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Quantitative Analysis of the Brachialis and Triceps Brachii Insertion Sites on the Proximal Epiphysis of the Ulna in Modern Hominid Primates and Fossil Hominins

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ABSTRACT

In several species of hominid primates with different types of locomotor behavior, we quantitatively studied the insertion sites of the brachialis and triceps brachii on the proximal epiphysis of the ulna. Our main objective was to evaluate the possibility of using the anatomical features of these insertion sites to infer the locomotor behavior of different species of fossil hominins. We measured the area of these muscle insertion sites using 3D bone meshes and obtained the value of each insertion site relative to the total size of the two insertion sites for each of the species studied. We also compared these relative values of the osteological samples with the relative mass of the brachialis and triceps brachii, which we obtained by dissecting these muscles in the same primate species. The relative values for the brachialis insertion were highest in orangutans, followed by bonobos, chimpanzees, gorillas, and humans. Fossil *Australopithecus* and *Paranthropus* had values similar to those of bonobos, while fossil *Homo* had values similar to those of *Homo sapiens*. The observed similarity in ulnar attachment sites between *Australopithecus* and *Paranthropus* and extant bonobos suggest that these hominins used arboreal locomotion to complement their bipedalism. These adaptations to arboreal locomotion were not observed in *Homo*.

1 | Introduction

Hominid primates use different types of locomotion—both arboreal forms like brachiation, suspension, and vertical climbing, as well as terrestrial forms like knuckle-walking and bipedalism (Fleagle 1999). Orangutans (*Pongo*) primarily use arboreal locomotion, while gorillas (*Gorilla gorilla*) and chimpanzees (*Pan troglodytes*) primarily use knuckle-walking and will occasionally combine this with different types of arboreal locomotion (Hunt 2004). Bonobos (*Pan paniscus*) are generally more arboreal than chimpanzees and frequently use suspensory locomotion (Doran 1993). Finally, modern humans (*Homo sapiens*) use only bipedal locomotion (Crompton, Vereecke, and Thorpe 2008), which eliminates the need for the upper limb in locomotion and frees it for specialization in manipulative tasks (Hunt 2004; Thorpe, Holder, and Crompton 2007).

Several indications of bipedalism have been identified in fossil hominins. One of the earliest fossil hominins with characteristics of bipedalism and a manipulative use of the upper limb similar to that of modern humans is *Australopithecus* (Drapeau 2004; Kivell et al. 2011; Ward 2015). The anatomy of their upper limb, however, suggests that they used a certain degree of arboreal locomotion in addition to bipedalism (Drapeau 2008a; Fleagle 1999;

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Summary

- There is a close relationship between the types of locomotion used by hominoid primates and the relative size of the brachialis and triceps brachii muscles.
- The relative mass of the brachialis and the triceps brachii muscles is related to the relative size of their insertion sites in the proximal epiphysis of the ulna.
- The morphology of the proximal epiphysis of the ulna can provide information on the locomotor behavior of fossil hominins.

Ryan et al. 2018). For example, their upper limb was relatively long and their elbow morphology was compatible with suspensory locomotion and vertical climbing, similar to that of *Pan* (Churchill et al. 2013; Drapeau 2008a; Green, Gordon, and Richmond 2007; Heaton et al. 2019; Rein et al. 2017; Ward 2015). Some of these characteristics were also present in *Paranthropus*, including an ulna with a high degree of curvature and an ape-like elbow morphology indicating the occasional use of arboreal locomotion (Domínguez-Rodrigo et al. 2013; Drapeau 2008a; Lague et al. 2019; Richmond et al. 2020). Finally, *Homo ergaster* showed habitual bipedalism and a lack of anatomical features in the upper limb that could be related to arboreal locomotion (Crompton, Vereecke, and Thorpe 2008; Ruff 2009; Stamos and Alemseged 2023).

The proximal epiphysis of the ulna has been used in several studies to infer the locomotor behavior of different species of fossil primates, first because a relatively high number of ulnae belonging to different species of the genera *Australopithecus* and *Paranthropus* have been identified (Aiello et al. 1999; Drapeau 2004, 2008a; Rein et al. 2017), and also because the anatomical characteristics of the ulna are closely related to different locomotor behaviors (Aiello et al. 1999; Drapeau 2004; Lague et al. 2019; Rein et al. 2017). For example, compared to nonhominoid primates, hominoid primates have a relatively short olecranon and a more proximal orientation of the trochlear notch of the ulna. These anatomical adaptations allow the greater degree of elbow extension that is necessary for suspensory locomotion and for knuckle-walking (Aiello and Dean 1990; Aiello et al. 1999; Drapeau 2004; Gebo 2014; Rein, Harvati, and Harrison 2015). In contrast, nonhominoid primates that use quadrupedal locomotion—especially those using quadrupedal terrestrial locomotion—generally have a longer and, in some cases, retroflexed olecranon, which makes the lever arm of the triceps brachii longer compared to that of hominoid primates and enables it to generate greater power during propulsion (Drapeau 2004; Gebo 2014; Rose 1993). The insertion sites of two muscles are located on the proximal epiphysis of the ulna: the brachialis and the triceps brachii, both of which play an important functional role in the elbow joint (de Diego et al. 2020, 2022). The brachialis, the main elbow flexor, originates from the anterior surface of the distal half of the humerus and inserts on the ulna tuberosity (Malagelada et al. 2014; Standring 2021), distal to the coronoid process; the triceps brachii, the main elbow extensor, originates from the infraglenoid tubercle of the scapula and the posterior surface of the humerus and inserts on the proximal surface of the olecranon process (Fornalski, Gupta, and Lee 2003; Malagelada et al. 2014; Standring 2021) (Figure 1).

