasale). The regression equations used for our approximation of LB1’s nasal morphology are those that do not include the acanthion (as the anterior nasal spine is missing), and are summarised as follows:

- $[(\text{rhinion-subnasale } 26.8\text{mm}) * 0.83] - 3.5 = 18.7\text{mm}$ anterior projection from the nasion-prosthion plane (valid for all populations studied)
- $[(\text{nasion-subnasale } 43.4\text{mm}) * 0.74] + 3.5 = 34.7\text{mm}$ nasal length from the soft tissue nasion to nasal tip (valid for ‘white’ populations only)
- $[(\text{nasion-subnasale } 43.4\text{mm}) * 0.63] + 17 = 44.3\text{mm}$ nasal height from the soft tissue nasion to subnasal (valid for female ‘white’ populations only)
- $[(\text{rhinion-subnasale } 26.8\text{mm}) * 0.5] + 1.5 = 15.7\text{mm}$ nasal depth from the nasal tip to soft tissue subnasal (valid for female ‘white’ populations only).

As detailed in Table 1 we approximate the rhinion (end of nasals) in the frontal view through reference to the preserved remains of the ethmoid plate and a pooled average nasal aperture shape (McDowell, L’Abbé, & Kenyhercz, 2012), which is illustrated in Figure 1b. The rhinion, however, is only used for the Rynn et al. (2010) equations referring to anterior nasal projection and nasal depth, and not to give shape to the upper nose in profile. As can be seen (Figure 1a), instead of following the undulation of the nasal bones (which were accidentally removed on excavation), our depiction of the nasal profile runs straight from nasion to nasal tip. Also detailed in Table 1, we identify the nasion in reference to Kaifu et al. (2011), and the subnasale is located 1.5mm superior to the preserved section of the right central incisor fossa.

In addition to deriving the regression equations listed above, Rynn et al. (2010) also add verification to Gerasimov’s (1955, 1971) observations that maximum nasal aperture width is very close to 2/3 the maximum width of the nasal wings, which for LB1 results in a

maximum nasal width of 35mm. Other observations of Gerasimov that Rynn et al. add verification to include: that in profile the maximum curve of the nasal wing is approximately 6mm anterior to the most posterior point on the lateral wall of the aperture; maximum nasal wing height closely corresponds to the *christa conchalis* on the lateral wall of nasal aperture; maximum nasal wing depth is 4mm lower than the lowest point on the curve of the lateral aperture border; that the shape of the alar groove generally correlates to the lateral curve of the aperture, and, overall, that individuals displaying ‘angular’ nasal apertures tend to have a pointed or angled nasal tip, and ‘rounded’ apertures, rounded tips.

For our approximation of LB1 the shape of the nasal wings and nasal tip are taken to have a close, rather than more general, correspondence with the shapes of the lateral curves of the nasal aperture. Although such a literal interpretation of Rynn et al. (2010) is not the published recommendation and unlikely to be accurate, it does remove the need for a more subjective interpretation which would be required to produce a somehow more analogous shape relationship. In addition, and because of excavation damage to the nasal aperture, our capture of the shape of the right lateral curve of the nasal aperture is more informed by the general arc of what remains of the lateral wall. Excavation damage also makes it impossible for us to apply a different, verified hard/soft tissue relationship involving the curvature of the superior nasal bones and the curvature of the nasal tip (Davy-Jow, Decker, & Ford, 2012). A further point is that in our approximation of LB1’s nasal tip, rather than Rynn et al.’s (2010) reading of Gerasimov as referring to the anterior nasal spine, we estimate nasal tip direction following the translation supplied by Ullrich and Stephan (2011), and identify nasal tip direction from two sagittal CT slices taken lateral to the nasal spine (see Figure 1c). As can be seen, this tangent passes through the centre of the nasal tip close to the approximated maximum nasal length (34.7mm).

