Title: Quantitative shape analysis of the deltoid tuberosity of modern humans (*Homo sapiens*) and common chimpanzees (*Pan troglodytes*)

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ABSTRACT

Purpose: To identify anatomical differences in the deltoid tuberosity of *Homo sapiens* and *Pan troglodytes,* potentially relating to the different uses of the forelimb in these two phylogenetically related species.

Basic procedures: We have used three-dimensional geometric morphometrics (3D GM) to analyze the deltoid tuberosity of scanned humeri from 30 *H. sapiens* and 27 *P. troglodytes*. We also used the 3D scans of the humeri to calculate the surface area of the deltoid tuberosity. Finally, we dissected the deltoid muscles of three *H. sapiens* and three *P. troglodytes* to determine the relative mass and the physiological cross-sectional area (PCSA) of each part of the muscle.

Main findings: The 3D GM analysis of the deltoid tuberosity identified an anteroposterior enlargement of the *P. troglodytes* tuberosity, with a lateral displacement of the middle segment, whereas in *H. sapiens*, there was a distal displacement of the middle segment. Muscle architecture analysis indicated higher normalized values of the PCSA of the clavicular and acromial deltoid in *P. troglodytes*.

Principal conclusions: The anatomical features observed in our *P. troglodytes* specimens serve to strengthen the three parts of the deltoid muscle. This fact can be related to the use of the forelimb in locomotion, both arboreal and knuckle-walking, in this species. Humans use the forelimb mainly in manipulative tasks, so they do not develop – as do chimpanzees – the anatomical features that increase the deltoid force. Our findings have shown that the different uses of the forelimb in modern humans and common chimpanzees can affect both muscle architecture and bone morphology, either jointly or separately.

Key words: deltoid muscle, morphometry, suspensory primates

1. INTRODUCTION

The deltoid muscle (Fig. 1) is divided into three parts: the clavicular deltoid (CD), the acromial deltoid (AD), and the spinal deltoid (SD) (Leijnse et al., 2008; Wysiadecki et al., 2014). All three parts converge at their insertion on the deltoid tuberosity, located on the lateral humeral shaft (Aiello and Dean, 1990). The primary function of the deltoid muscle in humans is the elevation of the forelimb in the scapular plane, with the CD acting as a flexor and internal rotator of the glenohumeral joint, the AD as an abductor, and the SD as an extensor and external rotator (Inman et al., 1944; Basmajian and De Luca, 1985; Levangie and Norkin, 2001; Gray and Standring, 2005; Gorelick and Brown, 2007; Michilsens et al., 2010).

The role of the deltoid muscle in elevating the forelimb is of utmost importance in primates using suspensory locomotion (Dunham et al., 2016), such as some members of the superfamily Hominoidea, which includes gibbons (*Hylobatidae*), orangutans (*Pongo spp.*), gorillas (*Gorilla spp.*), common chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*) and humans (*Homo sapiens*) (Gebo, 2014). Anatomical modifications in the glenohumeral joint of these primates increase their mobility (Ankel-Simons, 2000) and facilitate the elevation of the forelimb, which is the basis of brachiation, or arm swinging. These anatomical modifications that increase the biomechanical efficacy of the deltoid muscle in hominoid primates (Inman et al., 1944; Ashton and Oxnard, 1963; Aiello and Dean, 1990) include the presence of a wide deltoid tuberosity located relatively distally on the humeral shaft (Dunham et al., 2016). Moreover, the importance of forelimb elevation in hominoid primates results in a large deltoid muscle mass in these primates, which comprises 20.8% of total shoulder muscle mass in *P. troglodytes* (Oishi et al., 2008) and approximately 20% of total shoulder muscle mass in *H. sapiens* (Bassett et al., 1990; Lee and An, 2002; Rosso et al., 2014).

P. troglodytes and *P. paniscus* are the two primates of the superfamily Hominoidea that are most closely related phylogenetically to *H. sapiens* (Diogo et al., 2017). All three species, as is the case for all hominoid primates, share the anatomical pattern of a large deltoid muscle and a wide deltoid tuberosity located distally on the humeral shaft (Aiello and Dean, 1990). However, in spite of these common features, *H. sapiens* and the representatives of the genus *Pan* have developed different habitual behaviors for the forelimb, and therefore different uses of the glenohumeral joint and deltoid muscle. *P. troglodytes* is mostly terrestrial, spending approximately 90% of the time knuckle-walking (Doran, 1992; Hunt, 1992). In the relatively small amount of arboreal locomotion used by *P. troglodytes*, they tend to use vertical climbing 50% of the time and quadrupedal walking in trees 31% of the time, while other types of suspensory locomotion, such as arm swinging, occur more rarely (Hunt, 1992). In contrast, *H. sapiens* have a characteristic bipedal locomotion and the forelimbs are used mainly for manipulation, unlike *P. troglodytes*, which uses its forelimbs for both manipulation and locomotion. This has allowed modern humans to increase the complexity and versatility of the manual grips they can develop, while in chimpanzees these grips are primarily restricted to the hook grip and the pinch precision grip (Aiello and Dean, 1990).

Because of these different types of locomotion, the deltoid muscles of *P. troglodytes* and *H. sapiens* are used for quite different activities despite having similar anatomical patterns. In arboreal locomotion, the CD and the AD play a key role as elevators of the forelimb during the swing phase of vertical climbing or brachiating (Tuttle and Basmajian, 1978a; Larson and Stern, 1986), whereas the SD acts as a propulsive retractor of the humerus during the support phase (Larson and Stern, 1986). In knuckle-walking, the CD and the AD act to control the retraction of the forelimb and stabilize the glenohumeral joint during the support phase (Tuttle and Basmajian, 1978b; Larson and Stern, 1987), whereas the SD acts as an external rotator of the glenohumeral joint during the swing phase (Larson and Stern, 1987).

