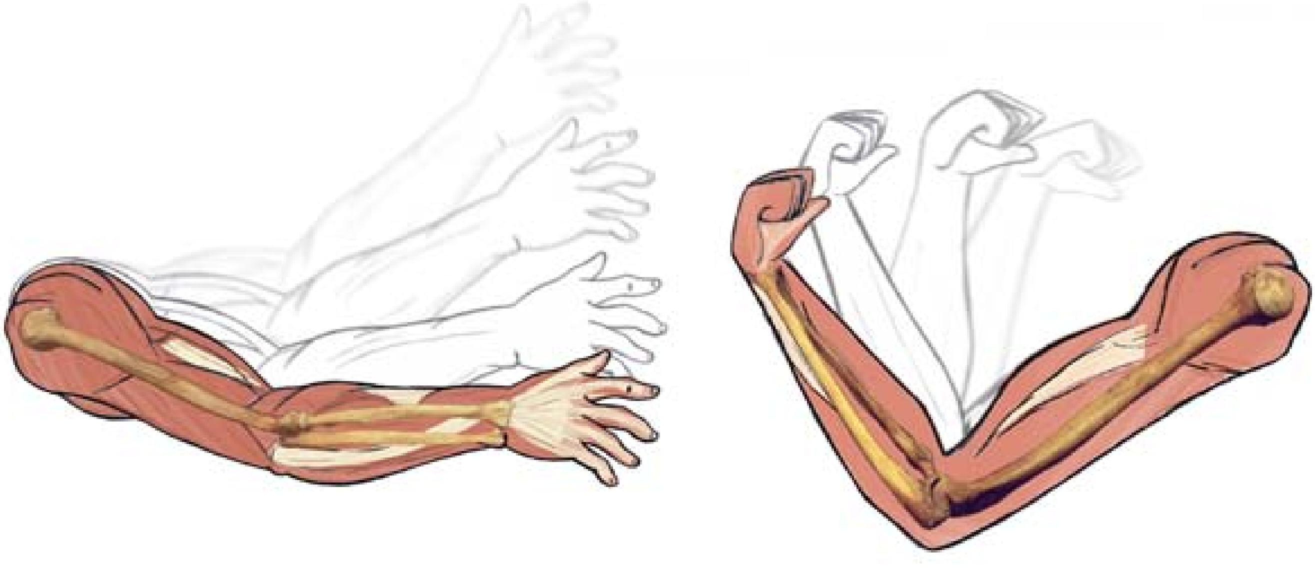
STRUCTURAL AND BIOMECHANICAL ANALYSES OF THE UPPER LIMB SKELETON: IMPLICATIONS FOR FUNCTIONAL RECONSTRUCTION IN HOMINOIDS.



PhD DISSERTATION

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STRUCTURAL AND BIOMECHANICAL ANALYSES OF THE UPPER LIMB SKELETON: IMPLICATIONS FOR FUNCTIONAL RECONSTRUCTION IN HOMINOIDS

Dissertation presented by Pere Ibáñez-Gimeno in fulfillment of the requirements for the Doctorate in Biodiversity of Departament de Biologia Animal, de Biologia Vegetal i d'Ecologia, Universitat Autònoma de Barcelona, directed by:

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Pere Ibáñez-Gimeno

The materials at present within my command hardly appeared adequate to so arduous an undertaking; but I doubted not that I should ultimately succeed. I prepared myself for a multitude of reverses; my operations might be incessantly baffled, and at last my work be imperfect; yet, when I considered the improvement which every day takes place in science and mechanics, I was encouraged to hope my present attempts should at least lay the foundations of future success.

Mary Shelley
Frankenstein

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When you start a research project, you never know how it is going to end up. You feel joy when something turns up to be statistically significant, unless that significance is completely unexplainable. You get stressed as a deadline gets closer, and you lose your sleep if Windows decides to erase a database that you had been filling up for weeks. You feel powerless when your advisors and you get stuck discussing about the font size of a figure legend and you have not even started to talk about the functional implications of the results. Nevertheless, those are moments when you realize that you care about what you are doing and that you are struggling to get things right. And the best part is that you find lots of people on the way that help you to keep following your path and reach your objectives.

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ABSTRACT

Some of the differences observed among nonhuman hominoids and among human groups in the upper limb skeleton are triggered by differences in their locomotion and in their activity patterns, respectively. Upper limb structural characteristics can be quantified using several approaches, e.g. scoring entheseal changes, calculating cross-sectional properties, analyzing shape or applying biomechanical models. Concerning the latter, the model to calculate forearm rotational efficiency (pronator teres rotational efficiency, E_{rot}) is of special interest, as pronation and supination are essential during locomotion and manipulation. This model uses osteometrical and geometrical measurements taken on three-dimensional images of humerii and on dry radii and ulnae to calculate E_{rot}, which is a measure of the capacity of pronator teres to rotate the radius around the ulna. The objective of this dissertation is to characterize the hominoid arm and forearm skeleton using E_{rot} and other function-related features and to use this characterization to reconstruct activity patterns and locomotor behaviors. Forearm rotational efficiency (E_{rot}) was calculated in a large sample of extant hominoids. The results indicate that the positions in the pronation-supination range where E_{rot} is maximal for each elbow angle differ among taxa, which reflects adaptations to locomotor modes: there are evident differences among knuckle-walkers, arboreal taxa and true brachiators. Humans present positions of the maximums that reflect the lack of locomotor requirements of their upper limb and the enhancement of manipulative capacities. The differences in the positions of maximum E_{rot} are caused by differences in the orientation of the humeral medial epicondyle, the proximal attachment site of pronator teres: more retroflexed epicondyles cause maximum E_{rot} in elbow extension to be in more pronated positions, whereas more proximally oriented epicondyles cause maximum E_{rot} in elbow flexion to be in more supinated positions. The effect of muscular activity on skeletal structure was explored by analyzing the components of pronator teres force and by assessing the relationship between entheseal development and other skeletal characteristics on a large sample of humans. The results suggest that pronator teres usage can cause plastic changes on characteristics related to E_{rot} calculation, especially to overcome functional disadvantages that occur when the forearm is used in positions of low E_{rot} or disequilibrium of forces. The correlation between the development of some entheseal changes and medial epicondylar orientation indicates that the latter can be probably modified by activity, and so forearm positions where E_{rot} is maximal can reflect activity patterns. Overall, skeletal features of the upper limb that are affected by activity, such as entheseal changes and humeral rigidity and shape, show covariance among them, which highlights their relevance to inferring function. The humeral shaft increases its rigidity and the anteroposterior width of its mid-proximal region in order to adjust to mechanical requirements related to muscles involved in shoulder motion. Cross-sectional properties and E_{rot} were also used to reconstruct the activity-related sexual dimorphism in Tigara (1200-1700CE) and Ipiutak (100BCE-500CE), Alaska. In Tigara, the greater values for humeral cross-sectional properties among males indicate that they were involved in more physically demanding tasks, such as hunting. The forearm positions where E_{rot} is maximal in elbow flexion are in more supinated

positions in females, which suggests that they probably engaged in manipulative labors more frequently. In Ipiutak, the results failed to find a relevant degree of sexual dimorphism. Forearm rotational efficiency (E_{rot}) was also used to infer the locomotor mode of Lucy (*Australopithecus afarensis*). The resemblance of the positions of its maximum E_{rot} with those of *Pongo* spp. throughout the entire flexion-extension range, and its resemblance with *Pan troglodytes* and *Gorilla gorilla* in elbow flexion, suggest that the upper limb of *Au. afarensis* was adapted to arboreal locomotion.

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1. INTRODUCTION

Everything we know is just barely being held together.

Claire Fisher

Six Feet Under

1.1. THE RELATIONSHIP BETWEEN UPPER LIMB STRUCTURE AND FUNCTION

The structure of biological systems is intimately related to the function that they perform (Darwin, 1859). As all tissues, bones undergo phylogenetic, ontogenetic and plastic changes in order to adapt to functional requirements (Ruff et al., 1993, 1994; Anapol et al., 2005; Shaw and Stock, 2009a, 2009b; Cowgill, 2010; Ryan and Shaw, 2012; Cambra-Moo et al., 2014). In hominoids, this is of special interest as far as the upper limb skeleton is concerned. The hominoid upper limb is a plesiomorphic structure that consists of the shoulder girdle, the arm, the forearm and the hand. Its major joints have seven degrees of freedom, and each of them is performed by several muscles (Table 1) (Kapandji, 2002; Dijkstra, 2010).

In nonhuman hominoids, the upper limb function is mainly associated to locomotor, positional and manipulative behaviors (Szalay and Dagosto, 1980; Hunt, 1991; Stern and Larson, 2001; Sarmiento, 2002). Suspensory and climbing hominoids, such as chimpanzees, bonobos, orangutans and, to a lesser extent, gorillas, present a cranially oriented glenoid fossa, which facilitates the use of the upper limb in elevated positions (Stern and Susman, 1983; Green, 2013), and a globular humeral head with low tubercles, which permit a wide range of movement (Fleagle, 1988). These hominoids also display a strong development of the ulnar wrist, which is related to climbing and other pulling actions (Tuttle, 1981), and elongated and rod-shape pisiforms, which are probably associated to an increased relative size of the flexor carpi ulnaris and increased leverage for carpal flexion (Stern and Susman, 1983). This is useful for arboreal locomotion as it leads to large and mechanically advantageous wrist flexors (Stern and Susman, 1983). They also show curved phalanges, which help alleviate the strain during these forms of locomotion (Stern and Susman, 1983; Richmond, 2007; Rein et al., 2011), and relatively long upper limbs and forearms (Jungers, 1982; Susman et al., 1984; Fleagle, 1988; Kimbel et al., 1994).

Besides arboreal locomotion, gorillas and chimpanzees commonly engage in knuckle-walking, a form of quadrupedalism in which pressure in the upper limb is taken by the knuckles, and which is also associated to several structural characteristics. Most of them are present in the hand and wrist, such as the bone ridges on the posterior aspect of the distal articular surface of the radius and the scaphoid and at the base of the posterior articular surface of each metacarpal head, which increase the stability of the wrist and the phalanges when they are extended (Tuttle, 1969a). Knuckle-walkers also have a broad, concavo-convex proximal articular surface for the capitate and corresponding morphology of the distal capitate, which limits eccentric motion during locomotion (Drapeau et al., 2005). Their central metacarpals are mechanically more robust, as they are used for load bearing (Marchi, 2005; Matsuura et al., 2010). Another structural feature characteristic of knuckle-walkers is their great medial rotation or torsion of the humeral head, which was suggested to be a response to the locomotion-related requirement of orienting the elbow in the sagittal plane (Aiello and Dean, 1990).

TABLE 1. Degrees of freedom and muscles of each major joint of the upper limb.

Joint	Degree of freedom	Muscles
Shoulder (glenohumeral joint)	Flexion and extension	Deltoid, coracobrachialis, pectoralis major, teres major, teres minor, latissimus dorsi
	Abduction and adduction	Deltoid, supraspinatus, infraspinatus, subscapularis, teres minor, teres major, latissimus dorsi, pectoralis major, triceps brachii
	Internal and external rotation	Latissimus dorsi, teres major, subscapularis, pectoralis major, infraspinatus, teres minor
Elbow (humeroulnar joint)	Flexion and extension	Brachialis, brachioradialis, biceps brachii, pronator teres, triceps brachii, anconeus
Proximal and distal radioulnar joints	Pronation and supination	Supinator, biceps brachii, brachioradialis, pronator quadratus, pronator teres
Wrist (radiocarpal joint)	Flexion and extension	Flexor carpi ulnaris, flexor carpi radialis, palmaris longus, extensor carpi ulnaris, extensor carpi radialis longus, extensor carpi radialis brevis
	Abduction and adduction	Flexor carpi ulnaris, flexor carpi radialis, palmaris longus, extensor carpi ulnaris, extensor carpi radialis longus, extensor carpi radialis brevis

Hylobatidae are arboreal primates, but they display a unique locomotor form, called ricochetal brachiation, in which they support their weight with their upper limbs beneath a superstrate employing both a contact and a flight phase in their gate (Bertram and Chang, 2001). This form of locomotion is enabled by a relatively long clavicle (Kagaya et al., 2010) and a markedly globular humeral head (Arias-Martorell et al., 2013). Hylobatidae also have long, curved, slender digits, and the longest upper limbs relative to body size of any primates, which facilitate this locomotor form (Fleagle, 1988; Dean and Begun, 2008).

Humans are adapted to an exclusively bipedal locomotion, which enabled a relaxation of the locomotor selection pressures in the upper limb and allowed an improvement of their preexisting manipulative skills in early hominines (Alba et al., 2003; Almécija et al., 2012; Almécija and Alba, 2014). The upper limb was probably co-opted for stone tool-making later, in early *Homo* (Marzke, 1997; Marzke and Marzke, 2000; Tocheri et al., 2008; Almécija et al., 2010). Therefore, the human upper limb is free from locomotor stresses and is only subjected to manipulative pressures, including carrying, transporting and throwing objects (Darwin, 1871; Alba et al., 2003), which entailed several unique structural changes. Human arms are shorter for their size than the arms of the rest of hominoids (Johanson and Edey, 1980; Susman et al., 1984). Humans also present a great torsion of the humeral head, even higher than gorillas and chimpanzees. As the shoulder joint is laterally oriented in humans, a great torsion of the humeral head allows the elbow joint to be anteriorly oriented, which enables the forearm and the hand to be used in front of the body during manipulation (Aiello and Dean, 1990). The humeral shaft, conversely to nonhuman hominoids, is not bowed because it is not a weight-bearing structure (Holliday and Friedl, 2013). The hand also displays several characteristics that enable humans to use the precision and the power grips, such as a long thumb in relation to the rest of the fingers (Almécija, 2009).

In nonhuman hominoids, therefore, interspecific dissimilarities in skeletal characteristics of the upper limb will usually be caused by differences in locomotion, posture or manipulative abilities. In humans, those intraspecific differences in the internal and/or external architecture of the upper limb skeleton that are mainly caused by prolonged and continued stress conditions will be basically derived from regular and occupation labors and will thus be reflecting differences in daily activities related to manipulative behaviors. For instance, sexual differences in the degree of bilateral asymmetry of the humeral diaphyseal rigidity may indicate sexual division of labor in a population (e.g. Nikita et al., 2011). Likewise, differences in the activity pattern among populations contribute to a differential development of their muscular insertions (e.g. Steen, 2003). Overall, all these premises justify the use of characteristics of the upper limb skeleton to infer activity patterns and reconstruct behavioral aspects of hominoid groups or taxa.