2.4.3 Mouth

For many years mouth width was taken to correspond to interpupillary width (Krogman & Iscan, 1986) and/or at some point radiating out from the canine/premolar junction (Krogman & Iscan, 1986; C Wilkinson, Motwani, & Chaing, 2003), while Gerasimov’s observation is that mouth width corresponds to the inter-premolar width of the maxilla (1955). Subsequent research (C. N. Stephan, 2003) has shown that in living subjects the interpupillary rule overestimates European mouth width (n=61), though is a reasonable approximation for a smaller group of South East Asian subjects (n=27), while the canine/premolar junction rule

consistently underestimates mouth width for both groups. Stephan's findings are that the medial border of the iris is a closer approximation of mouth corner location, but a more consistent guideline for all of the populations he studied is the following: (intercanine width) + $0.57 * [(interpupillary \text{ width}) - (intercanine \text{ width})]$. More recently, Stephan and Murphy (2008) further explored the results reported by Song et al. (2007), who's cadaveric study included an anthropometric analysis of the relationship between soft tissue landmarks and skeletal foramina. Song et al. examined 50 embalmed cadavers (32-101 years) of Korean population affinity, and found: the distance between the infraorbital foramina is close to identical to mouth width; for approximately half the individuals examined the infraorbital foramen and cheilion are located on the same sagittal plane; and, that the distance between the cheilion and the mental foramen is, on average, approximately 20mm (mean 20.9 mm, $s = 3.8\text{mm}$). Stephan and Murphy (2008) dissected nine cadavers of European population affinity (62-74 years), and their results add general support to that of Song et al. (2007).

For this facial approximation LB1's mouth corners are located on the same sagittal plane as the infraorbital foramina, and the resulting visible mouth width (43.7mm) is very close to the approximation arising from Stephan's algorithm reported above (i.e. $39\text{mm} + [0.57 * (48.5\text{mm} - 39\text{mm})] = 44.14\text{mm}$). Interestingly, however, our mouth width does not agree with a simplified algorithm developed by Stephan and Henneberg (2003), who show intercanine width to be approximately 75% of mouth width – which in this instance results in a mouth that is 8mm wider, and were it implemented would result in a mouth that is even wider than the interpupillary rule.

Transverse location of the oral fissure typically follows the recommendation of being within the lower third of the central incisor (K. T. Taylor, 2001), which is similar to the anatomical location of being slightly superior to the incisal edges of the anterior maxillary teeth (Standring, 2008). Location of the oral fissure for LB1 was taken to be slightly superior to the inferior edge of what remains of the dentine of the upper right canine, which is in accordance with the more general anatomical location, and is also approximately 20mm from each of the mental foramen (i.e. the average distance reported by Song et al. (2007)). Vermilion heights have also been examined in relation the height of the dentine of the central incisors. Digital calliper measures were taken of living subjects ($N=95$) (C Wilkinson et al., 2003), and the following formulae derived for 'white' Europeans:

- upper vermilion height = $(0.6 * \text{upper central incisor height}) + 0.4$

- lower vermilion height = $(0.4 * \text{lower central incisor height}) + 5.5$

Again due to the absence of the superior central incisors, upper vermilion height was calculated using the height of the dentine of the upper right canine (7.7mm) and lower vermilion height was calculated from the lower lateral right incisor (7.6mm) as it appears to display comparatively less tooth wear. This results in our approximation displaying an upper vermilion height of 5mm and a lower vermilion height of 8.5mm, which is close to the average lower vermilion height reported in this study (8.7mm), but nearly 1mm less than the average upper vermilion height (5.8mm). This could be because, in addition to our use of upper canine dentine, and not upper central incisor, Wilkinson et al.'s (2003) formulae are derived from extant Europeans, who presumably did not display extensive tooth-wear – which is a marked feature of LB1 (Peter Brown & Maeda, 2009).

Other recommendations for the mouth and used in our facial approximation of LB1 are that prominent canines may suggest lateral vermilion fullness (Caroline Wilkinson, 2004), and that philtral width may be related to the width of the central incisors (K. T. Taylor, 2001), which in this instance was approximated as possibly corresponding with the centre of the upper central incisor roots rather than the teeth themselves.

2.4.4 Ears

Recommendations to predict the shape, dimensions and angle of orientation of the ear from the skull have been evaluated by comparing each with both a CT scan analysis and a raft of published anthropometric data (Guyomarc'h & Stephan, 2012). The results of this study discredit all recommendations, and in some detail. Guyomarc'h and Stephan conclude that all non-Asian individuals should be approximated with free earlobes (as opposed to attached); that reliable anthropometric mean ear angles and mean ear width, such as those listed in Farkas (1994) are preferable, and that ear height is best approximated using their regression equation, derived from measurements taken from European CT scans (N=78, 43M, 35F; 18-84 years):

$$\text{ear length} = (4.85 * \text{sex}) + (0.10 * \text{age}) + 54.95, \text{ where male} = 1, \text{ female} = 0.$$

What this indicates is that males tend to have an ear that is 4.85mm longer, and that this regression usefully incorporates adult age-related changes to ear length. However, the need to enter a numerical age into the equation renders application impractical when age is only generally understood. LB1, for example, is estimated to be adult (Peter Brown & Maeda, 2009), which is a description spanning decades. Therefore we take ear height to be equivalent

to the soft tissue distance subnasal-menton (50mm), an anthropometric relationship described in Farkas (1994), and orient the tragus in its relation to the external acoustic meatus (Romanes, 1986). All other aspects of ear morphology depicted in our facial approximation are wholly subjective (refer Figure 2c).