In the present study, we have carried out a quantitative, three-dimensional geometric morphometric (3D GM) shape analysis of the deltoid tuberosity in *P. troglodytes* and *H. sapiens*. We chose *P. troglodytes* for our study because after *P. paniscus*, this species is the most phylogenetically related to *H. sapiens* (Diogo et al., 2017). The anatomical pattern of the deltoid tuberosity is similar in both *P. troglodytes* and *H. sapiens* (Aiello and Dean, 1990). However, the findings from previous electromyographic studies led us to hypothesize that the morphology of the deltoid tuberosity in *P. troglodytes* would be adapted to arboreal locomotion and to knuckle-walking. Specifically, *P. troglodytes* requires enhanced flexion and internal rotation by the CD, abduction by the AD, and extension and external rotation by the SD. Thus, our primary objective was to identify quantifiable morphological differences in the deltoid tuberosity related to the different ways of using the forelimb by each of these species. A secondary objective was to explore the potential correlation between morphological differences in the deltoid tuberosity and those in the functional anatomy of the deltoid muscle. With this aim, we have calculated the relative mass and the physiological cross-sectional area (PCSA) of the three parts of the deltoid muscle in the two species. The PCSA of a muscle is a parameter related to the number of parallel sarcomeres and to force-producing capacity (Carlson, 2006), and is calculated based on muscle mass, muscle fascicle length, and pennation angle (Michilsens et al., 2009). Thus, the muscular architecture can provide valuable information about its function, since muscles that present high PCSA values develop high force-producing capacity (Carlson, 2006).

Although the general anatomical features of the deltoid tuberosity in members of the superfamily Hominoidea are well known, specific differences between the species of this superfamily have not been examined in detail. Our findings will therefore shed further light on the anatomy and function of the shoulder area in hominoid primates. In addition, since *H. sapiens* and *P. troglodytes* are closely related phylogenetically, our findings will also be applicable to evolutionary studies. They may help to identify morphologies in keeping with different types of locomotion through an examination of fossil remains with a preserved deltoid tuberosity, which will help clarify morphological changes to the forelimb which hominids underwent during their transition from arboreal locomotion to bipedalism.

2. MATERIALS AND METHODS

2.1. Osteological samples

Thirty left humeri of *H. sapiens* and 27 of *P. troglodytes* were included in the study. The *H. sapiens* samples came from 14 male and 16 female cadavers from the Body Donation Service of the Unit of Human Anatomy and Embryology of the University of Barcelona (Barcelona, Spain). The median age was 77.8 years (range, 38-98). The *P. troglodytes* samples came from the Anatomy Museum of the University of Valladolid (Valladolid, Spain) and the Natural Science Museum of Barcelona (Barcelona, Spain). The samples were from 14 males and 13 females, all of which were adults, as determined by the full epiphyseal fusion of the humerus, and all of which had been raised in captivity in Spanish zoos and had died from causes unrelated to the present study. Although osteological samples of captive-bred chimpanzees are generally acceptable for morphometric studies, the results obtained with these samples must be interpreted carefully since the enrichment and nutrient content for captive chimpanzees may not represent their natural condition.

2.2. 3D GM and quantitative analysis

The proximal region of each humerus, where the deltoid tuberosity is located, was scanned with a 3D Next Engine Ultra HD laser surface scanner, at a resolution of 0.1 mm space-point separation with a density of 40k (2x) points. We obtained three 3D scans at different levels of the proximal region of the humerus in order to show as exactly as possible the complete deltoid tuberosity. The resulting triangle mesh was edited to merge the different scans in one 3D model with the open-source MeshLab software (Cignoni et al. 2008) and the models were imported into Landmark Editor software (v. 3.6) (Wiley et al. 2006) for placing the landmarks.

We applied a protocol of four landmarks and 19 semilandmarks to represent the morphology of the deltoid tuberosity (Table 1, Fig. 2). The L1 and L2 landmarks were placed at the proximal and distal ends of the ventral segment of the deltoid tuberosity, outlining the CD insertion site (Figs. 2 and 3a). The L3 and L4 landmarks were placed at the distal and proximal ends of the dorsal segment of the deltoid tuberosity, outlining the SD insertion site (Figs. 2 and 3b). The L2 and L3 landmarks were thus at the ventral and dorsal ends of the middle segment of the deltoid tuberosity and outlined the AD insertion site. Landmarks L1 to L4 were recorded as three semilandmark curves with Landmark Editor. This way, the 19 semilandmarks (8 in the curve representing the ventral segment, 3 in the curve representing the middle segment and 8 in the curve representing the dorsal segment) were automatically equally spaced from the landmarks on the curves (Fig. 2).

The raw data obtained with Landmark Editor software based on the landmark coordinates were exported into the MorphoJ statistical package (Klingenberg 2011). First, a generalized Procrustes analysis (GPA) was used to account for variability due to differences of size, placement or orientation and to minimize the sum of square distances between equivalent landmarks (Bookstein 1991; Zelditch et al. 2004; O'Higgins 2000). This procedure allows the resulting data, termed Procrustes coordinates, to be used in a multivariate analysis (Rohlf and Marcus 1993; Zelditch et al. 2004). A Principal Components Analysis (PCA) was then performed in order to reduce complex multidimensional data to fewer components, or eigenvectors, that could be used to explain the main differences between two groups (O'Higgins 2000; Zelditch et al. 2004; Klingenberg 2011). Finally, two parametrical T-square tests, for PC1 and PC2, and one non-parametric Mann-Whitney U test, for PC3, were used to determine the statistical significance of the differences in shape identified by the PCA.

In order to determine the influence of size on variation in shape (allometric scaling), a multivariate regression analysis (MRA) was performed, with Procrustes coordinates, indicative of shape, as the dependent variable and the centroid size (CS), indicative of the size of the deltoid tuberosity, as the independent variable (Bookstein 1991; O'Higgins 2000; Zelditch et al. 2004; Klingenberg 2011). MorphoJ can carry out multivariate regressions with a permutation test with 1000 randomizations and pool the regression within defined subgroups (the two species in the present study) as an external variable, which makes it an ideal procedure when a correction for size between groups is necessary.