1.2. QUANTIFYING FUNCTION-RELATED STRUCTURAL CHARACTERISTICS IN THE UPPER LIMB SKELETON

Several structural characteristics of the upper limb skeleton can be used to explore interspecific differences in locomotion, manipulation and positional behaviors in hominoids, as well as to obtain information on the manipulative labors that human individuals or groups were engaged in during life. The quantification of these characteristics enables to perform statistical comparisons to test the significance and strength of the interspecific and intraspecific differences, as well as the sexual dimorphism, the bilateral asymmetry and the influence of other factors, such as age and body size (Stock and Pfeiffer, 2004; Havelková et al., 2011; Lieverse et al., 2013; Ryan and Shaw, 2013).

The response of structures to specific loading conditions, for instance, can be assessed through finite element analysis (FEA), which consists of a computer simulation technique which frequently uses skeletal 3D images (Zienkiewicz, 1971; Richmond et al., 2005; Ross, 2005). FEA aims to assess the deformation and resistance of skeletal structures submitted to external loads by calculating the stress and strain that they undergo. Prior to this assessment, the complex geometry of the structures must be subdivided into a finite number of elements of simple geometry. Otherwise, stress and strain would be computationally unsolvable (Richmond et al., 2005). This method is useful not only to infer mechanical properties and function of structures, but also to interpret the ecological adaptations of these structures (Marcé-Nogué et al., 2013). Nevertheless, FEA has been scarcely used in studies involving the hominoid upper limb, and most of them addressed medical issues in humans (e.g. Boutroy et al., 2008; Rudang et al., 2013).

Bone microarchitecture studies are also employed when aiming to assess functional implications of the skeletal structure. These analyses generally focus on the quantification of the mineral density of the sub-articular cortical (subchondral) bone and of the trabecular bone, and on other trabecular bone properties (Rafferty and Ruff, 1994; Ryan and Walker, 2010; Zeininger et al., 2011; Shaw and Ryan, 2012; Ryan and Shaw, 2013; Scherf et al., 2013). For instance, the trabecular orientation uniformity of the proximal humerus has been shown to be lower in suspensory than in quadrupedal primate taxa, because the former are exposed to variable, non-repetitive loadings (Fajardo and Müller, 2001). Moreover, the locomotor forms of nonhuman hominoids and the manipulative capabilities of humans are reflected in the pattern of mineralization of the metacarpal heads, showing those areas with the greatest loads, and so with the greatest remodeling rates, the highest degrees of mineralization (Zeininger et al., 2011).

In humans, one of the most widespread methods to infer activity patterns of ancient populations from the upper limb skeleton are entheseal changes analyses and the assessment of diaphyseal cross-sectional properties (Meyer et al., 2011). The latter have also been used to explore locomotion-related differences between hominoid taxa (e.g. Marchi, 2005; Ruff et al., 2013). The study of shape as a structural parameter is also frequently used with these purposes, as well as biomechanical models implying theoretical approaches that focus on forces and moments applied to structures or generated by them (e.g. Galtés, 2008; Nikita et al., 2011; Holliday and Friedl, 2013). All these analyses (entheseal changes, cross-sectional properties, shape and biomechanical models) will be described in detail given their relevance for the development of the current thesis.

1.2.1. Entheseal changes

An enthesis is the point or area of the bone into which a muscle, tendon or ligament inserts. The alterations of entheses seen in skeletal materials are generically known as entheseal changes (Villotte and Knüsel, 2013). The development of these alterations is partially dependent on the mechanical loads that they are submitted to, and thus on the activities or amount of use that the individuals submitted their muscles to (Hawkey and Merbs, 1995; Galtés et al., 2006; Villotte et al., 2010). Nevertheless, a direct relationship between activity and entheseal development cannot be established, as entheseal changes are affected by several factors, such as age, sex, body size, gens that regulate muscle and bone size, hormonal levels, nutritional factors, pathological conditions and any other factor that influences muscular development and bone metabolism (Benjamin et al., 2002; Chen et al., 2007; Villotte et al., 2010; Mariotti and Belcastro, 2011; Schlecht, 2012).

Entheses can be classified following different criteria. According to their macroscopic classification, entheses can be tendinous or fleshy (Testut and Latarjet, 1990; Galtés et al., 2006). Tendinous entheses are those where the muscle attaches to the bone by means of a tendon. Fleshy entheses, or direct entheses, are those where the muscle attaches to relatively large areas of bone by fleshy fibers. On the bone, tendinous and fleshy entheses show different morphologies. A tendinous enthesis presents granular concretions, crests and bone deposits, i.e. irregularities on the bone cortex. A direct enthesis may show a concavity on the bone, but the cortex does not display the changes mentioned for tendinous entheses (Galtés et al., 2006, 2009b).

Although direct entheses are practically not influenced by age (Galtés et al., 2006), they have not been extensively analyzed in the literature. Only methods developed by Galtés et al. (2006, 2009b), and posteriorly revisited by Santana-Cabrera (2013), address the issue on how to study this type of entheses.

According to the tissue present at the skeletal attachment site, entheses can be fibrous or fibrocartilaginous (Benjamin et al., 2002; Schlecht, 2012). Fibrous entheses present dense fibrous connective tissue at the bone-tendon interface, whereas fibrocartilaginous entheses present fibrocartilage. Fibrous entheses are either bony, when the tendon attaches directly to the bone, or periosteal, when the tendon attaches to the periosteum. Fibrous entheses occur most commonly on the diaphyses of long bones, where there is a large surface area and the soft tissue does not move significantly during joint movement (Benjamin et al., 2002; Villotte et al., 2010; Schlecht, 2012).

Fibrocartilaginous entheses present four histological zones: the tendon, which is pure dense fibrous connective tissue, the uncalcified fibrocartilage, the calcified fibrocartilage, and bone (Fig. 1). There is no periosteum at the attachment. The tidemark is the boundary between hard and soft tissue, and it represents the point at which calcification ceased. It is thus the site where the soft tissues fall away from the bone after maceration (Benjamin et al., 2002; Schlecht, 2012). Fibrocartilaginous sites occur in close proximity to joints on epiphyses and are therefore constrained by limited attachment space, short moment arms of the soft tissue, and bending of the soft tissue at the interface during joint movement (Benjamin et al., 2002; Villotte et al., 2010; Schlecht, 2012). The gradual transition between tissue types with different elastic properties probably enhances the ability of tendons to dissipate force evenly during muscle contraction, thus resisting shear stresses at the bone surface (Benjamin et al., 2002; Alves Cardoso and Henderson, 2010). Nevertheless, fibrocartilaginous entheses are reported in the clinical literature as being most prone to injury (Alves Cardoso and Henderson, 2010).

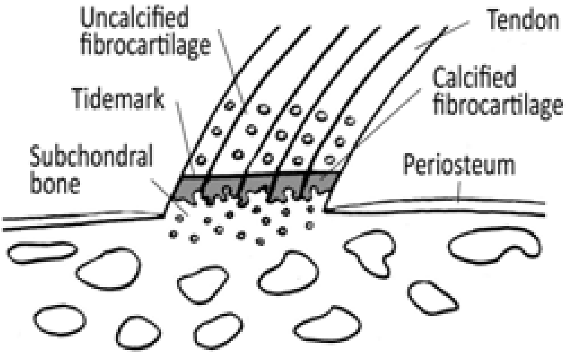

Figure 1. Schematic representation of the histological zones and structures present in fibrocartilaginous entheses. Adapted from Villotte (2013).

Bony fibrous attachments are the ones associated with raised ridges, or definite roughenings on the bone. Periosteal fibrous entheses show smooth markings on bones, but these are often far more extensive than fibrocartilaginous attachments and their boundaries less well defined. At healthy fibrocartilaginous attachments, as the tidemark is relatively straight and the fibrocartilage zones avascular, the enthesis is smooth, well circumscribed and devoid of vascular foramina. It should be noted, however, that the bony marking may be far less regular if the enthesis was the site of degenerative change that involved intratendinous calcification or bony spur formation (Benjamin et al., 2002; Schlecht, 2012).

Entheseal changes are used to infer activity patterns from ancient human populations, i.e. sexual dimorphism, bilateral asymmetry, intrapopulation and interpopulation differences, but they are not used in other species. Comparisons between species would not be informative, as the appearance of entheses is different in each taxon and there are no known methods to standardize by taxon. Intraspecific differences in nonhuman taxa are not informative either, because huge locomotion-related differences are not expected. Only experimental studies where animals are forced to perform different daily activities would be interesting as far as entheseal changes are concerned (Zumwalt, 2005; Rabey et al., 2015), as well as entheseal analyses assessing differences between free-ranging and captive animals (Niinimäki and Salmi, 2014).

The development of entheseal changes can be quantified using several methods. The most widespread methodologies imply grading the entheses in accordance to their appearance, development or robusticity. The first scoring system was proposed by Hawkey and Merbs (1995), which has been used by many researchers as foundation for new systems (e.g. Galtés et al., 2006; Mariotti et al., 2007; Alves Cardoso and Henderson, 2010; Santana-Cabrera, 2013). The greatest modifications from this original method are those systems that imply a separate gradation of the inner and the outer part of the entheses (Villotte et al., 2013) and those that consider fibrous and fibrocartilaginous entheses separately (Alves Cardoso and Henderson, 2010). Some authors support the idea that only fibrocartilaginous entheses should be used to infer activity patterns in ancient remains (Zumwalt, 2006; Villotte et al., 2010; Weiss, 2012; Henderson et al., 2013a, 2013b). Villotte (2006) found that fibrous entheseal changes scores have greater interobserver and intraobserver error rates than fibrocartilaginous scores. This is due to the fact that fibrocartilaginous entheses, being well-delimited, are easier to define and grade, whereas fibrous entheses are not that delimited. Furthermore, in fibrous entheses, a rough surface is expected even in unloaded insertions, whereas in fibrocartilaginous entheses, any kind of roughness or lack of smoothness on the surface is indicative of loading (Schlecht, 2012). Moreover, fibrous entheses are more affected by genes and body size (Chen et al., 2007; Jurmain and Roberts, 2008; Villotte et al., 2010).

Besides visual scoring systems, methodologies involving new techniques have been suggested, although they have not been widely explored. For instance, using a 3D laser scanner, Zumwalt (2005) assessed the fractal dimensions of entheseal surfaces, which were used as proxies for entheseal complexity and roughness. 3D technology also enabled to calculate the entheseal 3D surface area, which appears to be a good indicator of entheseal development (Noldner and Edgar, 2013; Nolte and Wilczak, 2013).

1.2.2. Cross-sectional properties

Long bone diaphyses behave much like engineering beams when they are submitted to mechanical loads, and so they can be considered as beam models and analyzed using the physical and engineering principles used to design structures (Ruff, 2000). Stresses derived from externally applied loading can thus be calculated by means of the cross-sectional geometric properties of the bone, measured perpendicular to the longitudinal axis of the bone. These properties can be proxies either for the strength of the diaphysis, which is the capacity to resist breaking, or for its rigidity, which is the resistance to deformation.

Cross-sectional properties can be calculated in relation to several kinds of loadings. Axial compression and tension occur when forces act along the long axis of the bone. Torsion is produced when the bone is twisted about its long axis, generating diagonal stress. Bending can occur on different planes, and causes compression and tension on the opposite surfaces of a cross-section (Ruff, 2000).

The main cross-sectional properties are areas of the sections, second moments of area and section moduli (Table 2). A second moment reflects how the points within an area are distributed with regard to an arbitrary axis. Mathematically, it is calculated as the product of small unit areas of material multiplied by the squared distances of these areas to the axis. Second moments of area of sections are used as proxies for diaphyseal rigidity. Section moduli are calculated by dividing the second moments of area by the distances from the outermost surface of the cross-section to the appropriate axis. As maximum stress under bending or torsion occurs on the surface of the section, section moduli are used as proxies for diaphyseal strength (Ruff, 1995, 2002).

TABLE 2. Main cross-sectional properties and their biomechanical definition. Modified from Ruff (2000).

Cross-sectional property	**Unit**	**Biomechanical definition**
Cortical area (CA)	mm^2	Strength or rigidity to tension and compression
Medullary area (MA)	mm^2	-
Total subperiosteal area (TA)	mm^2	-
Maximum second moment of area (I_{max})	mm^4	Maximum bending rigidity
Minimum second moment of area (I_{min})	mm^4	Minimum bending rigidity
Second moment of area about the mediolateral axis (I_x)	mm^4	Anteroposterior bending rigidity
Second moment of area about the anteroposterior (I_y)	mm^4	Mediolateral bending rigidity
Polar second moment of area (J)	mm^4	Torsional rigidity
Maximum section modulus (Z_{max})	mm^3	Maximum bending strength
Minimum section modulus (Z_{min})	mm^3	Minimum bending strength
Section modulus about the mediolateral axis (Z_x)	mm^3	Anteroposterior bending strength
Section modulus about the anteroposterior axis (Z_y)	mm^3	Mediolateral bending strength
Polar section modulus (Z_p)	mm^3	Torsional strength

The standard abbreviation of each property is shown in parentheses. MA and TA are not biomechanical properties of the bone, but they can be informative from a morphological point of view.

In order to calculate these variables, anatomically oriented images of sections of the diaphyses are needed (Ruff, 2002). Depending on the objectives of the study or the experimental design, researchers can choose to analyze one or several sections per bone. When aiming to analyze a single section to somehow assess a general estimation of the biomechanical properties of the overall diaphysis, the section at 50% of bone length is recommended (Ruff, 2000). In the humerus, the section at 35% from the distal end should be used, because at 50% there is the deltoid tuberosity. This insertion causes a marked morphological change that is caused by the insertion of a muscle and is not necessarily related to the biomechanical properties of the bone (Ruff, 2000).

Nevertheless, sections at different levels may be indicating different things. Therefore, several sections can be analyzed. Traditionally, five sections are studied in long bones: 20, 35, 50, 65 and 80% of bone length from the distal end, although some studies focus on other sections, normally in the mid-proximal and mid-distal diaphysis and in the mid-shaft of the bone (Ruff, 2000; Rhodes and Knüsel, 2005; Niinimäki, 2012).