2.4.5 Head shape

Upper head shape (Figure 2) is largely determined by the arc of the cranium, and the foreshortened forehead height is due to LB1 having a low cranial vault (P. Brown et al., 2004). In the mid-face the maximum width of the cheeks corresponds to the underlying bony bizygomatic width plus STD(-1s), and upper cheek protrusion and shape follows the protrusion and shape of the zygomaxillary bones. Bigonial width and overall jaw shape follows that indicated by the approximately reconstructed mandible plus STD(-1s), and as *Homo floresiensis* is without a bony chin (P. Brown et al., 2004) we assume this also holds true for the fleshed face.

2.5 Surface Appearance

The general consensus is that human skin is darker at the equator than at greater latitudes (Barsh, 2003), and Liang Bua (Flores, Indonesia) is located at 8.6°S. Research concerning the melanocortin 1 receptor (MC1R) locus indicates *Homo* has been hairless for at least 1.2 million years (Rogers, David Iltis, & Stephen Wooding, 2004), which has congruence with the ectoparasite theory, where a lack of thermal fur has an evolutionary advantage in reducing parasites (e.g. lice and fleas) (Rantala, 2007). We therefore approximate LB1 with fairly dark skin and lacking facial fur.

The cranium does not provide indicators regarding head hair colour or shape, and in all of the previous published research on which our method of approximation is based it has been argued that baldness is preferable in an evidence-based archaeological facial approximation (Hayes 2011; Hayes, et al. 2012; Hayes, et al. 2009). Hairless results, however, are typically interpreted as male (SH, personal observation), and LB1 is most likely female (Peter Brown, 2012; Peter Brown & Maeda, 2009; P. Brown et al., 2004). Therefore the likelihood that LB1 bore head hair is a more reasonable assumption than that she was bald². As can be seen (Figure 2c), we approximate an appearance of wet hair to allow for a more indefinite shape, length and texture, and to avoid an unjustifiable and yet enduring tendency to depict all early

hominins, including anatomically modern humans, as ungroomed and unkempt (Berman, 1999; Kemp, 2004).

2.6 LB1 facial variance

A 2D geometric morphometric analysis of an international selection of pre-existing faces of LB1 (n=9, with 2D images sourced from Anton, 2012; Balter, 2009; Carr, 2012; Davis & Deak, 2010; Daynès, 2008; Hall, 2010; Kemp, 2004; Roberts, 2011; Sawyer & Deak, 2007) together with our facial approximation (N=10) was undertaken using the shape analysis tool, *morphologika2* (v2.5) (O'Higgins & Jones, 2006). The 46 homologous soft tissue facial landmarks applied to these images are based on prior research exploring measurement of facial morphology in 2D images (Hayes, 2010), which has been further refined to explore patterns of distortion arising from mimetic portraiture (Hayes & Milne, 2011) and actual police witness descriptions of suspects (Hayes & Tullberg, 2012). In all of these previous analyses, the first Principal Component (PC), which captures the greatest variance between the individuals comprising the data set, concerned variations in head pose. Because we include Procrustes registration in our analysis of these LB1 faces (i.e. the landmarks are scaled, and rotated, for comparable fit), head canting (leaning the head towards one shoulder) does not impact on facial shapes, but head turning alters the horizontal dimensions of the face (and in particular cheek widths), and head pitching results in both vertical and horizontal changes (i.e. an upwards pose will contract the upper head, widen the jaw, give the appearance of an upturned nose and downturned mouth, and increase chin height).