With the same sample used in the 3D GM analysis, we performed a discriminant function analysis (DFA) with MorphoJ (Klingenberg, 2011) in order to determine if there was sexual dimorphism in the deltoid tuberosity of modern humans or chimpanzees.

We also used the 3D scans of the proximal humeri to obtain quantitative data on the size of the deltoid tuberosity. We used MeshLab to calculate the surface area of the deltoid tuberosity and we normalized these values relative to the total length of the humerus. We used the non-parametric Mann-Whitney U test to compare the relative surface of the deltoid tuberosity between *H. sapiens* and *P. troglodytes* and to compare the relative surface of the deltoid tuberosity between the males and the females of the two species studied. Statistical significance was set at $p<0.05$. Analyses were performed with SPSS 22.

2.3. Deltoid muscle samples

Three deltoid muscles of *H. sapiens* and three of *P. troglodytes* were dissected (Table 2). The *H. sapiens* samples came from three males with a median age of 82.3 years (range, 81-85). All the samples were from cadavers donated to the Body Donation Service of the University of Barcelona. None of the individuals had inflammation or degeneration of the rotator cuff tendons, muscular atrophy, injuries to the tendons of the long head of the biceps brachii, arthrosis, fractures, or any other pathology of the shoulder region. The *P. troglodytes* samples came from two adult males and one adult female obtained from the Anatomy Museum of the University of Valladolid. They had come from different Spanish zoos and had died from causes unrelated to the present study. All samples had been cryopreserved without fixation within 24-48 hours post mortem.

The same investigator (JMP) dissected the shoulder and the entire forelimb of each individual and weighed each muscle with a precision scale (model Sartorius PT610 and resolution of 0.1 g). The deltoid muscle of each individual was carefully dissected and disinserted and photographs of its multipennate structure were taken with a Canon Eos-50 digital camera. Finally, the CD, AD, and SD were separated and each part of the muscle was weighed separately to determine what percentage it represented of the total mass of the muscle.

The photographs of the multipennate structure of the deltoid were analyzed with ImageJ (https://imagej.nih.gov/ij). For each pennation unit, the length and orientation angle of three different fascicles were measured. These measurements were used to calculate the mean muscle fascicle length (MFL) and the mean pennation angle (Θ) for the deltoid and each of its parts. Using these mean values, the PCSA was calculated with the formula $PCSA = (MM \times \cos \Theta) / (\rho \times MFL)$, where MM=muscle mass of the deltoid in grams and ρ=muscle density (1.06 g cm^{-3}) (Kikuchi et al., 2012). The PCSAs were normalized to $MM^{2/3}$ (Michilsens et al., 2009).

No statistical analysis was performed to compare the muscle parameters between the two species due to the small size of the sample studied. However, we used the results of the present study together with those of previous studies (Carlson, 2006; Oishi et al., 2009; Kikuchi et al., 2012) for a statistical comparison of the normalized PCSA values between *Pan troglodytes* males and females (Table 3). We used the non-parametric Mann-Whitney U test to compare the two groups with SPSS 22 and significance set at $p<0.05$.

2.5. Ethical note

The research complied with protocols approved by the Institutional Animal Care and Use Committee of the University of Barcelona and adhered to the legal requirements of Spain.

3. RESULTS

3.1. Quantitative analysis of the surface area of the deltoid tuberosity

The quantitative analysis of the surface area showed that the deltoid tuberosity is larger in *P. troglodytes* than in *H. sapiens*. This difference is significant both when comparing the absolute values (1240.6 ± 238.6 mm2 in *P. troglodytes* vs. 1030.3 ± 308.4 mm2 in *H. sapiens*; p=0.006) and when comparing the normalized values relative to the total length of the humerus (4.35 ± 0.92 in *P. troglodytes* vs. 3.29 ± 0.85 in *H. sapiens*; p <0.001). The analysis of sexual dimorphism revealed differences in the relative size of the deltoid tuberosity between males and females in both species, with males having significantly higher normalized values than females: *H. sapiens*, 3.74 ± 0.70 vs. 2.89 ± 0.78 (p=0.004); *P. troglodytes*, 4.87 ± 0.69 vs. 3.79 ± 0.82 (p=0.003).

3.2. 3D GM analysis

The PCA yielded 56 principal components (PC), of which the first three explained 87.2% of the variance in shape of the deltoid tuberosity: PC1, 62.8%; PC2, 15.0%; and PC3, 9.4%. The remaining components accounted for <5.0% each. The scatter plot of PC1 vs. PC2 (Fig. 4) shows differences between the two species. Despite a high degree of overlapping, *P. troglodytes* showed more positive values for PC1, while *H. sapiens* showed more negative values. In contrast, for PC2, *P. troglodytes* showed negative and *H. sapiens* positive values. The positive values of PC1 and the negative values of PC2 in *P. troglodytes* are accompanied by a ventral displacement of the ventral segment, a dorsal displacement of the dorsal segment, and a proximal and lateral displacement of the middle segment of the deltoid tuberosity. In contrast, the negative values of PC1 and the positive values of PC2 in *H. sapiens* are accompanied by a dorsal displacement of the ventral segment, a ventral displacement of the dorsal segment, and a distal and medial displacement of the middle segment of the deltoid tuberosity. PC3 did not identify any differences between the two species. The T-square test of the first two PCs revealed significant differences between the species in PC1 ($p<0.0001$) but not in PC2 ($p=0.99$). The Mann-Whitney U test for PC3 found no significant differences between the two species ($p=0.50$). The multivariate regression analysis (MRA) of Procrustes distance onto centroid size was significant ($p=0.03$), but only 6.18% of the variance in shape of the deltoid tuberosity can be attributable to size.