Images of the sections can be obtained using several methods (O'Neill and Ruff, 2004). These can be invasive (cutting or breaking the diaphysis) or noninvasive. Among noninvasive methods, CT scanning is the one of choice if available, as it provides the most accurate images of both the periosteal contour and the medullary canal. Nevertheless, the periosteal contour can also be assessed from molds of the diaphyses or from 3D images obtained by means of laser scanners. The medullary canal can be reconstructed as an ellipse using biplanar radiographs of the diaphysis in the anteroposterior and the mediolateral planes (ellipse model method) (Fig. 2). All these estimating methods have been shown to be adequate, although a little less accurate than CT scanning (O'Neill and Ruff, 2004). The periosteal contour may also be reconstructed using the ellipse model method (Fig. 2), but this produces a bias that needs to be corrected (O'Neill and Ruff, 2004).

Even though reconstruction of both the periosteal contour and the medullary canal provides the greatest accuracy, several studies indicate that, in humans, great predictions of several cross-sectional properties can be obtained from periosteal external contours alone. These predictions have a strong correlation with properties calculated from sections including the medullary canal (Stock & Shaw, 2007; Sparacello & Pearson, 2010; Shaw and

Stock, 2011; Davies et al., 2012; Macintosh et al., 2013). This has only been tested in humans, and so for other species cross-sectional properties need to be measured using images with both the periosteal contour and the medullary canal.

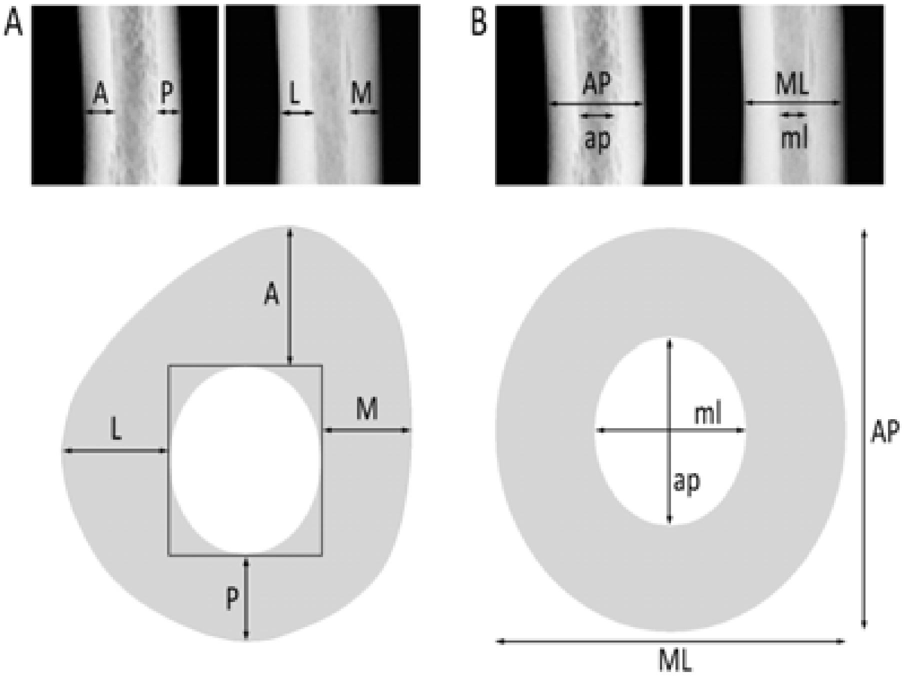

Figure 2. Reconstruction of diaphyseal cross-sections images. The section at 35% from the distal end of a human humerus is shown. **A:** Reconstruction of the medullary canal using the ellipse model method. Biplanar radiographs in the anteroposterior and mediolateral planes are used to measure the cortical thickness of the anterior (A), posterior (P), lateral (M) and lateral (L) aspects. The periosteal contour was obtained from a 3D image of the bone. **B:** Reconstruction of both the periosteal contour and the medullary canal using the ellipse model method. Biplanar radiographs in the anteroposterior and mediolateral planes are used to measure the anteroposterior (AP) and mediolateral (ML) diameters of the diaphysis and the anteroposterior (ap) and mediolateral (ml) diameter of the medullary canal. Adapted from O'Neill and Ruff (2004).

Cross-sectional properties have been widely used to infer activity patterns from human ancient remains (e.g. Holt, 2003; Stock and Pfeiffer, 2004; Rhodes and Knüsel, 2005; Shackelford, 2007; Sparacello and Marchi, 2008; Nikita et al., 2011; Sparacello et al., 2011). This usage of cross-sectional properties has been extensively justified by *in vivo* studies that explored how daily and common activities cause changes in these properties (Trinkaus et al., 1994; Johnson et al., 2001; Shaw and Stock, 2009a, 2009b; Wallace et al., 2014).

These properties have also been assessed in nonhuman hominoids in order to determine if they are influenced by the locomotor mode. For instance, metacarpal diaphyseal strength has been shown to be greater in knuckle-walkers than in humans, and intermediate in orangutans, which is in agreement with the locomotion and manipulation-related loadings that they are submitted to (Marchi, 2005). The relative humeral strength also displays a functional significance, as it is greater in juvenile mountain gorillas and in western lowland gorillas, which are more arboreal, than in adult mountain gorillas, which are the most terrestrial of all nonhuman hominoids (Ruff et al., 2013). The issue of lateralized arm behavior in hominoids has also been explored by examining cross-sectional properties (Sarringhaus et al., 2005).

When aiming to compare cross-sectional properties between individuals, populations or taxa, differences in body size must be controlled for, because it constitutes a mechanical load *per se* and is intimately related to factors that affect mechanical loading, such as muscular size (Ruff, 2000). Moreover, the fact that cross-sectional properties can be affected by factors unrelated to function should always be taken into consideration (Ruff, 2000; Carlson et al., 2008; Ruff et al., 2006).

Given that cross-sectional properties are structural changes that occur as consequence of mechanical loads derived from activity, it is expected that they present some sort of relationship with other function-dependent parameters. Although this has not been extensively explored, Shaw and Ryan (2012) found several significant correlations between humeral head sub-articular trabecular bone architecture and mid-humerus diaphyseal bone properties. Weiss (2003) observed that humeral robusticity, represented by a composite of several cross-sectional properties, and aggregated entheseal changes of seven major arm muscles showed a positive moderate correlation. Similarly, positive correlation and covariance between humeral torsional rigidity and entheseal development of pectoralis major, teres major and deltoid muscles was reported by Niinimäki (2012). Using a descriptive and theoretical approach, Rhodes and Knüsel (2005) indicated that the anteroposterior bending rigidity may be basically affected by movements involving the brachialis and the triceps brachii muscles. Conversely, Ogilvie and Hilton (2011) hypothesized that the triceps brachii, the brachialis and the brachioradialis contribute to the mediolateral bending rigidity of the mid-distal humerus.

1.2.3. Shape

The concept "shape" should not be confused for "form". The form of an object is unaffected by its position and orientation. Shape is not affected by position, orientation or size. Therefore, the shape of an object can be considered as its form corrected by its size (Kendall, 1977; Mitteroecker et al., 2013).

The analysis of shape variation and its covariation with other variables is known as morphometrics (Bookstein, 1991). Skeletal morphometrics has been widely used in phylogenetic and systematic studies (e.g. Lague and Jungers, 1996; Frost et al., 2003). Nevertheless, shape is affected by countless factors, and so it can also be analyzed in relation to many things. Recent analyses, for example, focus on the study of modularity, ontogenetic and evolutionary variation and response to external factors, among others (Bookstein et al., 2002; Marugán-Lobón and Buscalioni, 2006; Green and Alemseged, 2012; Tallman, 2012; Arias-Martorell et al., 2014b). The skeletal shape of the upper limb is also influenced by mechanical loadings, and so it can be used as a marker of activity in humans and a locomotion-related variable in the rest of hominoids.

Several approaches can be used to quantify shape (Meyer et al., 2011). Metrical indices from skeletal measurements are classically employed in the literature (Martin and Saller, 1957; Olivier, 1960; Howells, 1973; Feldesman, 1982; Rose, 1988; Lague and Jungers, 1996; Almécija et al., 2014). In the humerus and the radius, for instance, classical anthropological studies reconstruct human behavioral patterns from mid-distal and mid-shaft diaphyseal indices (robusticity and diaphyseal indices) (Olivier, 1960; Bass, 1971). There are also several upper limb indices that can be calculated in hominoids and used as proxies for the size and surface area of joints (Rafferty and Ruff, 1994; Ruff, 2002). Clear relationships between these indices and locomotor modes have been established in hominoids by investigating the articular size and surface area in relation to cross-sectional properties (Ruff, 2002). Nevertheless, these external indices are rather independent from sub-articular trabecular bone properties, and so they are probably adapted to different aspects of the mechanical environment (Rafferty and Ruff, 1994).

Besides these classical indices, new methodologies have recently arisen to measure shape. Among them, indices calculated from diaphyseal cross-sectional properties are of special interest in ancient human populations because they provide accurate information on the roundness of the sections (Holt, 2003; Stock and Pfeiffer, 2004; Shackelford, 2007; Sparacello and Marchi, 2008; Nikita et al., 2011; Sparacello et al., 2011). Basically, two types of indices can be assessed: I_x/I_y or Z_x/Z_y, which quantify the differences between the mediolateral and the anteroposterior diaphyseal development, and I_{max}/I_{min} or Z_{max}/Z_{min}, which quantify the differences between the planes of maximum and minimum rigidity or strength. Values of these indices close to one indicate a high degree of circularity. These shape indices provide information as to the orientation of the biomechanical loading (Shaw and Stock, 2009a), and thus the plausible functional role of upper limb muscular usage in humeral diaphyseal shape can be explored from a descriptive and theoretical point of view. Using a human skeletal assemblage, Rhodes and Knüsel (2005) suggested that the humeral insertion for the brachioradialis is related to the mediolateral broadening of the mid-distal diaphysis, because of the development of the lateral supracondylar ridge. At the midshaft, the deltoid development may broaden the diaphysis laterally, whereas the development of the coracobrachialis may broaden it medially. The anteroposterior breadth may be influenced by the brachialis and the triceps brachii. At the mid-proximal diaphysis, the anteroposterior breadth may be largely influenced by pectoralis major and deltoid attachment sites, whereas triceps brachii development may be influencing both the anteroposterior breadth and the medial margin of the diaphysis.

Indices from diaphyseal cross-sectional properties have also been assessed in nonhuman hominoids and their relationship with the locomotor form has been investigated. These studies mainly report that upper limb cross-sections tend to appear more circular in more arboreal and suspensory primates compared with terrestrial species (Carlson, 2005; Carlson et al., 2006; Patel et al., 2013). These data support the hypothesis that cross-sections that are more circular in shape are adapted for multidirectional loading regimes and bending moments encountered when using acrobatic locomotor behaviors.

The revolution in morphometrics did not occur until the development of geometric morphometric methods (Rohlf and Marcus, 1993), which capture the geometry of the morphological structures and preserve this information throughout the analyses. These include methods for both outline and landmarks data (Fig. 3). In outline methods, points are digitized along the outline of the specimen and then fitted with a mathematical function. The resulting curves can be compared by using the coefficients of functions as shape variables in multivariate analyses (Dean et al., 2004). Nevertheless, there is not a general consensus on the best statistical approach when analyzing outline data (Rohlf, 1986; Dean et al., 2004). Landmark methods are based on the collection of coordinates of biologically definable landmarks. The effects of position, orientation and scale are then mathematically eliminated by superimposing all the configurations of landmarks under study, so that shape variables can be used to perform comparisons. Depending on the nature of the landmark configurations, several superimposition methods may be used (Dean et al., 2004).

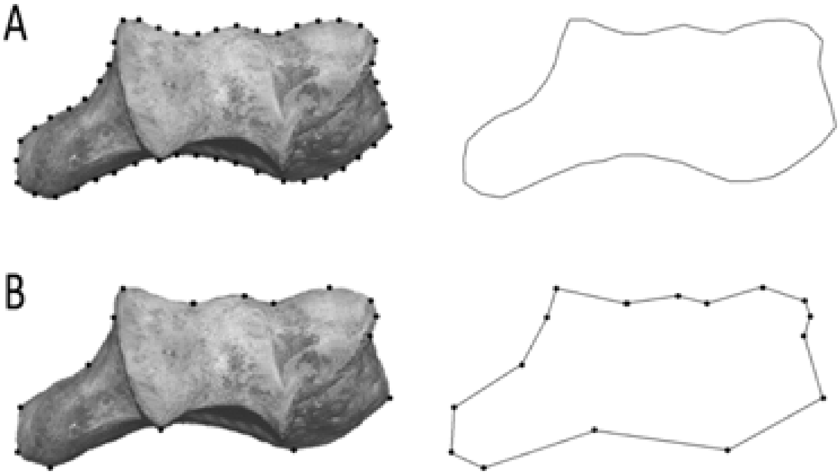

Figure 3. Representation of the geometric morphometric methods for data obtaining. A distal human humerus is shown. **A:** Outline method. Points are digitized along the outline. A curve is obtained from these points. **B:** Landmark method. Each landmark is a biologically definable coordinate (maximum convexity point, maximum concavity point, tip of a structure, intersection between structures, etc.).

Geometric morphometric analyses have found locomotion-related differences among hominoids focusing on several upper limb skeletal structures, such as the scapula (Bello-Hellegouarch et al., 2013; Green, 2013), the humerus (Lague and Jungers, 1999; Bacon, 2000; Tallman, 2010; Arias-Martorell et al., 2012; Holliday and Friedl, 2013; Arias-Martorell et al., 2014a; Lague, 2014; Arias-Martorell, 2015), and the proximal and distal radius and ulna (Tallman, 2013; Rein et al., 2015), although it is frequently difficult to distinguish between function-driven and phylogeny-driven differences.