As can be seen from the Procrustes registered wireframes of each of the LB1 images we analyse (Figure 3), there is some variation in head pose. Six LB1 faces are frontally orientated (Shapes 1, 2, 5, 7, 8, 10) with one of these displaying an upwards pitch (Shape 1), three display a head turn to the right shoulder (Shapes 3, 4, 9), and one has a slight head turn to the left (Shape 6). Furthermore, six of the images are photographs of 3D sculptures taken from unknown, and likely varying distances (Shapes 2, 3, 4, 6, 7, 8), and therefore, in addition to the small sample size, our analyses should only be read as indicative of depicted LB1 face shape variance.

Fig. 3. Wireframes of the LB1 faces analysed. Our facial approximation is Shape 5 (top row, far right). The remaining images were sourced as follows: Top row, from left: Shape 1 (Carr, 2012); Shape 2 (Daynès, 2008); Shape 3 (Davis & Deak, 2010); Shape 4 (Balter, 2009). Bottom row, from left: Shape 6 (Hall, 2010); Shape 7 (Roberts, 2011); Shape 8 (Sawyer & Deak, 2007); Shape 9 (Kemp, 2004); Shape 10 (Anton, 2012).

When all of the LB1 faces (N=10) are analysed, the thin plate spline (TPS) deformation grids show, as with previous studies, that the greatest variance is due to head pose (Figure 4: PC1 54.6%). The second greatest variance (PC2 16.6%) separates out the face shapes by relative eye roundedness, nose width, upper lip height (subnasal to superior vermillion border), and mouth width. Overall, PC2 indicates some LB1 depictions tend towards displaying LB1 with rounded eyes, short, narrow noses, narrow vermillion zones of the lips within wide mouths, and relatively narrow and long faces, with facial length being strongly influenced by upper lip height. The extreme of this group is the very first face given to LB1 (Shape 9 reproduced in Kemp, 2004), but it is possible that the variance displayed in PC2 is potentially compromised by including aspects of head pitch (Shape 1).

A second geometric morphometric analysis involving only the frontally orientated LB1 faces (n=5: Shapes 2, 5, 7, 8 and 10) does not capture variance related to head turning and pitch, and even without the prototype LB1 face (Shape 9), the results still show a tendency for LB1 faces to be narrow and display a marked upper lip height (Figure 5: PC1 38.1% variance). The next largest variance (PC2: 30.3%) concerns relative fullness of the vermillion zone of the lips, eye size, and that Shape 7 (reproduced in Roberts, 2011) depicts a face where excavation damage to the LB1 right orbital bones may possibly have been interpreted by the creators as an antemortem injury/pathology affecting both the size and orientation of the right palpebral fissure.

Fig. 4. Geometric morphometric analysis of all LB1 faces ($N = 10$) and Thin Plate Spline deformation grids showing overall variance for PC1 (x axis) and PC2 (y axis). The Thin Plate Splines were extracted from the following coordinates: PC1 -0.013 , PC1 ± 0.014 , PC2 -0.09 , PC2 ± 0.09 . The mean face for the group is shown bottom left, and includes some aspects of head turn facial morphology.

Fig. 5. Geometric morphometric analysis of only the frontally posed LB1 faces ($n = 5$) and Thin Plate Spline deformation grids showing overall variance for PC1 (x axis) and PC2 (y axis). The Thin Plate Splines were extracted from the following coordinates: PC1 -0.07 , PC1 ± 0.05 , PC2 -0.05 , PC2 ± 0.05 . The mean face for the group is shown bottom left, the overlay of Procrustes registered wireframes is shown bottom right.

The morphology of the mean LB1 face in this analysis (inset lower left Figure 5) and the pattern of distribution across PC1 and PC2 (capturing 68.4% of the variance) suggests our facial approximation of LB1 (Shape 5) is quite different from all of the other LB1 facial shapes. When the Procrustes registered wireframes are extracted from *morphologika2* prior to

running the PC analysis (inset lower right Figure 5), the wireframe of our facial approximation displays the widest face, the greatest hemiface asymmetry (the right mid-face and jaw are distinctly wider than the left), and the shortest upper lip distance.