The DFA of the effect of sexual dimorphism on the shape of the deltoid tuberosity found no significant morphological differences between males and females, either for Procrustes distances ($p=0.67$ in *H. sapiens* and $p=0.47$ in *P. troglodytes*) or for the T-square test ($p=0.51$ and $p=0.40$, respectively).

3.3. Deltoid muscle analysis

The mean mass of the deltoid muscle was 294.8 ± 177.4 grams in *P. troglodytes* and 164 ± 31.1 grams in *H. sapiens* (Table 2). The great variability of the mass of the deltoid muscle of the chimpanzees is due to the differences in body size of the three individuals analyzed. The CD accounted for 21.2% of the total mass of the deltoid in *P. troglodytes*, compared to 15.2% in *H. sapiens*. The AD accounted for 55.5% of the total mass of the deltoid in *P. troglodytes* and 56.4% in *H. sapiens*. The SD accounted for 23.3% of the total mass of the deltoid in *P. troglodytes* and 28.4% in *H. sapiens*. The mean PCSA of the deltoid muscle was 37.9 ± 21.5 cm^2 in *P. troglodytes* and 21.4 ± 2.8 cm^2 in *H. sapiens* and the mean normalized PCSAs were 0.85 ± 0.14 and 0.72 ± 0.04, respectively (Fig.5). The mean PCSA of the CD was 7.9 ± 5.2 cm^2 in *P. troglodytes* and 3 ± 0.1 cm^2 in *H. sapiens*; the mean PCSAs of the AD were 44 ± 21.6 cm^2 and 17.6 ± 2.9 cm^2, respectively; and the mean PCSAs of the SD were 5.8 ± 3.4 cm^2 and 4.9 ± 0.7

cm^2, respectively. The mean normalized PCSA of the CD was 0.48 ± 0.13 in *P. troglodytes* and 0.35 ± 0.01 in *H. sapiens*; the mean normalized PCSAs of the AD were 1.48 ± 0.21 and 0.87 ± 0.11, respectively; and the mean normalized PCSAs of the SD were 0.35 ± 0.04 and 0.38 ± 0.01, respectively (Table 2; Fig. 5).

When we analyzed our data and previously published data (Carlson, 2006; Oishi et al., 2009; Kikuchi et al., 2012) on sexual dimorphism in the PCSA of the deltoid in *P. troglodytes* (Table 3), we observed no significant differences between males (0.87 ± 0.11) and females (0.78 ± 0.16) in normalized PCSA values ($p=0.327$). We also observed similar NPCSA values for the different parts of the deltoid in male and female *P. troglodytes,* although it was not possible to perform a statistical analysis since we only had data on two females (Table 3).

4. DISCUSSION

Pan troglodytes and *H. sapiens* share the anatomical pattern that is characteristic of primates of the superfamily Hominoidea (Gebo, 2014), featuring a dorsal position of the scapulae and anatomical modifications that enhance the mobility of the glenohumeral joint (Aiello and Dean, 1990). On the one hand, this increased mobility facilitates certain types of locomotion, such as vertical climbing and brachiation (Larson and Stern, 1986), but on the other, it leads to relative instability in the glenohumeral joint (Dunham et al., 2016). The functional importance of the deltoid muscle is crucial in both cases, as it acts as flexor and abductor of the glenohumeral joint in the elevation of the forelimb in the scapular plane, and also helps to stabilize the glenohumeral joint. This stabilizing role is especially important in knuckle-walkers (Kikuchi et al., 2012) like common chimpanzees, bonobos and gorillas, as evidenced by their highly developed rotator cuff and other stabilizers of the glenohumeral joint (Potau et al., 2009).

Because of their need to stabilize the glenohumeral joint during knuckle-walking and to elevate the forelimb during vertical climbing and brachiation, *P. troglodytes* need a more powerful deltoid muscle than *H. sapiens* (Kikuchi et al., 2012). Accordingly, in our samples, the mass of the deltoid muscle in *P. troglodytes* (mean value of 294.8 grams) was greater than in *H. sapiens* (mean value of 164 grams). However, this fact must be interpreted with caution due to the small number of samples analyzed. The larger absolute size of the deltoid in *P. troglodytes* compared to *H. sapiens* (Table 2) is reflected in the larger relative size of the deltoid tuberosity shown in our quantitative analysis. This increased size of the deltoid and its insertion site in *P. troglodytes* may be related to the use of the forelimb in arboreal locomotion, which requires greater muscle development in this species (Aiello and Dean, 1990). At the same time, the relative size of the deltoid tuberosity may be affected by the sexual dimorphism we have observed in both *P. troglodytes* and *H. sapiens* (Schoonaert et al., 2007). Males of both species had a larger relative surface than females, which could be related to the greater muscle mass in the male upper arm (Jensen and Fletcher, 1994; Schoonaert et al., 2007).

Furthermore, the PCSA, which provides more reliable information on muscle force than muscle mass alone, was greater in *P. troglodytes* than in *H. sapiens*. The higher absolute PCSA and NPCSA values in chimpanzees than in humans may be related to the greater functional importance of the deltoid in chimpanzees, where it is used to elevate the forelimb during the swing phase of vertical climbing and brachiation (Tuttle and Basmajian, 1978a; Larson and Stern, 1986). The NPCSA values for the CD and AD, which are the two parts of the deltoid most involved in the elevation of the forelimb, were clearly greater in *P. troglodytes* than in *H. sapiens*, while the SD, which retracts the forelimb (Larson and Stern, 1986), had similar NPCSA values in the two species, though slightly higher in *H. sapiens* (Table 2). This higher overall NPCSA value in *P. troglodytes* was not affected by sexual dimorphism, since the males and females of this species, which is slightly dimorphic (Schoonaert et al., 2007), did not have significantly different NPCSA values either overall or for the different parts of the deltoid (Table 3). This finding is in line with the lack of differences in locomotion between adult male and female chimpanzees (Doran and Hunt, 1994; Sarringhaus et al., 2014). Nevertheless, our PCSA results for *H. sapiens* may have been affected by the advanced age of our specimens, since it is known that PCSA values decrease with age in certain hindlimb muscles (Narici et al., 2003). No previous study has explored possible modifications of the PCSA in forelimb muscles during chimpanzee ontogenesis, making it impossible for us to know if our results were influenced by the age of our chimpanzee specimens.