1.2.4. Biomechanical models

In order to know how structures respond to loads in terms of motion, and so to simulate dynamic aspects of the movements, biomechanical models can be used. Several analyses provide models of the musculoskeletal anatomy of the upper limb using bone mechanical properties, joint kinematics and muscular synergism, although they are basically focused on computer animation of human characters, rather than on biological issues (Mauler et al., 1996). In some cases, the results obtained from models were compared with data from *in vivo* observations (van der Helm, 1994), but functional implications were not explored. Many of these works modeled the shoulder joint, by employing fixed coordinates as the points of application of muscular forces (Högfors et al., 1987), by investigating the interplay between the motion of constituent parts of the shoulder (Högfors et al., 1991) or by describing the motion of the shoulder using theoretical vectors (Engin and Tümer, 1989; Tümer and Engin, 1989). The elbow joint, and so flexion-extension and pronation-supination, have also been extensively modelled using, for instance, inverse dynamic methods, which predict muscle and joint reaction forces by computing forces or torques based on the motion of joints (Rehbinder and Martin, 2001; Li et al., 2006). Other models calculated moment arms of elbow and forearm muscles by assessing the tendon displacement and joint angles (Murray et al., 1995, 2002; Bremer et al., 2006) and by simulating the path of the muscles as straight lines from the origin to the insertion point (Freund and Takala, 2001; Ramsay et al., 2002). Similar methods have been employed to generate models of the entire upper limb (Garner and Pandy, 2001; Rankin and Neptune, 2012), whereas other researches tried to improve those methods. For example, instead of using straight lines from the origin to the insertion point, curved lines following more realistic muscular paths have been suggested (Amis et al., 1979; Charlton and Johnson, 2001).

In general, all biomechanical analyses of the upper limb focus on calculating kinematic, ergonomic or mechanical parameters from computer or solid models or from cadaveric remains. None of these studies intend to analyze biomechanical parameters from dry skeletal remains, which would be very useful to study large samples and so to fully explore the natural variation of these parameters. Moreover, these works do not assess the relationship between these parameters and the functional advantages that they entail, and thus their etiology remains unknown. Therefore, analyses of the variation of the upper limb biomechanics and its functional significance are warranted.

1.2.4.1. Modeling forearm rotation

Forearm rotation (pronation-supination) occurs when the radius rotates around the ulna and enables the hand to face downwards, upwards and in any intermediate position. Therefore, forearm rotation is an essential degree of freedom of the upper limb. It allows primates to grab and manipulate objects, and entails an infinite number of positions of the hand in relation to the forearm, which provides with adequate means to perform a great variety of locomotion modes. Hominoids have greater pronation and supination capabilities as compared to monkeys in terms of range, strength and stability

(Stern and Larson, 2001; Sarmiento, 2002). The rotator specializations of the forearm in hominoids are notably distinctive, and it has even been suggested that they reflect adaptation to the stem locomotor mode of the hominoid linage (Hunt, 1991; Stern and Larson, 2001). Given the central role of pronation-supination in human manipulation and nonhuman hominoid locomotion, the analysis of the relationship between upper limb skeletal structure and the mechanical implications of forearm rotation is warranted. Studies on how structure and mechanics influence each other are indeed scarce in the literature. In this regard, a mathematical and physical model allowing to quantify the way in which the bone structure and the resulting muscular activity are related would be very useful. This model would enable to determine how changes in the structure affect function and how differences in activity, which may entail differences in muscular usage, cause skeletal structure to undergo plastic changes in order to adapt to the new functional requirements.

Galtés et al. (2008) developed a model to assess the ability of pronator teres to perform rotatory movements, i.e. to calculate forearm rotational efficiency (E_{rot}), from structural measurements taken on computed tomography images of the elbow and the forearm. This procedure was later adapted to calculate E_{rot} using skeletal remains (Galtés et al., 2009a) (Fig. 4). The capacity of pronator teres to rotate the radius around the ulna can be quantified if the torque of this muscle with respect to the pronation axis is known. The torque depends on the value of the force ($\vec{F}$) and the distance between the force vector and the rotation axis. The tangential component of the force ($\overrightarrow{F''}$) is the one that causes rotatory movements and its value can be calculated if the values of angles α and β are known (Fig. 4). As the distance between this component and the rotation axis is constant (rotational radius, $\overline{AO'}$), the value of the torque can be expressed as:

$$\vec{T} = \vec{F''} \times \overline{AO'} = \vec{F'} \times \cos\beta \times \overline{AO'} = \vec{F} \times \cos\alpha \times \cos\beta \times \overline{AO'}$$

The value of the torque in relation to the force exerted by pronator teres is a measure of the ability of the forearm to rotate:

$$E_{rot} = \frac{\vec{T}}{\vec{F}} = \frac{\vec{F} \times \cos\alpha \times \cos\beta \times \overline{AO'}}{\vec{F}} = \cos\alpha \times \cos\beta \times \overline{AO'}$$

$\overline{AO'}$ can be calculated from the curvature of the radius bone ($\overline{AO}$, Fig. 5) (Galtés et al., 2009a):

$$\overline{AO'} = \overline{AO} - \overline{OO'}$$

$\overline{OO'}$ can be obtained from trigonometric relationships between measurements shown in Fig. 6. Taking into account that d_r (radius of the radial head), d_c (ulnar distal epiphysis radius) and l_{pr} (vertical distance between the radial head proximal surface and point A) can be measured on dry bone (Galtés et al., 2009a), the values of a, b and e can be obtained from the following equations (Galtés, 2008):

$$\frac{d_r}{a} = \frac{d_c}{b}$$

$$a + b = l_{pr}$$

$$e = a - l_{pr}$$

$\overline{OO'}$ is thus calculated considering the following relation:

$$\frac{\overline{OO'}}{e} = \frac{d_r}{a} \Rightarrow \overline{OO'} = \frac{d_r \times e}{a}$$

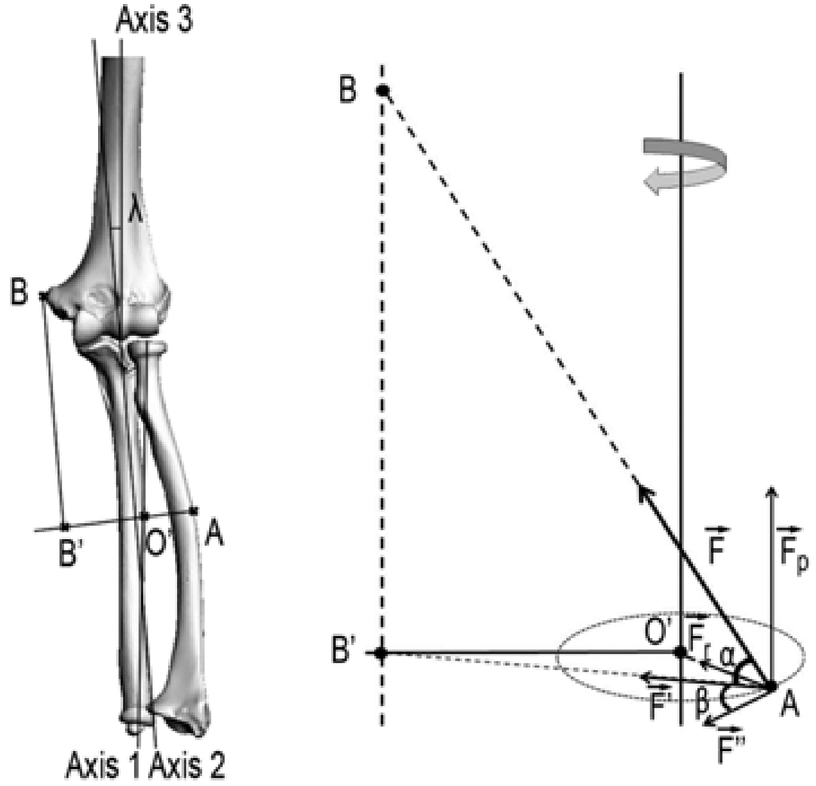

Figure 4. Representation of an upper limb skeleton of a *Gorilla gorilla gorilla* and diagram of the rotational movement of the forearm. The forearm rotation axis (axis 1), the forearm axis (axis 2) and the humeral axis (axis 3) are shown. Point A is the distal attachment site of pronator teres, at the apex of the radial curvature. Point B is the proximal attachment site of pronator teres, at the apex of the medial epicondyle. Point B′ is the projection of point B on the plane perpendicular to the forearm axis that passes through point A. Point O′ is the intersection between forearm rotational axis and the abovementioned plane. Angle λ is the angle between the humeral axis and the forearm axis (carrying angle) (Knussmann, 1967). $\vec{F}$ is the force exerted by pronator teres. $\vec{F'}$ is the projection of $\vec{F}$ on the plane perpendicular to forearm rotational axis. $\vec{F_p}$ is the vertical component of $\vec{F}$. $\vec{F_r}$ is the component of the force directed to the rotation center. $\overrightarrow{F''}$ is the component of the force tangential to the rotational movement. Angles α and β are the angles between $\vec{F}$ and $\vec{F'}$ and between $\vec{F'}$ and $\overrightarrow{F''}$, respectively.

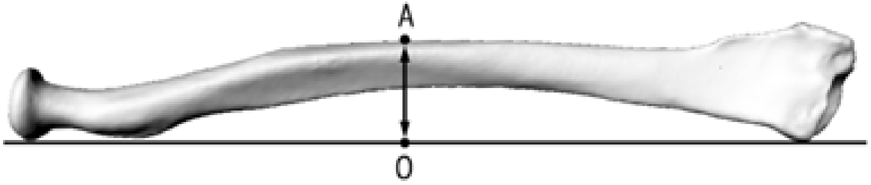

Figure 5. Representation of the parameter to assess the curvature of the radius ($\overline{AO}$). The radius of a *Gorilla gorilla gorilla* is shown. Point A is the apex of the radial curvature. Point O is the intersection between the forearm axis and the plane perpendicular to the forearm axis that passes through point A.

Distance $\overline{AO'}$ is constant throughout the pronation-supination and the flexion-extension ranges, but angles α and β are not and so they need to be assessed for each stage. In skeletal remains, this was achieved by calculating several relationships between osteometrical measurements (Galtés, 2008; Galtés et al., 2009a). Concerning the position of the elbow, two stages were considered in these works: full extension (180°) and intermediate flexion (90°), that basically cause distance $\overline{BB'}$, and so angle α, to vary (Fig. 7).

Forearm rotational efficiency (E_{rot}) is therefore dependent on several parameters. Amongst them, the curvature of the radius ($\overline{AO}$) was deeply investigated by Galtés et al. (2009b). They found that the entheseal development of pronator teres distal attachment site is positively correlated with the radial curvature. The muscular loading exerted on the apex of the radial diaphysis by pronator teres may thus play an important role in shaft bowing. This finding indicates that E_{rot} may be influenced by activity. This issue should be further investigated to understand what other parameters used to calculate E_{rot} are partially activity-dependent and how their variation affects E_{rot}.

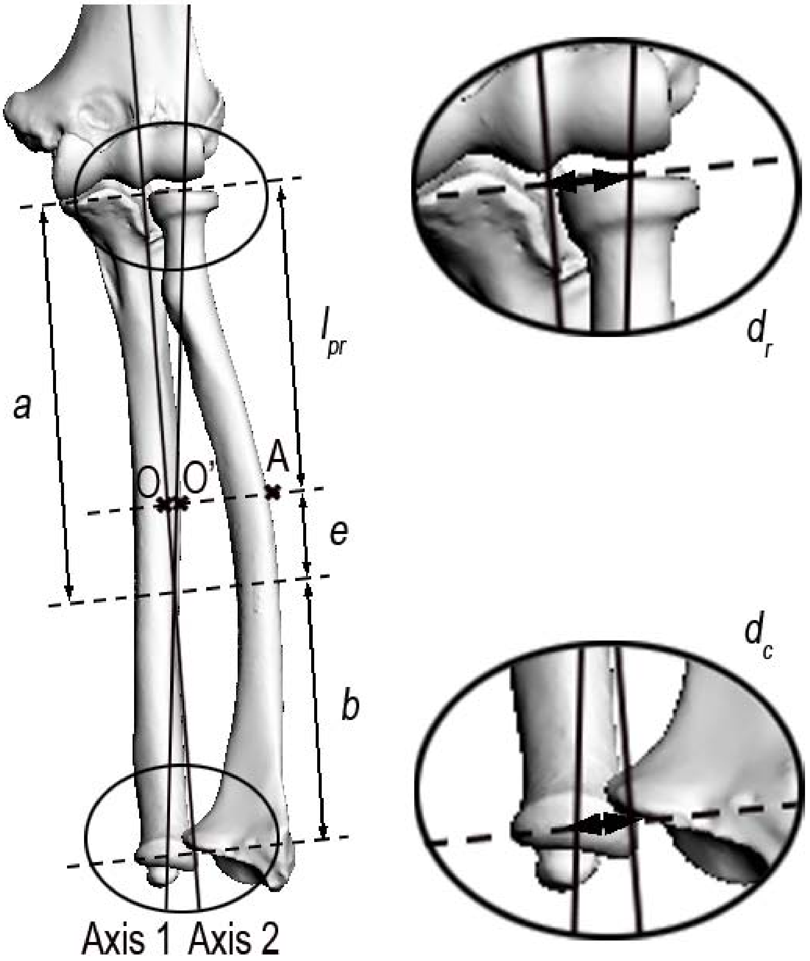

Figure 6. Skeletal measurements needed to calculate distance $\overline{OO'}$ on a *Gorilla gorilla gorilla* upper limb. Axes 1 and 2 are the forearm rotation axis and the forearm axis, respectively. The four transversal planes are perpendicular to the forearm axis and they pass, from the most proximal to the most distal, through the most proximal point of the radial head surface, through point A, through the intersection of both axes, and through the most distal point of the ulnar notch. Point A is the distal attachment site of pronator teres, at the apex of the curvature of the radius bone. Points O and O' are the intersections between the forearm axis and the forearm rotation axis, respectively, and the represented plane. The proximal and the distal parts of the forearm are zoomed in to show distances d_r and d_c. Distances l_{pr}, d_r and d_c can be measured on dry bone (Galtés et al., 2009a).