3. Discussion

The first stage in our facial approximation of LB1 was to reconstruct the mandible and cranium so as to best approximate its form prior to taphonomic, excavation and post-excavation damage. The actual extent of taphonomic and excavation damage is unknown, and therefore the remains are open to different reconstructions. For our facial approximation of LB1 we have applied predominantly robust relationships between the skull and its soft tissues, and all of the relationships that form our methodology are derived from studies of anatomically modern humans (Sections 2.2, 2.3 and 2.4.1-2.4.4). The applicability of these methods to the remains of archaic hominins is limited. LB1 is the holotype specimen of *Homo floresiensis*, and while sharing ancestry with *Homo sapiens*, LB1 is not an anatomically modern human. To test our results we conducted a geometric morphometric analysis including nine other pre-existing LB1 faces. Because of the influence of head pose and perspective on facial shapes, and the small number of faces analysed, these analyses are generally indicative rather than conclusive, and suggest our approximation of LB1's facial appearance displays a greater hemiface asymmetry, a proportionally wider face, and a shorter upper lip (subnasale-vermillion border), than most of the faces given to this archaic hominin.

Our reconstruction of the mandible involved splitting the body at the midline and re-articulating the left ramus and mandibular body so that both condyles were located within their mandibular fossae and in reasonable accordance with dental occlusion patterns (Section 2.1.1). Reconstruction of the zygomatic bones and right orbital bones was achieved through reflection, but with the reflected fragments manipulated so as to agree with information retained within relevant areas of preserved bone, such as the right zygomatic root, left marginal tubercle and left supraorbital notch (Section 2.1.2). Other skull reconstructions are possible, and justifiable. For example, it is likely that we have reduced the overall patterns of asymmetry which may have been an antemortem feature of this individual (see Y. Kaifu et al., 2009). However, even though LB1's asymmetry is a parallelogram skewing that is more apparent in the transverse plane, the Procrustes registered wireframe of our facial approximation shows a clear hemiface asymmetry that is in agreement with LB1's pattern of

cranial skewing, and further, that the right and left gonial angles differ (Figure 3, Shape 5) – at least, in so far as the soft tissue landmarks applied capture this aspect of facial morphology.

We apply, where possible, robust relationships to approximate the face of LB1. However, there are a number of ‘forensic’ recommendations that are still widely circulated and applied, even though many have proven to be less than reliable. These include STD data sets (Section 2.2) as well as recommendations for estimating the shapes, size and orientation of the eyes, nose, mouth and ears (Section 2.4). It is likely that the variance displayed between the LB1 faces analysed is due, in part, to the application of different skull/soft tissue relationships. Variance may also be due to some of the faces containing an admixture of extant non-human primate, as well as anatomically modern *Homo*, facial characteristics.

A number of the creators of LB1 faces describe their incorporation of “forensic” methods, such as applying STDs (e.g. as described in Balter, 2009; Daynès, 2008; Koepfer, 2003; Roberts, 2011; Sawyer & Deak, 2007), and therefore these would be depths derived from anatomically modern humans. It is likely that the STD data set, landmarks and angles of insertion selected for these LB1 faces will differ from each other, and from ours (i.e. C. N. Stephan & Simpson, 2008), and therefore slight differences in facial morphology is to be expected. However, because we have applied STD(-1s) (refer Section 2.2), our expectation was that, overall, our facial approximation would display a proportionally narrower face. However, the geometric morphometric analysis shows that our facial approximation is very likely the proportionally widest LB1 face (Section 2.6, Figures 3 and 5).

There are three possible reasons why our LB1 face appears wider. Firstly, our results are orthogonal (built from CT scans), whereas the other 2D images of LB1 faces probably include aspects of photographic and/or artistic perspective. Secondly, face shape, including facial width and facial asymmetry, will be influenced by how the mandible has been articulated, and the extent to which taphonomic and post-excavation damage has been addressed and/or incorporated (refer Section 2.1.1). Thirdly, some of the creators of the faces analysed here (Shapes 4, 7, 8) also describe including non-human primate anatomy in their work (detailed in Koepfer, 2003; Roberts, 2011; Sawyer & Deak, 2007), though these creators do not specify which aspects, or which primate.

Research involving dissection of *Pan troglodytes* shows that while human and chimpanzee facial musculature is close to identical, chimpanzee faces have very little adipose tissue (Burrows, Waller, Parr, & Bonar, 2006). Comparing the average STDs from a preliminary study using ultrasound measures taken from living, adult *Pan troglodytes* (n=16-19, Hanebrink, 2006) with Stephan and Simpson's (2008) weighted means, chimpanzee STDs are approximately half that of modern humans in the area of the cheeks (at the landmarks lateral to the superior and inferior second molars), which is where most of the fat in the human face is located (Raskin & LaTrenta, 2007). Use of *Pan troglodytes* STDs would, therefore, produce a thinner mid-face than a depiction based on anatomically modern human STDs, and perhaps explain why many LB1 faces appear to be proportionately narrower than our facial approximation. However, the Hanebrink's (2006) STD data also shows that chimpanzee STDs are nearly twice as thick as modern humans at the angle of the jaw (gonion), and this aspect of *Pan* anatomy does not seem to be a feature that has been incorporated into any of the LB1 faces analysed here.