The anatomical and functional differences in hominid primates of both the brachialis and the triceps brachii have been related to their different locomotor behaviors (de Diego et al. 2020, 2022; Kikuchi 2010; Michilsens et al. 2009; Oishi et al. 2008, 2009; Thorpe et al. 1999; Tuttle, Velte, and Basmajian 1983; Zihlman, Mcfarland, and Underwood 2011). For example, muscle mass, a parameter related to the power generation capacity of a muscle (Brand, Beach, and Thompson 1981; Michilsens et al. 2009), is relatively greater in the elbow flexors of *Pongo* than in those of *G. gorilla* and *P. troglodytes* (Oishi et al. 2008; Zihlman, Mcfarland, and Underwood 2011). This reflects the need for greater power generation in orangutans to propel the body upward during suspensory locomotion, especially in vertical climbing. In contrast, the relative muscle mass of the elbow extensors, mainly the triceps brachii, in gorillas and chimpanzees is greater than in orangutans, reflecting the greater functional importance of this muscle during knuckle-walking (Oishi et al. 2009; Zihlman, Mcfarland, and Underwood 2011). Compared to other species of hominoid primates, such as *P. troglodytes* or *Hylobates lar*, humans have a larger mass of the triceps brachii relative to the mass of the elbow flexor muscles (Kikuchi 2010), possibly related to the need to keep the elbow in flexion or semi-flexion for a long time when performing manipulative tasks (de Diego et al. 2020; Holzbaur et al. 2007; Thorpe et al. 1999).

Differences among the hominid primates in the brachialis and the triceps brachii are also evident when the muscles are studied from a functional point of view, since their activity pattern is related to the different locomotor behaviors (Aiello and Dean 1990; Swindler and Wood 1973; Tuttle, Velte, and Basmajian 1983). For example, the brachialis shows high electromyographic activity during the propulsion phase of vertical climbing (Tuttle, Velte, and Basmajian 1983), while the triceps brachii muscle presents high levels during knuckle-walking (Fleagle et al. 1981; Tuttle and Basmajian 1974; Tuttle, Velte, and Basmajian 1983; Tuttle and Watts 1985). Specifically, the triceps brachii remains active both during the swing phase of knuckle-walking, where it acts as an elbow extensor to place the hand in a more advanced position, and also during the stance phase, where it acts to stabilize the elbow (Oishi et al. 2009; Tuttle, Velte, and Basmajian 1983). In humans, the need to stabilize the elbow during manipulative functions explains why the triceps brachii presents a high level of electromyographic activity during both flexion and extension of the elbow (Chaytor et al. 2020; Landin, Thompson, and Jackson 2018).

In the present study, we measured the insertion sites (entheses) of the brachialis and triceps brachii on the proximal epiphysis of the ulna in different species of hominid primates. We also dissected these two muscles in specimens of the same species and calculated their muscle mass. In addition, we calculated the size of the muscle insertion sites in 3D bone meshes of seven fossil hominins. Our main objective was to determine if there were interspecies differences in the relative sizes of the brachialis and triceps brachii insertion sites in hominid primates and if such differences could be related to their different locomotor behaviors. If we were able to detect these differences, we could extrapolate our findings to infer the type of locomotion used by fossil hominins with a

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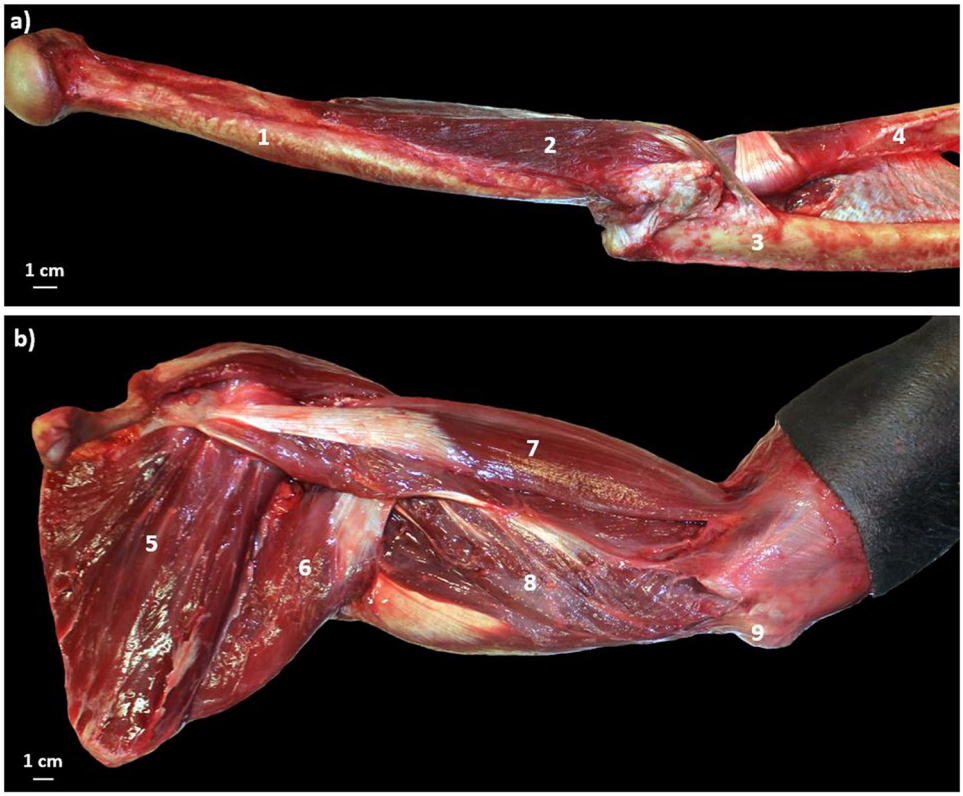

FIGURE 1 | Medial view of the insertion site of the brachialis muscle on the tuberosity of the ulna (a) and of the triceps brachii muscle on the olecranon (b) in a specimen of *Pan troglodytes*. 1 = Humerus; 2 = Brachialis muscle; 3 = Tuberosity of the ulna; 4 = Radius; 5 = Subscapularis muscle; 6 = Teres major muscle; 7 = Biceps brachii muscle; 8 = Triceps brachii muscle; 9 = Olecranon.