The 3D GM analysis of the shape of the deltoid tuberosity also identified significant differences between *H. sapiens* and *P. troglodytes*, which can be related to the larger and more powerful deltoid muscle in *P. troglodytes*. The lateral view of the deltoid tuberosity in *P. troglodytes* (Fig. 4) revealed a greater separation of the ventral and dorsal segments, which resulted in a larger overall width of the deltoid tuberosity. This was confirmed in our analysis of the deltoid tuberosity surface area, which was larger in *P. troglodytes* than in *H. sapiens*. The displacement of the ventral and dorsal segments of the deltoid tuberosity away from the transversal axis of the glenohumeral joint helps to increase the lever arms of the CD and SD, respectively. The increase of the CD lever arm makes it a more powerful flexor of the forelimb, which makes it easier for *P. troglodytes* to elevate the forelimb during the swing phase of vertical climbing and brachiation (Larson and Stern, 1986), and to control the degree of retraction of the forelimb in the support phase of knuckle-walking (Larson and Stern, 1987). The increase of the SD lever arm in *P. troglodytes* makes it a more powerful extensor of the glenohumeral joint, which enhances its function as propulsive retractor of the humerus in the support phase of vertical climbing and arm swinging (Larson and Stern, 1986) and its propulsive function during the stance phase of knuckle-walking (Tuttle and Basmajian, 1978b), where it retracts the humerus (Larson and Stern, 1987). The proximal view of the deltoid tuberosity in *P. troglodytes* (Fig. 4) also revealed a displacement of the ventral and dorsal segments away from the longitudinal axis of the glenohumeral joint, which increased the CD and SD lever arms and made them more powerful internal and external rotators, respectively, of the glenohumeral joint. Internal rotation is especially important during the first half of the support phase of arm swinging, where electromyographic studies have shown a high activity of the CD that produces a "rotatory torque tending to cause the body to pivot around the axis of the supporting limb" (Larson and Stern, 1986). External rotation is important during the swing phase of knuckle-walking (Larson and Stern, 1987). The proximal view also showed a lateral displacement of the middle segment of the deltoid tuberosity in *P. troglodytes*, which permitted an increase in the length of the AD lever arm relative to the sagittal axis of the glenohumeral joint, thus increasing the power of the AD as abductor of the glenohumeral joint, essential to the elevation of the forelimb in the scapular plane (Larson and Stern, 1986). In *H. sapiens*, the AD stabilizes the glenohumeral joint anteriorly during the elevation of the forelimb in the scapular plane (Lee and An, 2002) and also compresses the humeral head against the glenoid cavity (Yanagawa et al., 2008) in order to stabilize the glenohumeral joint. This stabilizing function of the AD is important in *H. sapiens*, whose muscles of the rotator cuff (the main stabilizer of the glenohumeral joint) are much smaller than those of *P. troglodytes* relative to the size of the deltoid muscle. This is an anatomical feature that facilitates manipulation (Potau et al., 2009). The functional importance of the AD in *H. sapiens* as abductor of the glenohumeral joint (Basmajian and de Luca, 1985; Gorelick and Brown, 2007) could be related to the distal displacement of the middle segment of the deltoid tuberosity (Fig. 4), which increases the abduction power and stabilizing function of the AD.

Although sexual dimorphism in *H. sapiens* and *P. troglodytes* (Schoonaert et al., 2007) impacts the relative size of the surface area of the deltoid tuberosity, our DFA results show that it does not seem to affect its shape. This may be due to the lack of differences in posture and locomotion between males and females of the same species (Sarringhaus et al., 2014), leading us to postulate that the relative size of the deltoid tuberosity may depend on both function and sexual dimorphism, while its shape may depend more on function and the different uses of the deltoid (Basmajian and de Luca, 1985; Tuttle and Basmajian, 1978a; Larson and Stern, 1986).

4.1. Conclusions

Our quantitative and 3D GM shape analysis of the deltoid tuberosity identified significant differences between the closely related species of *H. sapiens* and *P. troglodytes* that seem to be linked to the differential function of the glenohumeral joint in the two species. Since the forelimb in *P. troglodytes* is used for arboreal locomotion (like vertical climbing) or terrestrial locomotion (like knuckle-walking) the CD is more powerful in flexion and internal rotation, the AD in abduction, and the SD in extension and external rotation of the glenohumeral joint. In contrast, the forelimb in *H. sapiens* is used mainly to manipulate objects; therefore, the deltoid tuberosity does not show the adaptations observed in *P. troglodytes* that increase the power of the three parts of the deltoid. The only exception is the distal displacement of the middle segment of the deltoid tuberosity, increasing the power of the AD in *H. sapiens*, which may be related to the important role of the AD as a stabilizer of the glenohumeral joint in modern humans (Yanagawa et al., 2008). While anatomical variations in the deltoid tuberosity have previously been used to differentiate hominoid from non-hominoid primates (Aiello and Dean, 1990) and to differentiate postural behaviors of the forelimb among non-hominoid primates (Dunham et al., 2016), our results indicate that they can also be used to differentiate between two species of hominoid primates with vastly different uses of the forelimb. However, this differentiation is not as marked as that which separates hominoid from non-hominoid primates, since there is a high degree of overlap between humans and chimpanzees in the PCA. Our findings are along the lines of those of Dunham et al., (2016) showing that the deltoid tuberosity is significantly wider in non-hominoid primates that pick food located above their heads, which requires a greater use of the forelimb in flexion and greater degree of elevation of the humerus.