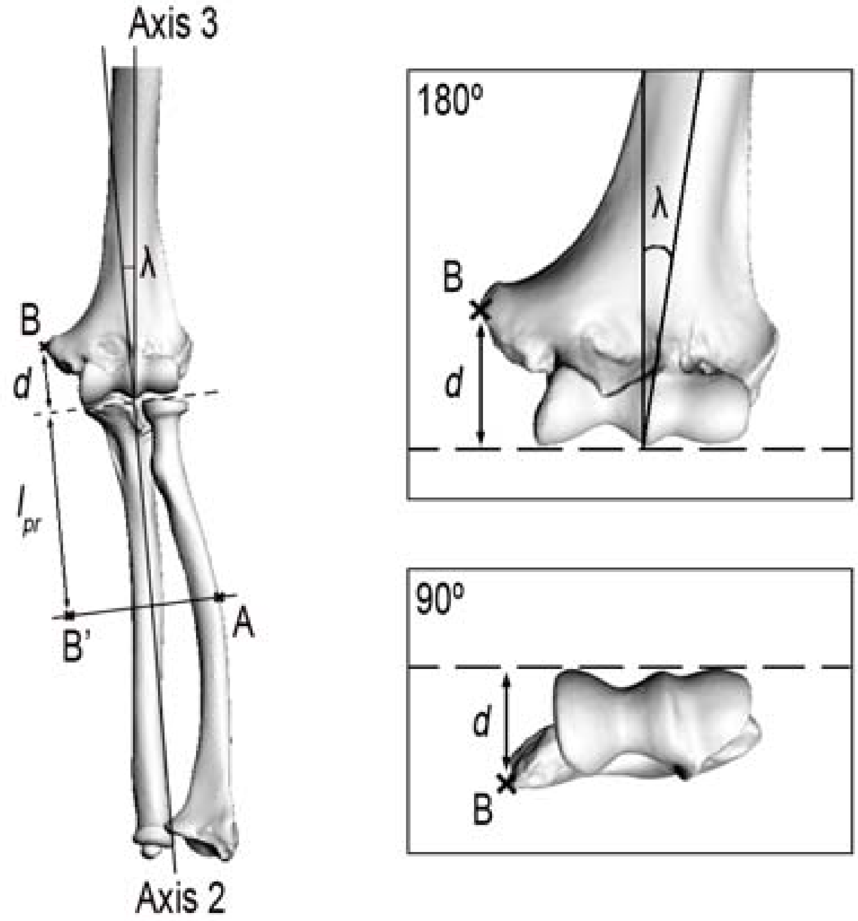

Figure 7. Calculation of distance $\overline{BB'}$, which is the addition of l_{pr} and d. The humerus, radius and ulna of a *Gorilla gorilla gorilla* are shown. Axes 2 and 3 are the forearm and the arm axes, respectively. Point A and point B are the radial and the humeral attachment sites of pronator teres, respectively. Point B’ is the projection of point B on a plane parallel to the forearm axis that passes through point A. The dashed line represents a plane parallel to the abovementioned plane that passes through the most proximal point of the radial head. Distance l_{pr} can be measured on dry bone (Galtés et al., 2009a). In full elbow extension (180°), distance d is influenced by the carrying angle of the individual (λ), which can also be measured on dry bone (Knussmann, 1967). In intermediate flexion (90°), carrying angle is null (Kapandji, 2002).

In humans, differences in E_{rot} influenced by differences in activity would most certainly be accounting for differences in manipulation. In nonhuman hominoids they probably account for differences in locomotor patterns rather than manipulation, considering the great stress that the upper limb bears during locomotion. Differences in E_{rot} among nonhuman hominoids may reflect the specific locomotor adaptation of each taxon. Testing this would indeed be extremely useful in paleoanthropological analyses, as E_{rot} could be used to reconstruct the role of the upper limb in the locomotion of fossil hominoids, and so to get further knowledge on their locomotor repertoire.

2. OBJECTIVES

These precepts would be merely anecdotal if they weren’t taken so much to heart.

Amélie Nothomb
Fear and trembling

The main goal of this thesis is to characterize structurally and biomechanically the hominoid arm and forearm skeleton in order to reconstruct activity patterns and locomotor behaviors. With this aim, the following specific objectives have been established:

1. Analyze pronator teres rotational efficiency (E_{rot}) in extant hominoids.
    - 1.1. Analyze the variation of E_{rot} and its functional implications.
    - 1.2. Characterize the relationship between the upper limb skeletal structure and E_{rot}.
2. Explore the functional plasticity of the human upper limb skeleton.
    - 2.1. Examine how pronator teres activity alters skeletal structure.
    - 2.2. Examine how overall muscular activity of the upper limb modifies skeletal structure.

3. Infer function-related aspects of the hominoid upper limb from structural and biomechanical parameters.

    3.1. Reconstruct activity patterns in human ancient populations.

    3.2. Reconstruct the locomotor behavior of fossil hominids.

3. PUBLICATIONS

They enjoy the goal but not the process. But the reality of it is that the true work of improving things is in the little achievements of the day.

Céline

Before Sunset

The objectives of the current thesis have been covered in six peer-reviewed publications and one study to be submitted:

1. Ibáñez-Gimeno P, Jordana X, Manyosa J, Malgosa A, Galtés I. 2012. **3D analysis of the forearm rotational efficiency variation in humans**. The Anatomical Record 295:1092-1100. DOI: 10.1002/ar.22483. Impact factor: 1.343 (2012); Q3 Anatomy and Morphology. **Objectives 1.1, 1.2**.

2. Ibáñez-Gimeno P, Galtés I, Jordana X, Malgosa A, Manyosa J. 2014. **Biomechanics of forearm rotation: Force and efficiency of pronator teres**. PLoS ONE 9:e90319. DOI: 10.1371/journal.pone.0090319. Impact factor: 3.534 (2013); Q1 Multidisciplinary Sciences. **Objectives 1.1, 1.2, 2.1**.

3. Ibáñez-Gimeno P, Galtés I, Manyosa J, Malgosa A, Jordana X. 2014. **Analysis of the forearm rotational efficiency in extant hominoids: New insights into the functional implications of the upper limb skeletal structure**. Journal of Human Evolution 76:165-176. DOI:

10.1016/j.jhevol.2014.08.004. Impact factor: 3.867 (2013); Q1 Anthropology; Q2 Evolutionary Biology. **Objectives 1.1, 1.2**.

4. Ibáñez-Gimeno P, Galtés I, Jordana X, Fiorin E, Manyosa J, Malgosa A. 2013. **Entheseal changes and functional implications of the humeral medial epicondyle**. International Journal of Osteoarchaeology 23:211-220. DOI: 10.1002/oa.2299. Impact factor: 1.070 (2013); Q2 Anthropology. **Objectives 1.2, 2.2**.

5. Ibáñez-Gimeno P, De Esteban-Trivigno S, Jordana X, Manyosa J, Malgosa A, Galtés I. 2013. **Functional plasticity of the human humerus: Shape, rigidity, and muscular entheses**. American Journal of Physical Anthropology 150:609-617. DOI: 10.1002/ajpa.22234. Impact factor: 2.514 (2013); Q1 Anthropology; Q3 Evolutionary Biology. **Objective 2.2**.

6. Ibáñez-Gimeno P, Galtés I, Jordana X, Manyosa J, Malgosa A. 2014. **Activity-related sexual dimorphism in Alaskan foragers from Point Hope: Evidences from the upper limb**. Anthropologischer Anzeiger (in press). Impact factor: 0.500 (2013); Q3 Anthropology. **Objective 3.1**.

7. Ibáñez-Gimeno P, Galtés I, Malgosa A, Manyosa J, Jordana X. 2014. **Forearm rotational efficiency in AL 288-1 (*Australopithecus afarensis*): Insights into its locomotor habits**. American Journal of Physical Anthropology (in preparation). Impact factor: 2.514 (2013); Q1 Anthropology; Q3 Evolutionary Biology. **Objective 3.2**.

3.1. 3D analysis of the forearm rotational efficiency variation in humans

– Objective 1.1 –

– Objective 1.2 –

See **Ibáñez-Gimeno P, Jordana X, Manyosa J, Malgosa A, Galtés I. 2012. 3D analysis of the forearm rotational efficiency variation in humans. The Anatomical Record 295:1092-1100. DOI: 10.1002/ar.22483.**

3.1.1. Corrigendum

See **Ibáñez-Gimeno P, Jordana X, Manyosa J, Malgosa A, Galtés I. 2014. Corrigendum: 3D analysis of the forearm rotational efficiency variation in humans. The Anatomical Record 297:2232. DOI: 10.1002/ar.23083.**

3.2. Biomechanics of forearm rotation: Force and efficiency of pronator teres

– Objective 1.1 –

– Objective 1.2 –

– Objective 2.1 –

See **Ibáñez-Gimeno P, Galtés I, Jordana X, Malgosa A, Manyosa J. 2014. Biomechanics of forearm rotation: Force and efficiency of pronator teres. PLoS ONE 9:e90319. DOI: 10.1371/journal.pone.0090319.**

3.3. Analysis of the forearm rotational efficiency in extant hominoids: New insights into the functional implications of the upper limb skeletal structure

– Objective 1.1 –

– Objective 1.2 –

See **Ibáñez-Gimeno P, Galtés I, Manyosa J, Malgosa A, Jordana X. 2014. Analysis of the forearm rotational efficiency in extant hominoids: New insights into the functional implications of the upper limb skeletal structure. Journal of Human Evolution 76:165-176. DOI: 10.1016/j.jhevol.2014.08.004.**

3.4. Entheseal changes and functional implications of the humeral medial epicondyle

– Objective 1.2 –

– Objective 2.2 –

See **Ibáñez-Gimeno P, Galtés I, Jordana X, Fiorin E, Manyosa J, Malgosa A. 2013. Entheseal changes and functional implications of the humeral medial epicondyle. International Journal of Osteoarchaeology 23:211-220. DOI: 10.1002/oa.2299.**

3.5. Functional plasticity of the human humerus: Shape, rigidity, and muscular entheses

– Objective 2.2 –

See **Ibáñez-Gimeno P, De Esteban-Trivigno S, Jordana X, Manyosa J, Malgosa A, Galtés I. 2013. Functional plasticity of the human humerus: Shape, rigidity, and muscular entheses. American Journal of Physical Anthropology 150:609-617. DOI: 10.1002/ajpa.22234.**

3.6. Activity-related sexual dimorphism in Alaskan foragers from Point Hope: Evidences from the upper limb

– Objective 3.1 –

See **Ibáñez-Gimeno P, Galtés I, Jordana X, Manyosa J, Malgosa A. 2014. Activity-related sexual dimorphism in Alaskan foragers from Point Hope: Evidences from the upper limb. Anthropologischer Anzeiger (in press).**

3.7. Forearm rotational efficiency in AL 288-1 (*Australopithecus afarensis*): Insights into its locomotor habits

– Objective 3.2 –

FOREARM ROTATIONAL EFFICIENCY IN AL 288-1 (*AUSTRALOPITHECUS AFARENSIS*): INSIGHTS INTO ITS LOCOMOTOR HABITS

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Abstract

The existence of ape-like traits in the upper limb skeleton of *Australopithecus afarensis* indicates that this taxon could have been partially arboreal. Nevertheless, there is an ongoing discussion on whether its arboreality was adaptively significant or not. In any case, the biological role of the upper limb in arboreal locomotion has never been analyzed from a biomechanical perspective. Using a previously reported biomechanical model, we aim to calculate forearm rotational efficiency (E_{rot}) in AL 288-1 and compare the results with a large sample of extant hominoids. As the pattern of E_{rot} is intimately associated with the locomotor mode in each taxon, this will be of special interest to reconstruct the locomotor habits of AL 288-1. The results show that, in AL 288-1, the positions in the pronation-supination range where E_{rot} is maximal for each elbow angle resemble those observed in *Pongo* spp. The positions of the maximums in AL 288-1 are also similar to *Pan troglodytes* and *Gorilla beringei*, but only in elbow positions close to full flexion. Overall, these findings indicate that the upper limb of *Au. afarensis* was probably adapted to climbing behaviors. Moreover, the differences between AL 288-1 and *Homo sapiens* are probably triggered by the existence of enhanced manipulative capacities in the latter, which were still not that marked in *Au. afarensis*.

Key words: Lucy, pronator teres, locomotion inference, functional reconstruction, fossil, humeral medial epicondyle.

Introduction

The evolution of the locomotor behaviors in early hominins has been an ongoing topic of discussion, especially intense since the description of the

Hadar fossils (Johanson et al., 1982). Several structural characteristics of the AL 288-1 partial skeleton (a.k.a. Lucy; 3.2 million years old; see Kimbel and Delezene, 2009) support the widely accepted hypothesis on the bipedality of *Australopithecus afarensis*, although there is a debate on whether it was functionally equivalent to the modern human condition (Stern and Susman, 1983; Jungers, 1988; Hunt, 1994; Stern, 2000; Ward, 2002; Kimbel and Delezene, 2009). The discovery of a relatively complete skeleton of *Australopithecus sediba* in Malapa (MH2; 1.98 million years old; Pickering et al., 2011) provided new evidences on the contention that the evolution of bipedalism was complex and its acquisition implied homoplasy (Harcourt-Smith and Aiello, 2004; Zipfel et al., 2011). Unlike *Au. afarensis* and *Australopithecus africanus*, *Au. sediba* displayed a foot with a mosaic anatomy and a hyperpronated gait (Berger et al., 2010; Zipfel et al., 2011, DeSilva et al., 2013). Therefore, there were probably multiple and kinematically different forms of bipedalism during the Plio-Pleistocene.

While not disputing that *Au. afarensis* were bipedal, several authors noted ape-like traits of the upper limb in these hominids, which are assumed to be primitive retentions (Oxnard, 1975; Senut, 1980, 1981; Tuttle, 1981; Feldesman, 1982; Marzke, 1983; Stern and Susman, 1983; McHenry, 1986; Duncan et al., 1994; Stern, 2000; Ward, 2002; Drapeau et al., 2005; Kimbel and Delezene, 2009; Arias-Martorell et al., 2012; Green and Alemseged, 2012). Nevertheless, there are two main lines of thought over the actual involvement of Lucy in arboreal locomotion and its ability to climb trees (Ward, 2002; Kimbel and Delezene, 2009). The first one states that the ape-like characteristics were retained by stabilizing selection and that *Au. afarensis* was indeed partially arboreal (Oxnard, 1975; Senut, 1980; Stern and Susman, 1983; Susman et al., 1984; McHenry, 1986; Duncan et al., 1994; Hunt, 1994; Stern, 2000; Green and Alemseged, 2012). The second one suggests that arboreality was adaptively insignificant and that the ape-like traits were neither selected for nor against (Lovejoy, 1978; Latimer, 1991; Drapeau et al., 2005). In any case, the biological role of the upper limb skeletal structure in Lucy's arboreal locomotion has been widely investigated, but mainly by descriptive and functional comparative studies using morphological and morphometric approaches. Whereas biomechanical analyses have been performed to test Lucy's bipedality (Kramer, 1999; Wang et al., 2004; Nagano et al., 2005) and hand-carrying ability (Wang et al., 2003), arboreal capabilities have never been biomechanically explored.