well-preserved proximal epiphysis of the ulna. Since the morphological characteristics of muscle insertion sites are related to the anatomical and functional characteristics of the muscles themselves (Drapeau 2008b; François, Braun, and Khan 2001; Judex and Carlson 2009; Turcotte et al. 2022), we hypothesized that the relative muscle mass of the brachialis and triceps brachii muscles would reflect the relative size of their insertion site, defined as a percentage of the total area of the two insertion sites. Taking this into account, we developed three working hypotheses: (1) orangutans, with predominantly arboreal locomotion, would have higher values for the brachialis insertion, while gorillas and chimpanzees, which are primarily knuckle-walkers, would have higher values for the triceps brachii insertion; (2) bonobos, with more frequent arboreal locomotion, would have higher values than chimpanzees for the brachialis insertion; and (3) humans would have relatively high values for the triceps brachii insertion as an adaptation to its use in performing manipulative tasks. We believe that our results will not only increase the currently available knowledge of the anatomy and function of the elbow joint in extant hominid primates but can also be applied to the study of locomotor behavior in fossil hominins.

2 | Methods

2.1 | Ethics Statement

The research complied with protocols approved by the Institutional Animal Care and Use Committee of the University of Barcelona (IRB00003099) and adhered to the legal requirements of Spain and to the principles of the American Society of Primatologists for the ethical treatment of nonhuman primates. We also dissected human cadavers and used human tissues in accordance with the recommendations and ethical guidelines of the University of Barcelona and the Body Donation Service.

2.2 | Quantitative Analysis of Muscle Insertion Sites

We studied 25 ulnae of *P. troglodytes* (13 male and 12 female), nine of *P. paniscus* (five male and four female), 12 of *G. gorilla* (five male and seven female), and nine of *Pongo pygmaeus* (two male and seven female). The chimpanzee, gorilla, and orangutan ulnae were provided by the Anatomical Museum of the University of Valladolid (Spain) and the Zoology Museum of Barcelona (Spain), while the bonobo ulnae came from the Royal Museum for Central Africa in Tervuren (Belgium). We also studied 20 human ulnae (nine men and 11 women), provided by the Human Anatomy and Embryology Unit of the University of Barcelona. The individuals were aged between 38 and 97 years (mean, 73.8). All the ulnae studied came from adult individuals that had died from causes unrelated to our study (Table 1).

In addition, we studied 3D bone meshes of the proximal epiphysis of the ulna of seven specimens of fossil hominins, which were provided by the Center for the Study of Human Origins (Department of Anthropology, New York University, NY):

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TABLE 1 | Summary of the samples included in the study.

	Species	Source	*N*	Sex
3D Bone Mesh	*Homo sapiens*	Human Anatomy and Embryology Unit (University of Barcelona)	20	9 Male/11 Female
	Pan troglodytes	University of Valladolid/Zoology Museum of Barcelona	25	13 Male/12 Female
	Pan paniscus	Royal Museum for Central Africa (Tervuren)	9	5 Male/4 Female
	Gorilla gorilla	University of Valladolid/Zoology Museum of Barcelona	12	5 Male/7 Female
	Pongo pygmaeus	University of Valladolid/Zoology Museum of Barcelona	9	2 Male/7 Female
	Australopithecus afarensis (AL-288-1)	Center for the Study of Human Origins (New York University)	1	
	Australopithecus africanus (STW-431)	Center for the Study of Human Origins (New York University)	1	
	Australopithecus sediba (UW-88-62)	Center for the Study of Human Origins (New York University)	1	
	Paranthropus boisei (OH-36)	Center for the Study of Human Origins (New York University)	1	
	Homo ergaster (KNMWT-15000)	Center for the Study of Human Origins (New York University)	1	
	Homo neanderthalensis (Spy)	Center for the Study of Human Origins (New York University)	1	
	Homo sapìens archaic (Skhul)	Center for the Study of Human Origins (New York University)	1	
Dissection	*Homo sapiens*	Body Donation Service (University of Barcelona)	18	11 Male/7 Female
	Pan troglodytes	Anatomical Museum (University of Valladolid)	9	4 Male/5 Female
	Pan paniscus	School of Veterinary Medicine (University of Antwerp)	2	1 Male/1 Female
	Gorilla gorilla	Anatomical Museum (University of Valladolid)	4	2 Male/2 Female
	Pongo pygmaeus	Anatomical Museum (University of Valladolid)	3	3 Female

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Australopithecus afarensis (AL-288-1), *Australopithecus africanus* (STW-431), *Australopithecus sediba* (UW-88-62), *Paranthropus boisei* (OH-36), *H. ergaster* (KNMWT-15000), *Homo neanderthalensis* (Spy) and *H. sapiens* (Skhul) (Table 1).

The size of the brachialis and the triceps brachii insertion sites was calculated as follows. The proximal epiphyses of all the ulnae were scanned with a Next Engine 2000 Ultra HD laser scanner (NextEngine, Inc., Santa Monica, CA, USA) and the resulting triangular meshes were edited with MeshLab 2021.05 software. The brachialis insertion on the tuberosity of the ulna and the triceps brachii insertion on the olecranon process were then identified in each of the 3D bone models formed by the triangular meshes obtained with the scanner (3D bone meshes) (Figure 2). Finally, the bone surface not belonging to these two insertion sites was manually eliminated with MeshLab to automatically obtain the area in mm^2 of the brachialis insertion (BIA) and the triceps brachii insertion (TBIA). These two values were then used to calculate the total area of the insertion sites of the two muscles. The relative value of the BIA and the TBIA as a percentage of the total area was then calculated (%BIA and %TBIA).