In addition, our findings have shown that the different uses of the forelimb can affect both muscle architecture and bone morphology – either jointly or separately. In *P. troglodytes*, the powerful role of the CD as flexor and internal rotator is enhanced by the morphological modification of the deltoid tuberosity, the larger proportional mass of the CD, and the higher values of the PCSA; the role of the AD as abductor is enhanced by the morphological modification of the deltoid tuberosity and the higher values of the PCSA; the role of the SD as extensor and external rotator is only supported by the morphological modification of the deltoid tuberosity. Furthermore, our results indicate that the size of the deltoid tuberosity depends not only on functional factors but also on others, such as sexual dimorphism, while its shape depends only on functional factors.

Our data on the anatomical and functional differences in the shoulder region of *H. sapiens* and *P. troglodytes* can be applied in diverse fields, including comparative anatomy, evolutionary anatomy, primatology, and anthropology. Moreover, our findings will be useful in interpreting the patterns of locomotion used by extinct hominoid primates through an examination of fossilized humeral shafts, which will help to clarify the evolutionary origins of knuckle-walking and bipedalism. Future studies including other species of hominoid primates can expand the interpretation of our results. For example, the inclusion of gorillas and orangutans could help to determine if the morphological characteristics that we have observed in *P. troglodytes* are the result of adaptation to knuckle-walking, arboreal locomotion, or both. Building upon our findings, such studies could provide further insights into the current debate over whether the origin of bipedalism is knuckle-walking (Richmond and Strait, 2000) or arboreal locomotion (Thorpe and Crompton, 2007). If distinctive morphologies were found in extant hominoids related to their particular locomotor behavior, the analysis of hominin humeral shafts could yield potentially valuable information on hominin locomotor behavior. For example, the degree of suspensory behavior in representatives of *Australopithecus* remains a controversial issue today (Sarringhaus et al., 2016). The analysis of preserved *A. sediba* humeri brought to light anatomical adaptations that were characteristic of hominoid primates with suspensory and climbing behavior (Churchill et al., 2013). The fact that these specimens had a well-preserved deltoid tuberosity would allow 3D analyses based on our findings that could corroborate well-defined types of arboreal locomotion in these species.

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7. CONFLICTS OF INTEREST

The authors declare that they have no conflicts of interest.

8. DATA ACCESSIBILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

9. AUTHORS' CONTRIBUTIONS

JM Potau, A Casado, J Arias-Martorell and JF Pastor dissected the samples. M Gómez and A Casado performed the 3D GM and the quantitative analysis. All the authors participated in the study design, in the collection, analysis and interpretation of data, in the writing and review of the manuscript and in the decision to submit the article for publication.

10. REFERENCES

Aiello, L., Dean, C., 1990. An introduction to human evolutionary anatomy. Academic

Press, London.

Ankel-Simons, F., 2000. Primate anatomy. Academic Press, San Diego.

Ashton, E.H., Oxnard, C.E., 1963. The musculature of the primate shoulder. Trans. Zool. Soc. London. 29, 553-650.

Basmajian, J.V., de Luca, C., 1985. Muscles alive. Their functions revealed by electromyography. Williams & Wilkins, Baltimore.

Basset, R.W., Browne, A.O., Morrey, B.F., An, K.N., 1990. Glenohumeral muscle force and moment mechanics in a position of shoulder instability. J. Biomech. 23, 405-415.

Bookstein, F.L., 1991. Morphometric tools for landmark data: geometry and biology. Cambridge University Press, Cambridge.

Bookstein, F.L., Schäfer, K., Prossinger, H., Seidler, H., Fieder, M., Stringer, C., Weber, G.W., Arsuaga, J.L., Slice, D.E., Rohlf, F.J., Recheis, W., Mariam, A.J., Marcus, L.F., 1999. Comparing frontal cranial profiles in archaic and modern *Homo* by morphometric analysis. Anat. Rec. 257, 217-224.

Carlson, K.J., 2006. Muscle architecture of the common chimpanzee (*Pan troglodytes*): perspectives for investigating chimpanzee behavior. Primates. 47, 218-229.

Churchill, S.E., Holliday, T.W., Carlson, K.J., Jashashvili, T., Macias, M.E., Mathews, S., Sparling, T.L., Schmid, P., de Ruiter, D.J., Berger, L.R., 2013. The upper limb of *Australopithecus sediba*. Science. 340 (6129), 1233477.

Cignoni, P., Callieri, M., Corsini, M., Dellepiane, M., Ganovelli, F., Ranzuglia, G., 2008. Meshlab: an open-source mesh processing tool. In: Sixth Eurographics Italian Chapter Conference, pp. 129-136.

Diogo, R., Shearer, B., Potau, J.M., Pastor, J.F., de Paz, F.J., Arias-Martorell, J., Turcotte, C., Hammond, A., Vereecke, E., Vanhoof, M., Nauwelaerts, S., Wood, B., 2017. Photographic and descriptive musculoskeletal atlas of bonobos. Springer, Cham.

Doran, D.M., 1992. Comparison of instantaneous and locomotor bout sampling methods: a case study of adult male chimpanzee locomotor behavior and substrate use. Am. J. Phys. Anthropol. 89, 85-99.

Doran, D.M., Hunt, K.D., 1994. Comparative locomotor behavior of chimpanzees and bonobos: species and habitat differences. In: Wrangham, R.W., McGrew, W.C., de Waal, F.B.M., Heltne, P.G. (Eds.), Chimpanzee Cultures. Harvard University Press, Cambridge.

Dunham, N.T., Kane, E.E., McGraw, W.S., 2016. Humeral correlates of forelimb elevation in four West African cercopithecid monkeys. Am. J. Phys. Anthropol. 162, 337-349.

Gebo, D.L., 2014. Primate comparative anatomy. Johns Hopkins University Press, Baltimore.

Gorelick, M.L., Brown, J.M.M., 2007. Mechanomyographic assessment of contractile properties within seven segments of the human deltoid muscle. Eur. J. Appl. Physiol. 100, 35-44.