In this regard, a biomechanical model to calculate the rotational efficiency of pronator teres (E_{rot}) can be particularly useful (Galtés et al., 2008, 2009; Ibáñez-Gimeno et al., 2012, 2014a, 2014b). Forearm rotation is essential for the locomotion of primates (Tuttle, 1969; Myatt et al., 2012). In fact, hominoids present a greater range, strength and stability of pronation and supination than monkeys, in order to adapt to their locomotor, positional and manipulative behaviors (Stern and Larson, 2001). Forearm rotational efficiency (E_{rot}) in each elbow angle has a maximum value, which is located in a specific pronation-supination position. The positions of these maximums, which differ among taxa, reflect the locomotor repertoire of each nonhuman hominoid taxon and the enhanced manipulative ability of humans (Ibáñez-Gimeno et al., 2014b). These function-related differences are mainly caused by dissimilarities in the orientation of the humeral medial epicondyle, the origin attachment site of the muscle (Ibáñez-Gimeno et al., 2012, 2014b).

The current work is the first biomechanical insight into the arboreal capabilities of AL 288-1 based on its upper limb skeleton. Here, we apply the biomechanical model to calculate E_{rot} in this australopithecine specimen. We aim to explore the functional implications concerning locomotion derived from this parameter and from the comparison with extant hominoids. The analysis of E_{rot} has provided valuable information on the relationship between structure and function in extant hominoids, and it is therefore a very useful method to reconstruct locomotor habits of fossil taxa.

Material and methods

Reconstructed plaster casts of the right upper limb skeleton of the adult female AL 288-1 (Lucy, *Australopithecus afarensis*) from the Cleveland Museum of Natural History were used. The head, the anatomical neck and the greater tubercle of the right humerus (AL 288-1m) were exploded (Johanson et al., 1982), and so they were inferred from the left humerus (AL 288-1r) in the reconstruction. The right ulna and radius (AL 288-1n, AL 288-1o, AL 288-1p and AL 288-1q) lacked part of their shafts, which were thus reconstructed. Although the right radial shaft (also originally named AL 288-1p) was displayed in a figure of a paper by Johanson and Edey (1981) and was described by Johanson et al. (1982), it does not appear in subsequent literature (except for a photograph in Fleagle (1988)), and not a single reconstruction of AL 288-1 uses this radial portion. The lengths of the reconstructed specimens are consistent with observed and estimated measurements of previous studies (Johanson et al., 1982; Jungers, 1982; Hartwig-Scherer and Martin, 1991; Asfaw et al., 1999; Reno et al., 2005). The results obtained in AL 288-1 are compared with a sample of wild-shot extant hominoids housed at the American Museum of Natural History, Naturhistorisches Museum Wien, Anthropological Institute and Museum of Universität Zürich, Smithsonian National Museum of Natural History, and Estación Biológica de Doñana (Table 1).

Forearm rotational efficiency (E_{rot}) is a measure of the capacity of the forearm to rotate, and it is defined as the value of the torque in relation to the force exerted by pronator teres. It was calculated for AL 288-1 and for the comparative sample of wild-shot hominoids using a previously described biomechanical model (Ibáñez-Gimeno et al., 2014a) from both osteometrical and geometrical parameters of the elbow and forearm. Some measures were taken directly on the casts or bones, whereas others were assessed on a 3D images of the humeri, which were obtained using NextEngine's 3D Scanner and processed using ScanStudio HD (2006) and Rhinoceros 4.0 SR1 (2007). See Ibáñez-Gimeno et al. (2014a) for further information about the parameters and the biomechanical model.

TABLE 1. Comparative sample of extant hominoids.

Taxon	**N**			**Total**
	M	**F**	**U**	
Hylobatidae	8	15	2	25
Pongo spp.	5	13	3	21
Gorilla beringei	5	5	-	10
Gorilla gorilla	12	7	1	20
Pan troglodytes	17	11	2	30
Homo sapiens	19	15	-	34

M: males. F: females. U: unknown sex.

Results

The parameters measured for E_{rot} calculation are shown in Table 2. In AL 288-1, E_{rot} for each elbow position is maximal when the forearm is close to the neutral position and is minimal in the extremes of the pronation-supination range (Fig. 1). The value of maximum E_{rot} in full elbow extension (180°) is 0.43, and it does not vary until 160°. As the elbow flexes from this position, maximum E_{rot} rises, reaching 0.48 in full elbow flexion (40°). Regarding the position in the pronation-supination range where E_{rot} is maximal in AL 288-1 (Figs. 1 and 2), in full extension it is in a slightly pronated position (-11°). As the elbow is flexed, this position shifts to the neutral position of the forearm, reaching 0° when the elbow is between 140° and 150° of flexion. Further in flexion, the position of maximum E_{rot} shifts to supination. In elbow semi-flexion

(90°), the maximum is located at 13° of supination, and it reaches 15° in full elbow flexion (40°).

The positions in the pronation-supination range where E_{rot} is maximal for each elbow angle in AL 288-1 were compared to the positions of maximum E_{rot} in several extant hominoid taxa (Fig. 2). The comparisons were performed using the 95% confidence interval for the mean of the positions of the maximums for each elbow angle. Maximum positions of AL 288-1 are outside the 95%CI for *H. sapiens* throughout the entire flexion-extension range. When compared to *P. troglodytes*, the maximum positions of AL 288-1 only fall inside the 95%CI at 40° and 60°-90° of elbow flexion. The maximum positions of AL 288-1 are within the 95%CI for *G. beringei* at 40°-50° of elbow flexion and within the 95%CI for *G. gorilla* at 70°-90° of elbow flexion. The greatest coincidence is found for *Pongo* spp. In this case, maximum positions of AL 288-1 fall within the 95%CI at 40°, 70°-80° and 100°-160° of the elbow. In the rest of elbow angles, despite falling outside the 95%CI, the maximum positions are close to the margin of the interval that approaches the most to the neutral position of the forearm. As regards Hylobatidae, the maximum positions of AL 288-1 only fall within the 95%CI at 130°-140° of elbow flexion.

The positions of maximum E_{rot} were reported to be mainly influenced by the orientation of the humeral medial epicondyle (Ibáñez-Gimeno et al., 2012, 2014a, 2014b). In this regard, the anteroposterior and proximodistal orientation of the epicondyle in AL 288-1 has been compared with the extant hominoid sample (Fig. 3). The retroflexion (anteroposterior orientation) of the epicondyle in AL 288-1, which is assessed by angle φ (180°) (Ibáñez-Gimeno et al., 2012, 2013, 2014a, 2014b), is greater than in Hylobatidae, but it is lower than in the rest of hominoids. Nevertheless, the value for AL 288-1 falls close to the lower margin of the 95%CI for the mean of *Pongo* spp.'s φ (180°) angle. Concerning the proximodistal orientation of the epicondyle, which is assessed by angle φ (90°) (Ibáñez-Gimeno et al., 2012, 2013, 2014a, 2014b), AL 288-1 displays a more proximally oriented epicondyle than *H. sapiens*, *G. beringei* and Hylobatidae. The value for φ (90°) in AL 288-1 falls within the 95%CI for *P. troglodytes* and *G. gorilla*, and is very close to the lower margin of the 95%CI for *Pongo* spp.

Discussion

The positions in the pronation-supination range where E_{rot} is maximal in *Au. afarensis* are virtually identical to those of *Pongo* spp. throughout the entire flexion-extension range. This is due to the fact that, considering both the retroflexion and the proximal-distal orientation of the humeral medial epicondyle, AL 228-1 is more similar to *Pongo* spp. than to any other extant hominoid taxa, and the positions of maximum E_{rot} are almost exclusively determined by the orientation of the epicondyle (Ibáñez-Gimeno et al., 2012, 2013, 2014a, 2014b). In both taxa, maximum positions are greatly shifted to supination when the elbow is fully flexed. In fact, in elbow flexion, Lucy presents its maximum E_{rot} in similar positions to taxa involved in climbing behaviors (*Pongo* spp., *P. troglodytes* and *G. gorilla*). This great shift of the maximum position towards supination in elbow flexion causes pronator teres capacity to rotate the forearm to be greater in those positions essential during climbing, i.e. flexion of the elbow with the forearm supinated (Sarmiento, 1987, 1988; Stern and Larson, 2001; Ibáñez-Gimeno et al., 2014b). This would, therefore, be suggesting that Lucy's upper limb skeleton was still adapted to arboreal locomotion. Although there is also a similarity between Lucy's and *G. beringei*'s maximum E_{rot} positions, this is restricted to a narrow range of elbow flexion (40° and 50°). *Gorilla beringei* presents a basically terrestrial locomotion (Gregory, 1927; Gregory and Raven, 1937), and so it would not need a gain of E_{rot} in such supinated positions of the forearm.

TABLE 2. Osteometrical and geometrical parameters used to calculate forearm rotational efficiency (E_{rot}) in AL 288-1.

Parameter and definition		AL 288-1	Hylobatidae	*Pongo* spp.	*G. beringei*	*G. gorilla*	*P. troglodytes*	*H. sapiens*
d_r: Radial head radius		0.70	0.65 ± 0.07	1.12 ± 0.13	1.52 ± 0.22	1.51 ± 0.21	1.18 ± 0.08	1.02 ± 0.09
d_c: Ulnar distal epiphysis radius		0.69	0.56 ± 0.07	1.10 ± 0.09	1.40 ± 0.18	1.40 ± 0.22	1.05 ± 0.08	0.98 ± 0.07
l_f: Physiological length of the radius		20.00	26.86 ± 2.62	34.25 ± 2.93	30.83 ± 2.75	32.29 ± 3.59	26.91 ± 1.57	22.01 ± 1.55
l_{pr}: Distance between P_2 and P_3 planes		9.80	8.32 ± 1.45	14.31 ± 1.94	15.19 ± 1.92	15.53 ± 2.67	11.80 ± 1.44	10.92 ± 0.90
λ: Carrying angle (Knussmann, 1967)		2.50°	13.44° ± 3.96°	5.57° ± 3.26°	3.50° ± 2.55°	5.20° ± 3.86°	3.63° ± 3.55°	8.79° ± 4.54°
ε: Angle between the positive *x*-axis and the position vector of point B		30.79°	25.77° ± 10.12°	32.41° ± 7.63°	54.47° ± 13.18°	44.19° ± 7.69°	39.09° ± 8.40°	47.49° ± 12.17°
d_e: Distance between flexion-extension axis and point B		0.80	0.37 ± 0.11	1.51 ± 0.31	2.05 ± 0.40	2.36 ± 0.52	1.36 ± 0.22	1.03 ± 0.17
R_c: Humeral capitulum radius		0.66	0.62 ± 0.06	1.19 ± 0.16	1.38 ± 0.19	1.43 ± 0.22	1.05 ± 0.09	0.96 ± 0.08
B: Coordinates of point B (humeral attachment site of pronator teres)	*x*-coordinate	0.68	0.33 ± 0.11	1.26 ± 0.24	1.16 ± 0.44	1.67 ± 0.41	1.05 ± 0.21	0.68 ± 0.20
	y-coordinate	-0.41	-0.15 ± 0.06	-0.81 ± 0.29	-1.63 ± 0.42	-1.63 ± 0.45	-0.85 ± 0.20	-0.75 ± 0.19
$\overline{XB}$: Distance between point B and humeral axis		2.46	1.59 ± 0.22	4.01 ± 0.51	5.74 ± 0.76	5.59 ± 0.75	3.62 ± 0.30	3.56 ± 0.30
$\overline{XC}$: Distance between P_1 and P_2		1.44	0.80 ± 0.16	2.28 ± 0.36	2.58 ± 0.58	3.18 ± 0.59	2.02 ± 0.26	1.55 ± 0.23
$\overline{AO}$: Radial curvature		2.00	1.73 ± 0.28	3.02 ± 0.63	3.84 ± 0.66	3.82 ± 0.61	3.14 ± 0.35	2.33 ± 0.22

Distances are shown in cm. Values for extant hominoids are shown as mean ± SD. See Ibáñez-Gimeno et al. (2014a) for further information on the parameters. In AL 288-1, l_f is an approximation, as part of the radial shaft is reconstructed, but it is consistent with previous estimates (Hartwig-Scherer and Martin, 1991; Asfaw et al., 1999). l_{pr} and $\overline{AO}$ are also approximations in AL 288-1. These parameters influence the value of maximum E_{rot}, but they do not affect the position in the pronation-supination range where E_{rot} is maximal (Ibáñez-Gimeno et al., 2012, 2014a, 2014b), which is the variable discussed in this study.