2.3 | Relative Muscle Mass of the Brachialis and Triceps Brachii

We dissected the upper limbs of 18 human cadaver specimens (11 men and seven women; aged between 38 and 97 years [mean, 76.8]) provided by the Body Donation Service of the University of Barcelona. In addition, we dissected nine adult *P. troglodytes* (four male and five female), two adult *P. paniscus* (one male and one female), four adult *G. gorilla* (two male and two female), and three adult *Pongo pygmaeus* (three female). The chimpanzees, gorillas, and orangutans came from different Spanish zoos and were dissected at the Anatomical Museum of the University of Valladolid, while the bonobos came from the Antwerp Zoo (Belgium) and were dissected at the School of Veterinary Medicine of the University of Antwerp (Belgium) as part of the international Bonobo Morphology Initiative. The Bonobo Morphology Initiative was organized by the Center for Research and Conservation of the Royal Zoological Society of Antwerp (KMDA/RZSA), which made several of their bonobo, chimpanzee, and siamang cadavers available for dissection. All dissected hominid primates died from causes unrelated to our study and were cryopreserved without chemical fixation at 24–48 h postmortem (Table 1).

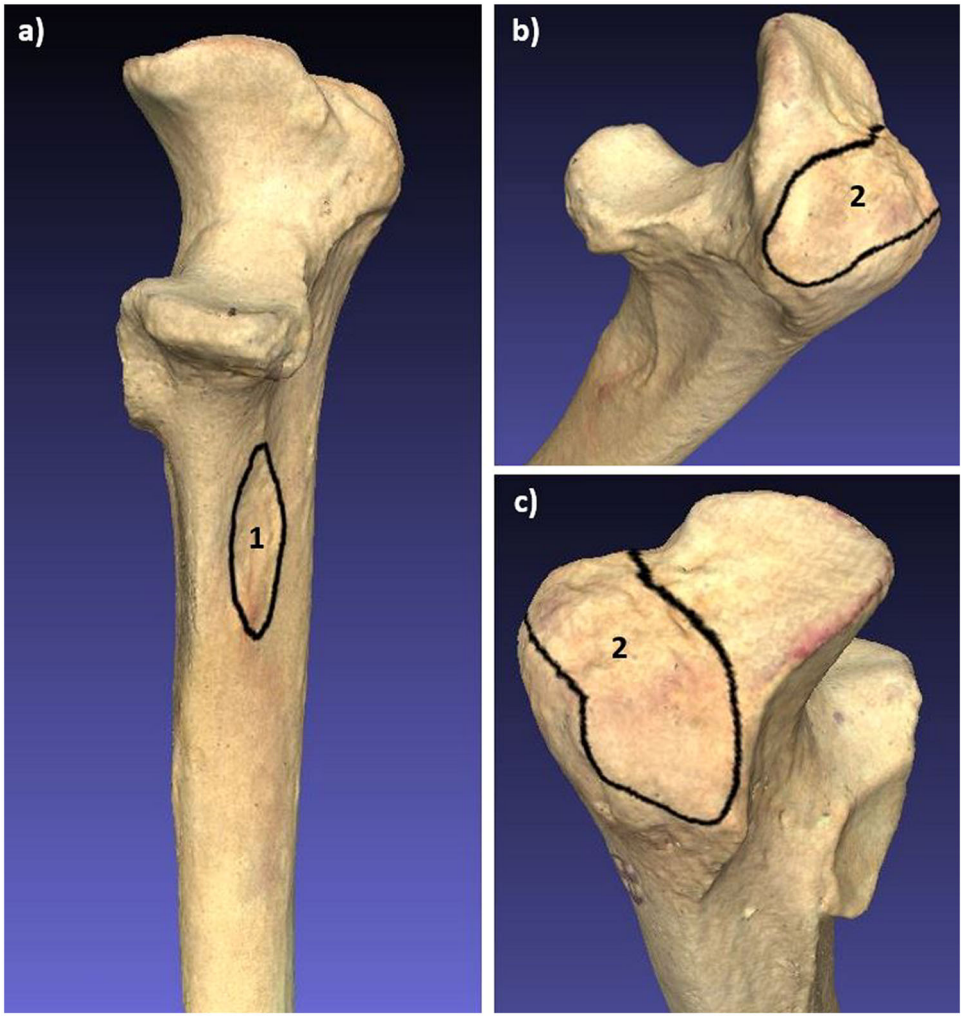

FIGURE 2 | Three-dimensional model of the proximal epiphysis of the ulna in a specimen of *Pan troglodytes*: anteromedial view (a), proximomedial view (b), and proximolateral view (c). 1 = Insertion site of the brachialis muscle on the tuberosity of the ulna; 2 = Insertion site of the triceps brachii muscle on the olecranon.

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The same researcher (Josep M. Potau) performed all the dissections. He identified and isolated the brachialis and triceps brachii as part of a dissection of all the muscles of the upper limb. Once he had isolated the two muscles and freed them from any remaining connective or adipose tissue, he removed them and obtained the muscle mass in grams of the brachialis (BMM) and the triceps brachii (TBMM) using a precision scale (model Sartorius PT610 and resolution of 0.1 g). Finally, he obtained the total mass of the two muscles and calculated the relative value of each of the two muscles as a percentage of the total mass (%BMM and %TBMM).

2.4 | Statistical Analyses

The normality of the sample was tested using the Shapiro–Wilk test, which indicated that none of the variables followed a normal distribution. To confirm the reliability and repeatability of our method for measuring the size of the insertion sites of the brachialis and triceps brachii in the 3D bone meshes, we established a protocol to calculate the intra/interobserver error. Two investigators repeated the measurements of the insertion sites in five specimens of each species and in all the fossil hominin specimens on 4 days spread over 2 weeks, with a minimum separation of 24 h between 2 days. The intra/interobserver errors were calculated using Kruskal-Wallis one-way ANOVA with the Dwass-Steel-Critchlow-Fligner *post hoc* pairwise comparison test to detect any unreliability in the data. A correlation test was also performed between the BIA-BMM and TBIA-TBMM variables to determine the degree of relationship between the size of the insertion site and the muscle mass in both muscles studied. This correlation test was carried out with specimens for which we had both 3D bone mesh and muscle mass values: 17 humans, eight chimpanzees, four gorillas, and three orangutans.