Gray, H., Standring, S., 2005. Gray's anatomy: the anatomical basis of clinical practice. Elsevier, New York.

Hunt, K.D., 1992. Positional behavior of *Pan troglodytes* in the Mahale mountains and Gombe Stream National Parks, Tanzania. Am. J. Phys. Anthropol. 87, 83-105.

Inman, V.T., Saunders, J.B., Abbott, L.C., 1944. Observations on the function of the shoulder joint. J. Bone Joint Sur. 26, 1-30.

Jensen, R.K., Fletcher, P., 1994. Distribution of mass to the segments of elderly males and females. J. Biomech. 27, 89-96.

Kikuchi, Y., Takemoto, H., Kuraoka, A., 2012. Relationship between humeral geometry and shoulder muscle power among suspensory, knuckle-walking, and digitigrade⁄palmigrade quadrupedal primates. J. Anat. 220, 29-41.

Klingenberg, C.P., 2011. MorphoJ: an integrated software package for geometric morphometrics. Mol. Ecol. Resour. 11, 353-357.

Larson, S.G., Stern, J.T., 1986. EMG of scapulohumeral muscles in the chimpanzee during reaching and arboreal locomotion. Am. J. Anat. 176, 171-190.

Larson, S.G., Stern, J.T., 1987. EMG of chimpanzee shoulder muscles during knuckle-walking: problems of terrestrial locomotion in a suspensory adapted primate. J. Zool. 212, 629-655.

Lee, S.B., & An, K.N., 2002. Dynamic glenohumeral stability provided by three heads of the deltoid muscle. Clin. Orthop. Relat. Res. 400, 40-47.

Leijnse, J.N.A.L., Han, S.H., Kwon, Y.H., 2008. Morphology of deltoid origin and end tendons a generic model. J. Anat. 213, 733-742.

Levangie, P.K., Norkin, C.C., 2001. Joint structure and function: a comprehensive analysis. FA Davis, Philadelphia.

Michilsens, F., Vereecke, E.E., D'Aout, K., Aerts, P., 2009. Functional anatomy of the gibbon forelimb: adaptations to a brachiating lifestyle. J. Anat. 215, 335-354.

Michilsens, F., Vereecke, E.E., D’Août, K., Aerts, P., 2010. Muscle moment arms and function of the siamang forelimb during brachiation. J. Anat. 217, 521-535.

Narici, M.V., Maganaris, C.N., Reeves, N.D., Capodaglio, P., 2003. Effects of aging on human muscle architecture. J. Appl. Physiol. 95, 2229-2234.

O'Higgins, P., 2000. The study of morphological variation in the hominid fossil record: biology, landmarks and geometry. J. Anat. 197, 103-120.

Oishi, M., Ogihara, N., Endo, H., Asari, M., 2008. Muscle architecture of the upper limb in the orangutan. Primates. 49, 204-209.

Potau, J.M., Bardina, X., Ciurana, N., Camprubi, D., Pastor, J.F., de Paz, F., Barbosa, M. 2009. Quantitative Analysis of the Deltoid and Rotator Cuff muscles in humans and great apes. Int. J. Primatol. 30, 697-708.

Richmond, B.G., Strait, D.S., 2000. Evidence that humans evolved from a knuckle-walking ancestor. Nature. 404, 382–385.

Rohlf, F.J., Marcus, L.F. 1993. A revolution in morphometrics. Trends Ecol. Evol. 8, 129-132.

Rosso, C., Mueller, A.M., McKenzie, B., Entezari, V., Cereatti, A., Della Croce, U., Ramappa, A.J., Nazarian, A., DeAngelis, J.P., 2014. Bulk effect of the deltoid muscle on the glenohumeral joint. J. Exp. Orthop. 1, 14.

Sarringhaus, L.A., MacLatchy, L.M., Mitani, J.C., 2014. Locomotor and postural development of wild chimpanzees. J. Hum. Evol. 66, 29-38.

Sarringhaus, L.A., MacLatchy, L.M., Mitani, J.C., 2016. Long bone cross-sectional properties reflect changes in locomotor behavior in developing chimpanzees. Am. J. Phys. Anthropol. 160, 16-29.

Schoonaert, K., D'Aout, K., Aerts, P., 2007. Morphometrics and inertial properties in the body segments of chimpanzees (*Pan troglodytes*). J. Anat. 210, 518-531.

Thorpe, S.K.S., Crompton, R.H., 2007. Origin of human bipedalism as an adaptation for locomotion on flexible branches. Science. 316, 1328-1331.

Tuttle, R.H., Basmajian, J.V., 1978a. Electromyography of pongid shoulder muscles II: deltoid, rhomboid and rotator cuff. Am. J. Phys. Anthropol. 49, 47-56.

Tuttle, R.H., Basmajian, J.V., 1978b. Electromyography of pongid shoulder muscles III: quadrupedal positional behavior. Am. J. Phys. Anthropol. 49, 57-70.

Wiley, D.F., Amenta, N., Alcantara, D.A., Ghosh, D., Kil, Y.J., Delson, E., Harcourt-Smith, W., Rohlf, F.J., St. John, K., Hamann, B., Motani, R., Rosenberger, A.L., Tallman, L., Disotell, T., O’Neill, R., 2006. Evolutionary Morphing, Landmark Editor 3.0. IDAV, Davis: University of California, Avalaible at: http://www.idav.ucdavis.edu/research/EvoMorph.

Wysiadecki, G., Polguj, M., Krasucki, K., Żytkowski, A., Śmigielski, J., Topol, M., Orkisz, S., 2014. Morphology and a proposed model of innervation of the human deltoid muscle: a pilot study. Folia Morphol. 73, 216-223.

Yanagawa, T., Goodwin, C.J., Shelburne, K.B., Giphart, J.E., Torry, M.R., Pandy, M.G., 2008. Contributions of the individual muscles of the shoulder to glenohumeral joint stability during abduction. J. Biomech. Eng. 130, 021024.