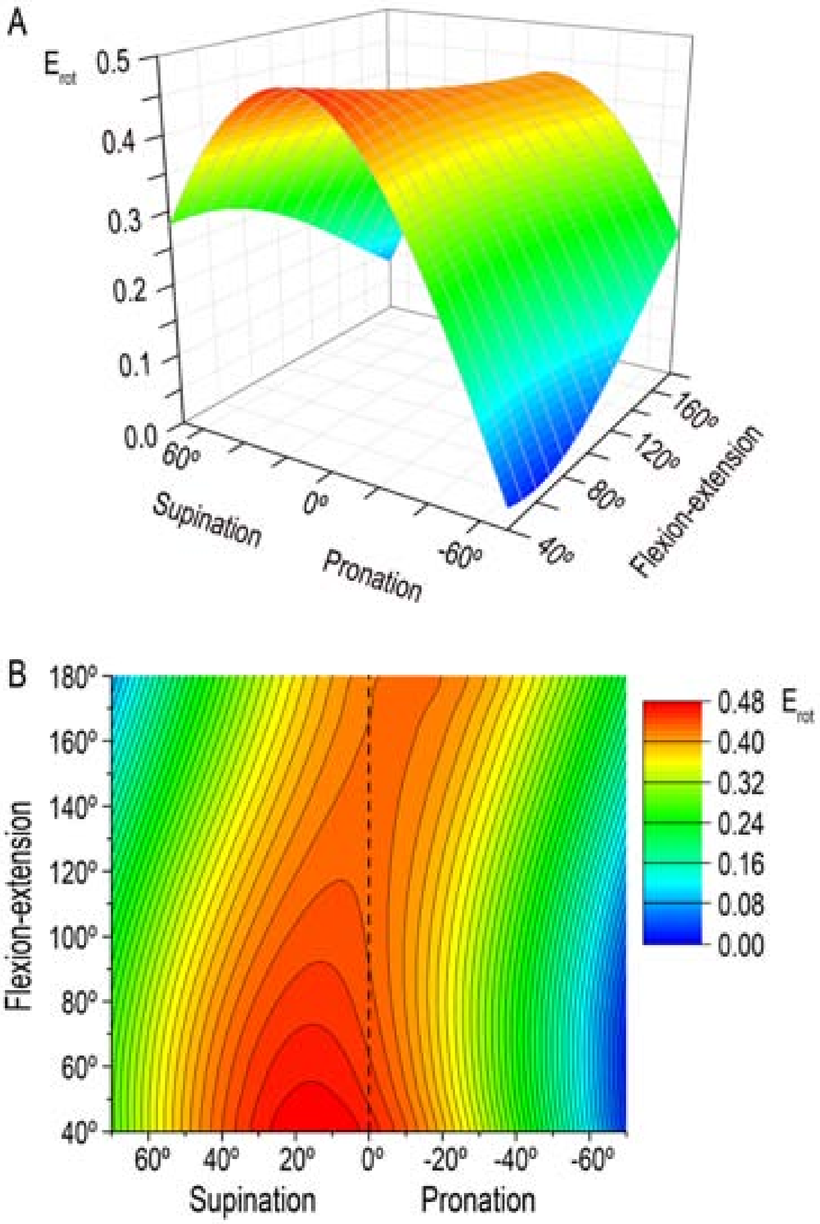

Figure 1. Forearm rotational efficiency (E$_{rot}$) as a function of pronation-supination and flexion-extension angles for AL 288-1. **A:** Three-dimensional surface showing E$_{rot}$ values at each forearm and elbow angles. **B:** Projection of the three-dimensional surface on XY plane showing E$_{rot}$ ranges at each forearm and elbow angles. The dashed line indicates the neutral position of the forearm.

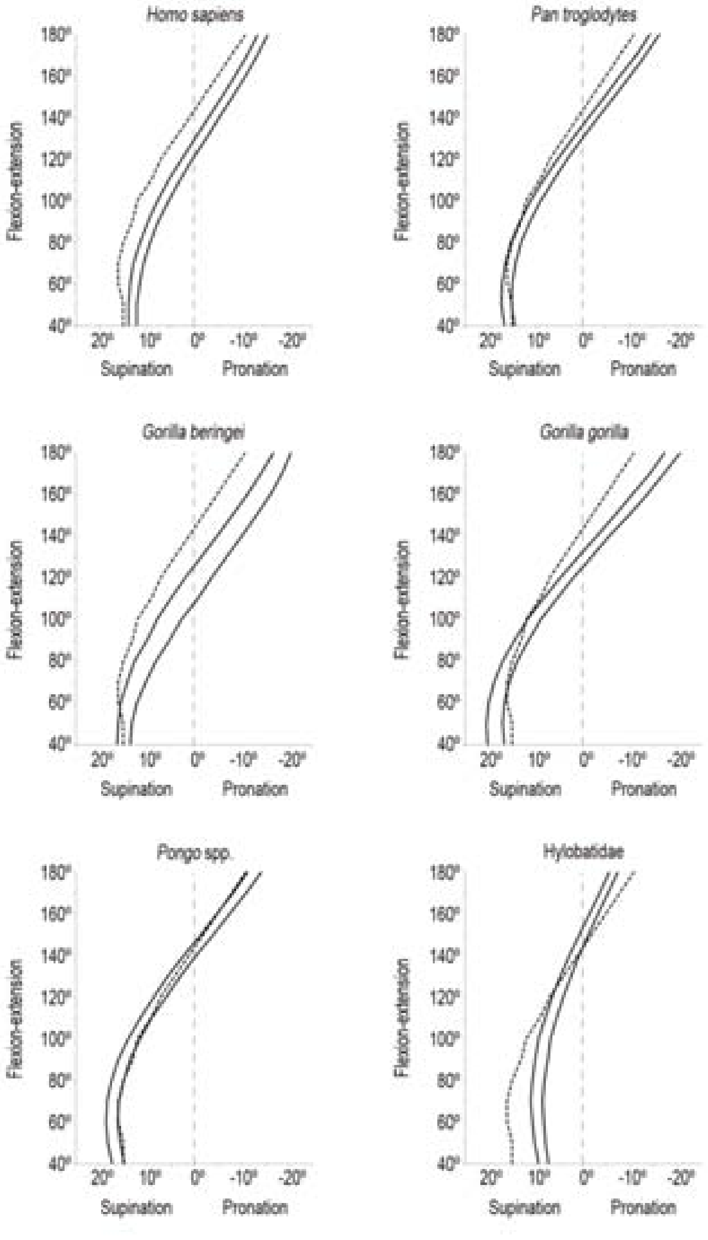

Figure 2. Comparison between AL 288-1 and extant hominoid taxa for the position of maximum forearm rotational efficiency (E_{rot}) in the pronation-supination range for each elbow angle. The continuous lines encompass the 95%CIs for the mean of the positions of the maximums for each extant hominoid taxon, and the thick dashed line shows the positions of the maximums for AL 288-1. The vertical dashed line indicates the neutral position of the forearm (0° of pronation-supination).

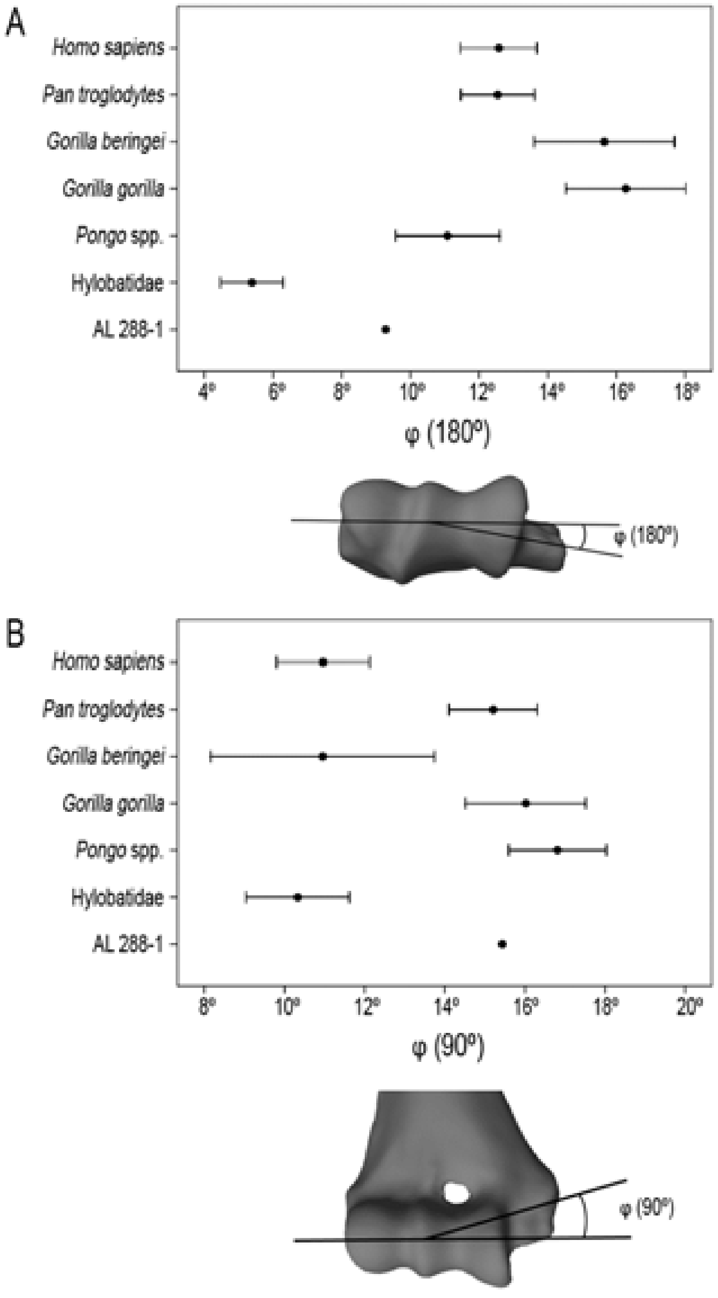

Figure 3. 95% confidence intervals for the mean of angles φ (Ibáñez-Gimeno et al., 2012). Both angles are displayed on 3D images of the distal humerus of AL 288-1. **A:** Angle φ (180°). It is a proxy for the retroflexion of the medial epicondyle. **B:** Angle φ (90°). It is a proxy for the proximodistal orientation of the medial epicondyle.

As the elbow extends, the positions of the maximum E_{rot} in Lucy and *Pongo* spp. shift towards the neutral position of the forearm, which they reach at approximately 140° of flexion. Further in extension, the maximum positions shift towards pronation, reaching less pronated positions in full elbow extension than knuckle-walker taxa. Unlike *Pongo* spp., *P. troglodytes* and *Gorilla* spp. benefit from presenting their maximums in elbow extension in a greatly pronated position of the forearm, as that is the position that they attain during knuckle-walking. The similarity between Lucy and *Pongo* spp. in these elbow angles supports the accepted idea of lack of knuckle-walking in *Au. afarensis* (Kimbel et al., 1994; Drapeau et al., 2005; Kimbel and Delezene, 2009) and suggests that its upper limb was probably used only in arboreal contexts as far as locomotion is concerned.

The maximums for Lucy are located in different forearm positions than those for modern humans. *Homo sapiens* present their maximums between 40° and 120° of elbow flexion closer to the forearm neutral position than Lucy. Between 130° and 180° of the elbow, the maximums for modern humans are in a more pronated position. These changes could have occurred in the human lineage due to the requirements related to the increasing manipulative capacities. Nevertheless, some characteristics of the upper limb may have suffered evolutionary reversals along the hominid linage, such as limb proportions, which are more ape-like in *Au. africanus*, *Australopithecus garhi* and *Homo habilis* than in *Au. afarensis* (McHenry and Berger, 1998; Richmond et al., 2002; Berger, 2006; Green et al., 2007; but for contrasting view, see Dobson, 2005; Reno et al., 2005; Churchill et al., 2013). Several morphological characteristics of the upper limb skeleton also suggest a greater degree of arboreality in *Au. africanus* than in *Au. afarensis* (McHenry and Berger, 1998; Green et al., 2007; Churchill et al., 2013), and the former appears to be closely related to *Au. sediba* (Berger et al., 2010). Therefore, further research is warranted to assess if more modern species were actually more human-like concerning the positions of maximum E_{rot}.

In any case, in modern humans, the shift to supination of the position of the maximum in elbow flexion was not necessary because arboreal repertoires were not selected for. Humans required the use of the precision grip, which is commonly used for manipulative behaviors, thus in short distances. Therefore, their maximums in flexed positions of the elbow are closer to the neutral position of the forearm, in which the precision grip is enhanced (Kapandji, 2002; Ibáñez-Gimeno et al., 2012). In positions close to elbow extension, Lucy does not present its maximums in greatly pronated position probably because that was not useful for arboreal locomotion (Ibáñez-Gimeno et al., 2014b). Nevertheless, in humans the maximums in these positions are in a more pronated position, which is favorable during the reach-and-grasp task, where humans use their prone hand to grab objects that are far from the body (Kapandji, 2002). Although *Au. afarensis* was probably capable of enhanced manipulation (Alba et al., 2003; Almécija and Alba, 2014), the results indicate that concerning pronator teres rotational efficiency, these capabilities were far from those observed in modern humans.

Conclusions

The analysis of E_{rot} indicates that the upper limb of AL 288-1 was adapted to climbing behaviors, similarly to *Pongo* spp. The differences between *Au. afarensis* and nonhuman Homininae are especially important in elbow extension, and are probably reflecting a derived behavior in the latter, the use of knuckle-walking. In humans, the pattern of E_{rot} is likely related to the appearance of manipulative requirements, which accounts for the differences observed with AL 288-1, although analyses involving other hominid taxa are required to explore the evolutionary pathway of this parameter in the human lineage.

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4. GENERAL DISCUSSION

I stand upon my desk to remind myself that we must constantly look at things in a different way.

John Keating

Dead Poets Society

4.1. FOREARM ROTATIONAL EFFICIENCY IN EXTANT HOMINOIDS

4.1.1. An overview of the analysis of forearm rotational efficiency

Forearm rotational efficiency (E_{rot}) was first defined by Galtés et al. (2008). They used a biomechanical model that calculated E_{rot} in full elbow extension from structural measurements taken on *in vivo* computed tomography (CT) images of the elbow and the forearm. This model was later adapted to calculate E_{rot} in two elbow positions (full extension and semi-flexion) from photographs of the distal epiphysis of the humerus instead of CT images (Galtés et al., 2009a). Although this enabled to assess this parameter in skeletal remains, some assumptions about the mechanics of the arm and forearm and the representation of the geometrical points and planes needed for the analysis had to be made.

In order to properly study the natural variation of E_{rot}, the accuracy of the model needed to be improved. In this thesis, the model was readapted to calculate E_{rot} from three-dimensional images of the humerus instead of photographs (Ibáñez-Gimeno et al., 2012; Publication 3.1). The use of 3D modelling techniques enabled to assess with great precision the points and measures needed for the calculation of E_{rot}, as well as to work with planes that actually crossed the humerus, which was impracticable when using photographs (Ibáñez-Gimeno et al., 2012; see Figs. 3 and 4 in Publication 3.1). This version of the model was used to calculate E_{rot} in full elbow extension and intermediate flexion in a large sample of humans, in order to determine if the functional specializations of the human upper limb were reflected in their E_{rot} pattern, and to explore the effect of the skeletal structure on the determination of E_{rot}.

The biomechanical model was later improved in order to calculate E_{rot} not only in two elbow positions, but throughout the entire flexion-extension range (Ibáñez-Gimeno et al., 2014a; Publication 3.2), which obviously provided a greater amount of information. By applying this model to a human upper limb and performing several simulations, some aspects on how skeletal structure and E_{rot} (and so pronator teres biomechanics) influence each other were clarified. Moreover, the components of pronator teres force were explored, which provided further insight into the functional implications of E_{rot} pattern.