Perspective, mandibular articulation and selective incorporation of mid-face *Pan* STDs may explain why geometric morphometric analyses suggest a tendency towards depicting LB1 with a narrower mid-face, but not the trend towards depicting LB1 with a long upper lip. As discussed (Sections 2.1 and 2.2), excavation of the LB1 cranium included inadvertent removal of the surface of the subnasal region of the maxilla, and this damage confounds all of the upper and mid-face anterior dimensions, such as STDs along the midline when the skull/face is in profile. This excavation damage does not, however, confound bone orientation on the sagittal plane. LB1's nasal aperture base, maxilla, alveolar ridges and remaining maxillary dentition retain their vertical orientations, even though the surfaces have been inadvertently sheared away. Therefore, the tendency to depict LB1 with a long upper lip is not strongly justified by the skeletal evidence.

Our approximation of LB1's nasal dimensions sits within the range of noses depicted for LB1. Some are narrower, and some are broader, though broader noses could be an artefact of artistic/photographic perspective. A narrower appearing nose is not related to perspective, and is a feature of three LB1 faces (Shapes 2, 6 and 9). This could be due to an interpretation of LB1's nasal aperture as more similar to non-human primates. Research regarding *Pan troglodyte* nasal apertures finds they are less elongated (Schmittbuhl, Le Minor, Allenbach, & Schaaf, 1998) and narrower (Neaux, Guy, Gilissen, Coudyzer, & Ducrocq, 2013) than

modern humans, and in *Pongo*, *Gorilla* and *Pan*, the nasospinale and premaxilla have very different orientations (e.g. McCollum & Ward, 1997). However, the relationship between the hard/soft nasal tissues of non-human primates does not appear to be as well studied, or verified, as modern *Homo*. A further point is that of the creators who include aspects of non-human primates in their work (as described in Koepfer, 2003; Roberts, 2011; Sawyer & Deak, 2007), all depict a broad, and not narrow, LB1 nasal morphology (Shapes 4, 7, 8). Quite what the justification could be for depicting LB1 with a narrower nose is therefore unknown at this time.

Other aspects that could influence the facial morphology of LB1 include the quality of the casts on which the faces were based, and the knowledge underpinning interpretation of the remains. It is likely that an LB1 face would be severely compromised if the skeletal cast was estimated from photographs and/or the creators did not perceive many of the distortions to the mandible and cranium as having occurred postmortem (as appears to be the case with Shape 7 – see Section 2.6). It is also likely that some LB1 faces would be discordant with the remains if they were created without due reference to the existing body of research, and/or before there was widespread consensus (e.g. Aiello, 2010; Argue, Morwood, Sutikna, Jatmiko, & Saptomo, 2009; Yousuke Kaifu et al., 2011) concerning LB1's status as an archaic hominin (with this being most likely with the first LB1 face, Shape 9). A further possibility is that some of the LB1 faces could also have been (mis)guided by a common, and well-documented, assumption within archaeology that archaic hominins fall into the socio-historical categories encompassing “wild men”, “missing links” and “ape-men” (Berman, 1999; Montagu, 1947; Moser, 1992). This last point could also be related to why there appears to be a marked tendency to generally, or selectively, reference or allude to non-human primate morphologies in LB1's facial features, even though LB1 is a member of the *Homo* genus, and much more is known, and verified, regarding the relationship between the skull and soft tissues of modern *Homo sapiens*.

3. Conclusion

Our facial approximation of the *Homo floresiensis* holotype is the result of our virtual reconstruction of the LB1 mandible and cranium and subsequent application of known and verified data, algorithms and guidelines derived from the faces of anatomically modern humans. However, although we approximate the face and features of LB1 using statistical averages, and therefore unavoidably average her facial appearance, these results still

incorporate differences due to the unique bony morphology of the skeletal remains. In the case of LB1 these include a low forehead, prominent brow ridges, distinct cheek bones, facial asymmetry, a comparatively short upper lip, and a jaw lacking a chin.

Footnotes:

1. We are grateful to Mark Collard for alerting us to this
2. Thank you to Debbie Argue for providing this reasoning

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