The %BIA and %TBIA parameters were compared between the different primate species with a Kruskal Wallis one-way analysis of variance (ANOVA) with the Dwass-Steel-Critchlow-Fligner *post hoc* pairwise comparison test. The %BMM and %TBMM parameters were compared between humans and chimpanzees with a nonparametric Mann–Whitney *U* test.

The values for the muscle mass of bonobos, gorillas, and orangutans were not included in the comparison of muscle mass since there were fewer than five individuals in each group. All statistical analyses were performed with SPSS 22 and Jamovi (The Jamovi Project, 2020) and statistical significance was set at $p < 0.05$.

3 | Results

Table 2 summarizes the main results of our study (see also Supporting Information S1: Table S1). The intra/interobserver analysis showed no significant difference between the results obtained by the two investigators (BIA $\chi^2 = 0.125$, $df = 7$, $p = 1.000$; TBIA $\chi^2 = 0.210$, $df = 7$, $p = 1.000$) (Supporting Information S1: Table S2). The correlation test carried out between the size of the insertion site and the muscle mass (Figure 3) indicated a significant positive correlation between these two parameters for both the brachialis (Spearman's Rho = 0.895; $p < 0.001$) and the triceps brachii (Spearman's Rho = 0.851; $p < 0.001$). The Kruskal–Wallis one-way ANOVA indicated significant differences between the different species of hominid primates for both %BIA ($\chi^2 = 36.5$; $df = 4$; $p < 0.001$) and %TBIA ($\chi^2 = 36.5$; $df = 4$; $p < 0.001$). The results of the Dwass-Steel-Critchlow-Fligner *post hoc* pairwise comparison test for the parameters %BIA and %TBIA are summarized in Table 3.

Orangutans, with mainly arboreal locomotion, had a significantly greater %BIA (41.2 ± 1.1) than the chimpanzees (28.1 ± 2.6; $df = 33$; $p < 0.001$) and the gorillas (28.1 ± 4.0; $df = 20$; $p = 0.001$), which use primarily knuckle-walking. The %BIA was significantly higher (32.0 ± 3.4) in bonobos, which combine knuckle-walking with arboreal locomotion, than in chimpanzees ($df = 33$; $p = 0.047$) and significantly lower than in orangutans ($df = 17$; $p = 0.003$). The %BIA was also higher

TABLE 2 | Mean and standard deviation of the relative area of the insertion sites of the brachialis (%BIA) and the triceps brachii (%TBIA) and of the relative muscle mass of the brachialis (%BMM) and the triceps brachii (%TBMM) in five species of modern hominid primates and seven fossil hominins.

	Species	%BIA	%TBIA	%BMM	%TBMM
Hominid primates	*Homo sapiens*	26.0 ± 2.2	74 ± 2.2	25.2 ± 2.7	74.8 ± 2.7
	Pan paniscus	32.0 ± 3.4	68.0 ± 3.4	32.5 ± 7.3	67.5 ± 7.3
	Pan troglodytes	28.1 ± 2.6	71.9 ± 2.6	29.3 ± 3.4	70.7 ± 3.4
	Gorilla gorilla	28.1 ± 4.0	71.9 ± 4.0	27.8 ± 2.6	72.2 ± 2.6
	Pongo pygmaeus	41.2 ± 1.1	58.8 ± 1.1	41.0 ± 2.3	59.0 ± 2.3
Fossil hominins	*Australopithecus afarensis*	31.9	68.1		
	Australopithecus africanus	33.2	66.8		
	Australopithecus sediba	31.8	68.2		
	Paranthropus boisei	34.9	65.1		
	Homo ergaster	27.5	72.5		
	Homo neanderthalensis	24.7	75.3		
	Homo sapiens (archaic)	27.9	72.1		

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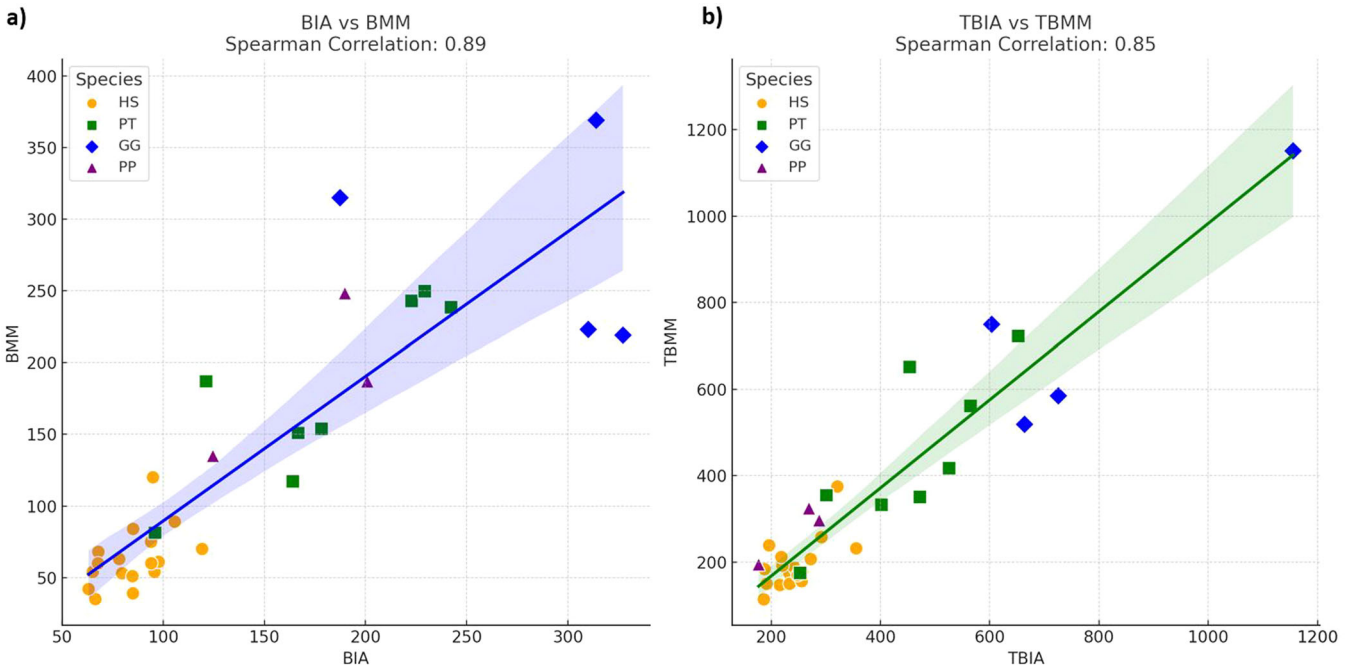