Zelditch, M.L., Swiderski, D.L., Sheets, H.D., Fink, W.L., 2004. Geometric Morphometrics for Biologists: A Primer. Academic Press, New York.

TABLE LEGENDS

Table 1. Numbering, description and types of landmarks (Bookstein et al., 1999; O'Higgins, 2000).

Landmark	**Description**	**Type**
L1	Proximal end of the ventral segment of the deltoid tuberosity	II
L2	Distal end of the ventral segment of the deltoid tuberosity	II
L3	Distal end of the dorsal segment of the deltoid tuberosity	II
L4	Proximal end of the dorsal segment of the deltoid tuberosity	II

Table 2. Mass in grams and normalized PCSA (NPCSA) of the entire deltoid muscle and of its individual parts in three *Homo sapiens* and three *Pan troglodytes*. D = deltoid muscle; CD = clavicular deltoid; AD = acromial deltoid; SD = spinal deltoid; NPCSA = normalized physiological cross-sectional area; HS = Homo sapiens; PT = Pan troglodytes; M = male; F = female; SD = standard deviation.

SAMPLE	SEX	D	CD	AD	SD	D NPCSA	CD NPCSA	AD NPCSA	SD NPCSA
HS052	M	136.5	23.4	78.1	35.0	0.75	0.37	0.98	0.39
HS053	M	157.9	27.0	82.1	48.8	0.67	0.34	0.77	0.37
HS090	M	197.7	24.7	117.3	55.7	0.73	0.35	0.85	0.38
Mean		***164.0***	***25.0***	***92.5***	***46.5***	***0.72***	***0.35***	***0.87***	***0.38***
SD		***31.1***	***1.8***	***21.6***	***10.5***	***0.04***	***0.01***	***0.11***	***0.01***
PT04	M	494.7	102.6	273.9	118.2	1.00	0.63	1.63	0.40
PT07	M	233.6	51.1	119.5	63.0	0.72	0.39	1.24	0.33
PT08	F	156.1	33.9	97.5	24.7	0.82	0.42	1.56	0.32
Mean		***294.8***	***62.5***	***163.6***	***68.6***	***0.85***	***0.48***	***1.48***	***0.35***
SD		***177.4***	***35.7***	***96.1***	***47.0***	***0.14***	***0.13***	***0.21***	***0.04***

Table 3. Comparison of the NPCSA values of the deltoid and its three parts between male and female *Pan troglodytes*. DM = deltoid mass in grams; D = deltoid muscle; CD = clavicular deltoid; AD = acromial deltoid; SD = spinal deltoid; NPCSA = normalized physiological cross-sectional area; M = male; F = female; DS = standard deviation; NA = not available.

SAMPLE	SEX	DM	D PCSA	D NPCSA	CD NPCSA	AD NPCSA	SD NPCSA
PT04	M	494.7	62.6	1.00	0.63	1.63	0.40
PT07	M	233.6	27.5	0.72	0.39	1.24	0.33
Oishi et al. 2009	M	429.6	53.5	0.94	0.50	0.92	0.38
Oishi et al. 2010	M	366.4	40.8	0.80	0.35	0.81	0.28
Oishi et al. 2011	M	340.5	43.3	0.89	0.36	0.91	0.30
Mean				**0.87**	**0.45**	**1.10**	**0.34**
SD				**0.11**	**0.12**	**0.34**	**0.05**
PT08	F	156.1	23.7	0.82	0.42	1.56	0.32
Oishi et al. 2009	F	205.4	27.5	0.79	0.37	0.80	0.29
Carlson 2006	F	172.7	17.4	0.56	NA	NA	NA
Kikuchi et al. 2012	F	180.9	29.8	0.93	NA	NA	NA
Mean				**0.78**	**0.40**	**1.18**	**0.30**
SD				**0.16**	**0.03**	**0.40**	**0.10**

p=0.327

FIGURE LEGENDS

Figure 1. Dissection (a) and schematic diagram (b) of the shoulder and arm muscles in *Pan troglodytes* (common chimpanzee). 1 = clavicular deltoid muscle, 2 = acromial deltoid muscle, 3 = spinal deltoid muscle, 4 = biceps brachii muscle, 5 = brachialis muscle, 6 = brachioradialis muscle, 7 = triceps brachii muscle (caput laterale), 8 = triceps brachii muscle (caput longum), 9 = teres major muscle.

Figure 2. Lateral view of the insertion sites of the three parts of the deltoid muscle and of the placement of landmark and semilandmark points on the deltoid tuberosity of the left humerus of *H. sapiens*. CD = clavicular deltoid, AD = acromial deltoid, SD = spinal deltoid.

Figure 3. Dissection of the insertion sites of the deltoid muscle in *P. troglodytes*. **a)** Anterior view. 1 = clavicular deltoid, * = clavicular deltoid insertion at the ventral segment of the deltoid tuberosity, 2 = brachialis muscle, 3 = teres major muscle, 4 = greater tubercle of the humerus, 5 = coracoid process. **b)** Posterior view. 6 = spinal deltoid, * = spinal deltoid insertion at the dorsal segment of the deltoid tuberosity, 7 = humeral shaft, 8 = teres minor muscle, 9 = triceps brachii muscle.

Figure 4. Location of the deltoid tuberosity in a lateral view and in a transparent proximal view of a three-dimensional model of the left humerus of *P. troglodytes* and a scatter plot of PC1 vs. PC2 derived from the PCA of the GM analysis. The ellipses include 95% confidence intervals of the group mean. Dark wireframes show the extreme shape of each PC and light wireframes represent the mean shape (coordinates 0,0).

Figure 5. Box and whisker plots of the normalized PCSA values of the deltoid muscle (a) and its parts (b, c y d). NPCSA = normalized PCSA, D = deltoid, CD = clavicular deltoid, AD = acromial deltoid, SD = spinal deltoid, PT = *Pan troglodytes*, HS = *Homo*

sapiens.