FIGURE 3 | Scatter plot of the bivariate comparison of the brachialis insertion site versus brachialis muscle mass (a) and of the triceps brachii insertion site versus triceps brachii muscle mass (b). The scatter plots were created using Python with the Seaborn and Matplotlib libraries. BIA, brachialis insertion area; BMM, brachialis muscle mass; GG, *Gorilla gorilla*; HS, *Homo sapiens*; PP, *Pongo pygmaeus;* PT, *Pan troglodytes*; TBIA, triceps brachii insertion area; TBMM, triceps brachii muscle mass.

TABLE 3 | Results of the Dwass-Steel-Critchlow-Fligner *post hoc* pairwise comparison test for the parameters %BIA and %TBIA.

	Pairwise comparison of %BIA		Pairwise comparison of %TBIA	
	W	**P**	**W**	**P**
HS versus PT	3.7471	0.062	−3.7471	0.062
HS versus PPa	5.0000	0.004	−5.0000	0.004
HS versus GG	2.0368	0.602	−2.0368	0.602
HS versus PG	6.0000	< 0.001	−6.0000	< 0.001
PT versus PPa	3.8920	0.047	−3.8920	0.047
PT versus GG	0.0918	1.000	−0.0918	1.000
PT versus PG	6.2106	< 0.001	−6.2106	< 0.001
PPa versus GG	−3.2161	0.153	3.2161	0.153
PPa versus PG	5.0576	0.003	−5.0576	0.003
GG versus PG	5.4272	0.001	−5.4272	0.001

Abbreviations: BIA, brachialis insertion area; GG, *Gorilla gorilla*; HS, *Homo sapiens*; PG, *Pongo pygmaeus*; PPa, *Pan paniscus*; PT, *Pan troglodytes*; TBIA, triceps brachii insertion area.

in bonobos than in gorillas but this difference was not significant ($df = 20$; $p = 0.153$). Humans had the highest %TBIA of all the specimens (74.0 ± 2.2). The difference in %TBIA was significant when humans were compared with bonobos (%TBIA $= 68.0 \pm 3.4$; $df = 28$; $p = 0.004$) or orangutans (%TBIA $= 58.8 \pm 1.1$; $df = 28$; $p < 0.001$), but not when compared with chimpanzees (%TBIA $= 71.9 \pm 2.6$; $df = 44$; $p = 0.062$) or gorillas (%TBIA $= 71.9 \pm 4.0$; $df = 31$; $p = 0.602$).

Our muscular results were in line with our osteological results (Table 2), and the %BMM and %TBMM values mirrored those of the %BIA and %TBIA. When we compared the %BIA-%BMM and %TBIA-%TBMM values in humans and chimpanzees (the only two groups with more than five dissected individuals), we found no significant differences (human %BIA-%BMM, $U = 145.000$; $df = 37$; $p = 0.306$; human %TBIA-%TBMM, $U = 145.000$; $df = 37$; $p = 0.306$; chimpanzee %BIA-%BMM, $U = 88.000$; $df = 33$; $p = 0.339$; chimpanzee %TBIA-%TBMM, $U = 88.000$; $df = 33$; $p = 0.339$).

Among the fossil hominins, the %BIA and %TBIA values in specimens from *Australopithecus* and *Paranthropus* were similar to those of *P. paniscus* (Table 2). This similarity was even more pronounced when *A. afarensis*, *A. africanus*, *A. sediba*, and *P. boisei* were grouped together. The mean %BIA for these four species was 32.9 ± 1.4, compared to 32.0 ± 3.4 in bonobos,

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while the mean %TBIA for the four species was 67.1 ± 1.4, compared to 68.0 ± 3.4 in bonobos. Moreover, the three fossil *Homo* specimens (*H. ergaster*, *H. neanderthalensis*, and *H. sapiens*) had %BIA and %TBIA values similar to those of modern humans. The mean %BIA for the three species was 26.7 ± 1.6, compared to 26.0 ± 2.2 in modern humans, while the mean %TBIA for the three species was 73.3 ± 1.8, compared to 74.0 ± 2.2 in modern humans.

4 | Discussion

In the present study, we explored the potential relationship between the size of the brachialis and triceps brachii insertion sites and locomotor behavior in hominid primates. Interestingly, we found a close connection between the relative mass of these two muscles, the relative size of their insertion sites, and the types of locomotion used by orangutans, gorillas, chimpanzees, and bonobos.

Our findings on the relative muscle mass of the brachialis and triceps brachii are in line with those of other studies. Thorpe et al. (1999), Carlson (2006), Oishi et al. (2009), and Kikuchi (2010) studied eight *P. troglodytes* (four male, three female, and one specimen of indeterminate sex) and reported %BMM of 20.3%–38.0% and %TBMM of 62.0%–79.7%. In our study of nine chimpanzees (four male and five female), we found %BMM of 24.8%–34.5% and %TBMM of 65.5%–75.2%. Zihlman, Mcfarland, and Underwood (2011) studied five male gorillas and found % BMM of 24.4%–30.2% and %TBMM of 69.8%–75.6%, while in our four gorillas (three female and one male), %BMM was 24.3%–30.1% and %TBMM was 69.9%–75.7%. Finally, Oishi et al. (2009) and Zihlman, Mcfarland, and Underwood (2011) studied seven orangutans (six male and one female) and reported % BMM of 33.3%–46.3% and %TBMM of 53.7%–66.7%, compared to our findings of 38.6%–43.3% and 56.7%–61.4%, respectively, in three female orangutans.

Orangutans, which had the highest %BIA (41.2 ± 1.1) and % BMM (41.0 ± 2.3) in our study, rely mostly on arboreal locomotion, in which the brachialis shows high electromyographic activity, particularly during the swing phase of suspensory locomotion and during the propulsion phase of vertical climbing (Fleagle et al. 1981; Tuttle and Basmajian 1974; Tuttle, Velte, and Basmajian 1983). In contrast, gorillas and chimpanzees had the highest %TBIA (71.9 ± 4.0 for gorillas and 71.9 ± 2.6 for chimpanzees) and %TBMM (72.2 ± 2.6 for gorillas and 70.7 ± 3.4 for chimpanzees). Both these species of hominid primates primarily use knuckle-walking (Hunt 2004), in which the triceps brachii shows high electromyographic activity, acting as an extensor of the elbow during the swing phase and a stabilizer of the elbow during the stance phase of knuckle-walking (Tuttle, Velte, and Basmajian 1983). The larger relative muscle mass of the triceps brachii that we observed in gorillas and chimpanzees may also compensate for their short olecranon compared to humans (Aiello and Dean 1990; Aiello et al. 1999; Drapeau 2004; Gebo 2014; Rose 1993), an anatomical adaptation that allows hyperextension of the elbow during the stance phase of knuckle-walking (Aiello et al. 1999). These results obtained in orangutans, chimpanzees, and gorillas regarding the parameters %BIA, %BMM, %TBIA, and %TBMM fully support our first hypothesis—that orangutans, with predominantly arboreal locomotion, would have higher values for the brachialis insertion, while gorillas and chimpanzees, which are primarily knuckle-walkers, would have higher values for the triceps brachii insertion.

Bonobos had higher %BIA (32.0 ± 3.4) and %BMM (32.5 ± 7.3) than gorillas and chimpanzees but lower than orangutans. This may be a reflection of their locomotor behavior, which combines knuckle-walking with some arboreal locomotion (Doran 1993). These results fully support our second hypothesis—that bonobos, with more frequent arboreal locomotion, would have higher values than chimpanzees for the brachialis insertion.

Finally, our modern humans showed high %TBIA (74 ± 2.2) and %TBMM (74.8 ± 2.7). The strictly bipedal locomotion in modern humans has allowed their upper limb to adapt to manipulative functions (Hunt 2004), where the triceps brachii shows high electromyographic activity during both the flexion and the extension of the elbow, contributing to the stabilization of both the elbow joint and the upper limb as a whole (Chaytor et al. 2020). The great importance of the triceps brachii during manipulative activities in modern humans is also reflected in their longer lever arm compared to that of other hominid primates; in fact, humans are the hominid with the greatest relative length of the olecranon (Thorpe et al. 1999). Our findings in humans fully support our third hypothesis—that humans would have relatively high values for the triceps brachii insertion as an adaptation to its use in performing manipulative tasks. The lower value of %BIA and % BMM in humans compared to the other primate species studied (Table 2) can be related to the smaller relative size of the elbow flexor muscles in *H. sapiens* when compared to other primate species such as *P. troglodytes* (Kikuchi 2010). This lesser development of the elbow flexor muscles in humans is also reflected in the position of the brachialis insertion site closer to the trochlear notch of the ulna compared to chimpanzees, making the lever arm of the brachialis relatively shorter in *H. sapiens* than in *P. troglodytes* (de Diego et al. 2020).

There is a certain degree of controversy regarding the validity of obtaining information on the anatomical and functional characteristics of a muscle through the morphological analysis of the muscle insertion site (enthesis) at the bone level. Some experts affirm that entheses adapt their morphology to the anatomical and functional characteristics of the muscles and that the size and robustness of the insertion sites are related to the morphology and activity of the muscles (Drapeau 2008b; Foster, Buckley, and Tayles 2014; Niinimäki 2011). Others, however, suggest that the size and robustness of the entheses are not related to muscle morphology or activity but to other factors, such as age (Cardoso and Henderson 2010; Milella et al. 2012) or body size (Weiss, Corona, and Schultz 2012; Zumwalt, Ruff, and Wilczak 2000). In the present study, we found a significant positive correlation between the size of the insertion site and the muscle mass of both muscles studied (Figure 3), which suggests a relationship between the morphology of the enthesis of the brachialis and triceps brachii and the anatomical and functional characteristics of the respective muscles. Furthermore, the information obtained with the quantitative analysis of the insertion sites of the brachialis and triceps brachii on the proximal epiphysis of the ulna was corroborated by the similar results

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obtained with the study of the muscles themselves in the same species of hominid primates (Table 2). Therefore, we can conclude that the relative size of the insertion sites of the two muscles may well be related to their relative muscle mass and to the type of locomotion in each of the species of primates, since the different types of locomotion entail functional differences in the brachialis and triceps brachii (Fleagle et al. 1981; Tuttle and Basmajian 1974; Tuttle, Velte, and Basmajian 1983).

Our findings of a close relationship between the relative size of the brachialis and triceps brachii insertion sites, their relative muscle mass, and the locomotor behavior of our modern hominid primates allowed us to extrapolate these results to the locomotor behavior of several fossil hominins with well-preserved proximal epiphyses of the ulna. The earliest hominins that we studied—AL-288-1, dating to 3.2 MYA (Drapeau 2004) and STW-431, dating to 2.6–2.8 MYA (Drapeau 2008a), belong to the species *A. afarensis* and *A. africanus*, respectively. They had %BIA values very similar to those obtained in *P. paniscus*, which frequently use arboreal locomotion (Doran 1993). This finding suggests that these early hominins also used some arboreal locomotion, like vertical climbing or suspensory locomotion, to complement their bipedalism. Arboreal postural behavior and locomotion in these early representatives of *Australopithecus* has been suggested by various authors (Green, Gordon, and Richmond 2007; Stamos and Alemseged 2023) based on anatomical characteristics of their upper limb, including the shape of the trochlear notch of the ulna (Drapeau 2008a), the relatively long upper limb, the cranial orientation of the glenoid cavity of the scapula, the relatively long pisiform bone and the presence of curved phalanges in the hand (Fleagle 1999; Stamos and Alemseged 2023). Such arboreal behavior would be of vital importance when searching for food, building nests or avoiding predators.

We also studied a later representative of *Australopithecus*, *A. sediba*—UW-88-62, dating to 1.98 MYA (Rein et al. 2017). Based on the presence of a relatively long upper limb and the morphology of the trochlear notch and the radial notch of the ulna (Churchill et al. 2013; Rein et al. 2017), investigators have postulated that *A. sediba* used primarily bipedal locomotion that was complemented by vertical climbing and suspensory behavior (Holliday et al. 2018). Along this same line, our *A. sediba* had %BIA values very similar to those of *A. afarensis* and *P. paniscus* (Table 2), indicating a similar locomotor behavior. Our fourth fossil hominin was *P. boisei*—OH-36, dating to 1.1–1.2 MYA (Aiello et al. 1999)—a more recent species than the *Australopithecus* (Jurmain et al. 2018). Osteological analyses of the upper limb in *P. boisei* revealed the presence of a relatively long upper limb (Fleagle 1999; Lague et al. 2019), a unique morphology of the trochlear notch of the ulna (Drapeau 2008a; Lague et al. 2019), and a lateral eccentricity of the articular fovea of the head of the radius similar to that of orangutans (Domínguez-Rodrigo et al. 2013). These findings indicate that *P. boisei* also combined bipedalism with different types of arboreal postural behavior and locomotion, including vertical climbing and suspensory locomotion (Aiello et al. 1999; Domínguez-Rodrigo et al. 2013; Lague et al. 2019). The proximal epiphysis of the ulna in our specimen of *P. boisei* showed slightly higher values for %BIA than those of *P. paniscus* or *Australopithecus*, suggesting the use of arboreal locomotion in this species (Table 2).

Finally, the %BIA and %TBIA of our three fossil *Homo* specimens (*H. ergaster*, *H. neanderthalensis*, and archaic *H. sapiens*) were very similar to those observed in modern humans (Table 2). This finding corroborates the generally accepted theory that the appearance of body proportions characteristic of modern humans and the loss of arboreal locomotion in favor of strict bipedalism occurred with the appearance in Africa of *H. ergaster*, dating to 1.7 MYA (Crompton, Vereecke, and Thorpe 2008; Ruff 2009; Stamos and Alemseged 2023).

Our study has several limitations, including the low number of dissected hominid primates, especially *P. paniscus*, *G. gorilla*, and *P. pygmaeus*. Although the number of *P. troglodytes* dissected in our study is relatively high considering the generally limited access to these primates, ideally a larger study with more specimens of bonobos, gorillas, and orangutans is warranted. Additionally, most of our samples came from captive-bred primates, with the exception of the 3D bone meshes of *P. paniscus*, which were provided by the Royal Museum for Central Africa in Tervuren (Belgium). Although some studies indicate that captive-bred hominid primates are good models for osteometric studies (Bello-Hellegouarch et al. 2013), we cannot be sure to what extent their locomotor behavior is comparable to that of their wild-caught counterparts. Our results should ideally be validated in 3D bone meshes of ulnae from wild primates of the same species included in our study. A further limitation of our study is that we have only analyzed the insertion of the distal end of the brachialis and triceps brachii muscles. Although this distal end is usually the mobile and functional end in many movements, especially those performed in an open kinetic chain, in some movements performed in a closed kinetic chain the mobile and functional end of the muscle is inverted. This occurs, for example, in the support phase of vertical climbing or knuckle-walking. To obtain a more complete view of the morphological and functional characteristics of these two muscles, their proximal insertion sites should also be analyzed, which would improve our understanding of the anatomical adaptations to the different types of locomotion in these species. Finally, our human specimens came from cadavers provided by the Body Donation Service, which are generally from older individuals. The advanced age of our human specimens may have affected our findings on muscle mass, since elderly individuals often suffer from muscle atrophy or sarcopenia. However, we have compensated for this limitation by using values for relative muscle mass.

In conclusion, our findings indicate that the relative size of the brachialis and triceps brachii insertion sites on the proximal epiphysis of the ulna in modern hominid primates, including humans, is closely related both to the relative mass of these two muscles and to the types of locomotion used by these primates. This information can be extrapolated to determine the locomotor behavior of fossil hominins with a well-preserved proximal epiphysis of the ulna. Our use of 3D bone meshes to calculate the area of the insertion sites provided more precise information than 2D images, since the insertion site of the brachialis is markedly concave and that of the triceps brachii is markedly convex. Our results help to expand our knowledge of the anatomical and functional details of the elbow joint in hominid primates and to better understand the locomotor behavior of fossil hominins.

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Author Contributions

Neus Ciurana: conceptualization, data curation, formal analysis, investigation, methodology, validation, visualization, writing–original draft preparation. **Aroa Casado:** data curation, formal analysis, investigation, methodology, validation, visualization. **Patrícia Rodríguez:** data curation, formal analysis, investigation, methodology, validation, visualization. **Marcel García:** data curation, formal analysis, investigation, methodology, validation, visualization. **Francisco Pastor:** data curation, formal analysis, investigation, methodology, resources, supervision, validation, visualization. **Josep M. Potau:** conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, visualization, writing–original draft preparation.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

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

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