One of the focuses of this thesis was to analyze E_{rot} in nonhuman hominoids, in order to determine whether it is associated to the locomotor form of each taxon. Although a preliminary analysis was performed with three individuals (Ibáñez-Gimeno et al., 2012; Publication 3.1), the main findings were established using a sample of more than one hundred wild-shot specimens (Ibáñez-Gimeno et al., 2014b; Publication 3.3). In the latter, the relationship between E_{rot} and locomotion was widely discussed, and several aspects on the influence of upper limb skeletal structure on E_{rot} were interpreted.

In the following sections of the discussion, the main findings concerning E_{rot} variation and its relationship with skeletal structure and function will be exposed.

4.1.2. Variation of forearm rotational efficiency and its functional implications

The results indicate that, in all of the extant hominoids analyzed here, E_{rot} for each elbow angle is maximal when the forearm is close to the neutral position (0° of pronation-supination) and it is minimal in the extremes of the pronation-supination range (Ibáñez-Gimeno et al., 2012, 2014a, b; Publications 3.1, 3.2 and 3.3). Regardless of the taxa, maximum E_{rot} increases from extension (180°) to full flexion (40°) (Ibáñez-Gimeno et al., 2014a, b; Publications 3.2 and 3.3). These findings are concordant with kinematic studies that assessed the torque and the moment arm of pronator teres in humans (Murray et al., 1995; Haugstvedt et al., 2001; Bremer et al., 2006). The increase of rotational efficiency during flexion may be closely linked to the central role of arboreal locomotion and vertical climbing in apes (Hunt, 1991; Crompton et al., 2008; Green, 2013), in which flexed positions of the elbow are essential (Schmitt, 2003; Oishi et al., 2008).

Nevertheless, the existence of marked differences among taxa in the biomechanics of pronator teres muscle has also been observed. Hominoids with a greater size of the upper limb have higher E_{rot} values (Ibáñez-Gimeno et al., 2014b; Publication 3.3). In this regard, *Gorilla beringei* and *Gorilla gorilla gorilla* present the greatest values of maximum E_{rot} throughout the entire flexion-extension range, followed by *Pan troglodytes*, *Pongo* spp., *Homo sapiens* and Hylobatidae (Ibáñez-Gimeno et al., 2014b; see Fig. 3 in Publication 3.3). The relative upper limb size may reflect locomotor specializations. For instance, in suspensory species the upper limb is longer than the lower limb, whereas in quadrupedal taxa both pairs of limbs are similar in size (Fleagle, 1988). Nevertheless, the absolute upper limb size is mainly determined by general body size, which is highly variable among apes (Aiello and Dean, 1990). As the absolute upper limb size is influenced by many features independent of locomotion, differences among taxa for the values of rotational efficiency are not used here to explore functional dissimilarities.

Concerning the position in the pronation-supination range where E_{rot} is maximal, in full extension, *P. troglodytes* and especially *Gorilla* spp. are the taxa that present the maximum E_{rot} in the most pronated positions, followed by *H. sapiens* and *Pongo* spp., whereas in Hylobatidae this maximum is closer to the neutral position of the forearm. This pattern changes as the elbow flexes. In full flexion of the elbow, *G. gorilla gorilla* is the taxa with the maximum E_{rot} in the most supinated position, which is significantly different from *G. beringei*. The latter, in addition to *Pongo* spp., *P. troglodytes* and *H. sapiens*, display their maximum in a less supinated position, whereas Hylobatidae present their maximum closer to the neutral position of the forearm (Ibáñez-Gimeno et al., 2014b; see Fig. 5 in Publication 3.3). The functional implications of these differences will be discussed for each taxon.

The fact that *P. troglodytes* and *Gorilla* spp. are the taxa that present the maximum E_{rot} in the most pronated positions and are the only taxa that display an increase of maximum E_{rot} from semi-flexion to extension (Ibáñez-Gimeno et al., 2014b; Publication 3.3) could be related to their habitual involvement in knuckle-walking, which implies an extension of the elbow with the prone hand (Hunt, 1991; Tuttle et al., 1992; Myatt et al., 2012; Green, 2013). This is in agreement with pronator teres being reported as markedly active during several stages of knuckle-walking in electromyographic analyses in both taxa (Tuttle et al., 1992). The broad repertoire of locomotor modes in *P. troglodytes* (Hunt, 1991; Carlson et al., 2006; Matsumura et al., 2010; Congdon, 2012; Sarringhaus et al., 2014) and the fact that *Gorilla* spp. employ a more pronated hand during knuckle-walking (Tuttle, 1969b) probably contribute to the fact that the former present their maximum E_{rot} in full elbow extension closer to the forearm neutral position than the latter (Ibáñez-Gimeno et al., 2014b; see Fig. 5 in Publication 3.3).

Probably because of the highly predominant arboreal locomotion in *Pongo* spp. (Thorpe and Crompton, 2005; Congdon, 2012; Myatt et al., 2012), which does not require a great pronation range with the elbow extended, this taxon displays its maximum E_{rot} slightly closer to the neutral position of the forearm than does *P. troglodytes* (Ibáñez-Gimeno et al., 2014b; Publication 3.3). Arboreal locomotion modes such as vertical climbing require a large range of supination (Sarmiento, 1987, 1988; Stern and Larson, 2001), and so a great shift of the maximum to pronation would not be useful for *Pongo* spp. Moreover, an approach of the maximum to the neutral position is advantageous for suspensory locomotion, in which the neutral position is adopted by the supporting forelimb when elbow extension is maximal (Larson, 1988). Nevertheless, the slight shift of the maximum to pronation in elbow extension benefits *Pongo* spp. during their terrestrial fist-walking or modified palmigrade locomotion, which, even if not frequent, requires a slight pronation of the forearm (Tuttle, 1969a).

The fact that, in full elbow flexion, *G. gorilla gorilla* display their maximum E_{rot} in a more supinated position than *G. beringei* (Ibáñez-Gimeno et al., 2014b; Publication 3.3) may account for their differentiated locomotor specializations. The latter has been described as an essentially terrestrial herbivore, whereas the former has been reported as more arboreal and frugivorous (Gregory, 1927; Gregory and Raven, 1937). In this regard, a maximum E_{rot} in a more supinated position in elbow flexion would enhance the arboreal capabilities of *G. gorilla gorilla* (Sarmiento, 1987, 1988; Stern and Larson, 2001). This is consistent with previous studies reporting differences between both species in several morphological characteristics linked to locomotor abilities, such as pedal, limb and scapular shape (Schultz, 1927, 1930, 1934; Taylor, 1997; Dunn et al., 2013; Holliday and Friedl, 2013) and long bone strength proportions (Ruff et al., 2013).

The increasing shift to supination of the position of maximum E_{rot} observed in *P. troglodytes* and *Pongo* spp. from semi-flexion to full flexion (Ibáñez-Gimeno et al., 2014b; Publication 3.3) may also be associated with the advantage of a great supination range in arboreal locomotion (Sarmiento, 1987, 1988; Stern and Larson, 2001).

In Hylobatidae, the maximums being close to the neutral position of the forearm throughout the entire flexion-extension range (Ibáñez-Gimeno et al., 2014b; Publication 3.3) may indicate that the necessity of engaging in extreme forearm positions is lower in this taxon than in great apes, which contrasts with the high rotational demand described for this taxon by previous works (Swartz, 1990; Rose, 1993). Nevertheless, Hylobatidae depend on brachiation for up to 80% of their total locomotion (Andrews and Groves, 1976), and during brachiation they show a greater recruitment of rotator cuff muscles than other apes (Larson, 1988). In fact, shoulder muscles of Hylobatidae have the highest power-generating capacity and are well suited to gain speed and to change direction (Michilsens et al., 2009, 2010). Therefore, the rotation of the trunk during brachiation in this taxon would be basically dependent on the shoulder rotatory ability (Bertram and Chang, 2001), which is consistent with their humeral head being more globular (Arias-Martorell et al., 2013). Moreover, the neutral position of the forearm is the one that provides the greatest stability of the joints, as it is the position in which contact between radial and ulnar articulation structures is maximal (MacConnaill and Basmajian, 1969).

In *H. sapiens*, the upper limb skeleton is free from locomotor behaviors and thus is only subjected to manipulative selection pressures, but it maintains the basic structures that are common to all hominoid species (Darwin, 1871;

Alba et al., 2003). Therefore, the nature of the human pattern may be related to the main manipulative function of the human upper limb. In this regard, the fact that E_{rot} is maximal when the forearm is close to the neutral position (Ibáñez-Gimeno et al., 2012, 2014a, b; Publications 3.1, 3.2 and 3.3) supports the relationship between this position and the functional position of the forearm, which implies a state of natural equilibrium between the antagonistic muscle groups in order to minimize expenditure of muscular energy (Kapandji, 2002). This forearm position also implies an optimum position of the hand for grasping. In neutral position, the axis of the grip is in line with the axis of pronation-supination (Kapandji, 2002), in order to enhance the precision of the grip (Marzke, 1997). Nevertheless, the maximum positions in humans are not as close to the forearm neutral position as in other taxa (Ibáñez-Gimeno et al., 2014b; Publication 3.3). This may be related to the advantage that pronation with the elbow extended and supination with the elbow flexed would entail during reach-and-grasp and manipulation tasks in humans (Lan and Baker, 2004).

4.1.3. Forearm rotational efficiency and skeletal structure

The results of the studies provided afore indicate that E_{rot} values, and so the values of maximum E_{rot}, increase as the radius bone is more curved and as the medial humeral epicondyle is more medially projected (Ibáñez-Gimeno et al., 2012, 2014a, b; Publications 3.1, 3.2 and 3.3). A more distally located radial enthesis of pronator teres and a greater carrying angle of the elbow cause E_{rot} to be lower (Ibáñez-Gimeno et al., 2014a, b; Publications 3.2 and 3.3). These structural effects are the reasons behind maximum E_{rot} being the highest in *Gorilla* spp., followed by *P. troglodytes*, *Pongo* spp. and *H. sapiens*, and the lowest in Hylobatidae (Ibáñez-Gimeno et al., 2014b; Publication 3.3). Because of the fact that the curvature of the radius, the medial projection of the epicondyle and the location of the radial enthesis of pronator teres are dependent on the size of arm and forearm bones, E_{rot} values are influenced by upper limb size (Ibáñez-Gimeno et al., 2014b; Publication 3.3).

The orientation of the humeral medial epicondyle also has an effect on the value of E_{rot}. When the epicondyle is more proximally oriented or when its retroflexion is low, maximum E_{rot} rises in elbow flexion and decreases in extension. Conversely, when it is more distally oriented or when it is greatly retroflexed, maximum E_{rot} decreases in flexion and rises in extension (Ibáñez-Gimeno et al., 2014a; Publication 3.2). Nevertheless, the greatest effect of the medial epicondylar orientation on E_{rot} occurs on the position in the pronation-supination range where E_{rot} is maximal for each elbow angle (Ibáñez-Gimeno et al., 2012, 2013b; Publications 3.1 and 3.4). In this regard, the taxa or individuals with greater values of epicondylar retroflexion, such as *Gorilla* spp., *P. troglodytes* and *H. sapiens*, display their maximum E_{rot} values in elbow extension in more pronated positions of the forearm. Those taxa or individuals with more proximally oriented epicondyles, such as *Pongo* spp., *G. gorilla gorilla* and *P. troglodytes*, present their maximum E_{rot} values in elbow flexion in more supinated positions. Hylobatidae, which is the taxon with the lowest epicondylar retroflexion and the less proximally oriented epicondyles among hominoids, present their maximum E_{rot} values closer to the forearm neutral position than the rest of the taxa (Ibáñez-Gimeno et al., 2014b; Publication 3.3). The rest of the parameters have no effect or virtually no effect on the position in the pronation-supination range where E_{rot} is maximal (Ibáñez-Gimeno et al., 2012, 2014a; Publications 3.1 and 3.2).

The increase from extension to flexion observed in the E_{rot} pattern of all hominoids is due to the changes in the distance between pronator teres humeral and radial attachment sites (distance l_1) and in the value of $\overline{O'B'}$, that occur as the position of the elbow is modified (Ibáñez-Gimeno et al., 2014b; see Fig. 1 in Publication 3.3). As the elbow flexes, the distance between both entheses diminishes. The decrease of this distance is caused by two factors: when the extended elbow flexes, (i) the carrying angle diminishes (Kapandji, 2002; Goto et al., 2004), and (ii) the apex of the humeral medial epicondyle gets closer to the distal enthesis of pronator teres. Concerning $\overline{O'B'}$, it rises as the elbow flexes. In full extension, this parameter is minimal because the carrying angle is maximal. As the elbow flexes, the carrying angle decreases, and so this parameter increases. The decrease of l_1 and the increase of $\overline{O'B'}$ that occur as the elbow flexes cause a rise of maximum E_{rot} (Ibáñez-Gimeno et al., 2014b; Publication 3.3).

The increase of maximum E_{rot} from semi-flexion to full extension observed in *P. troglodytes* and *Gorilla* spp. is due to the orientation of the medial epicondyle. In both species, epicondylar retroflexion is high and proximal orientation is comparatively low, i.e. values for angle ε are high (Ibáñez-Gimeno et al., 2014b; see Fig. 11 in Publication 3.3). This causes the apex of the humeral epicondyle to be closer to the distal enthesis of pronator teres in semi-flexion than in extension. *Homo sapiens* also present a great retroflexion in comparison to the proximal orientation of the epicondyle, but they do not show this increase of maximum E_{rot} in full extension. This is due to the high values for their carrying angle, which, in full extension, cause the radial attachment site of pronator teres to be closer to the humeral attachment site, blurring the effect of the epicondyle orientation (Ibáñez-Gimeno et al., 2014b; Publication 3.3).

4.2. FUNCTIONAL PLASTICITY OF THE HUMAN UPPER LIMB SKELETON

Skeletal structure and function are intimately related, but there are many basic aspects concerning structure that remain unknown. For instance, the effect of muscular activity and mechanical loadings on many morphological characteristics has been poorly explored. Moreover, the relationship between skeletal features should be further investigated, as it would be very informative as regards their etiology and the nature of their development.

4.2.1. The effect of pronator teres on skeletal structure

The study of the components of pronator teres force suggests that the upper limb skeletal characteristics related to E_{rot} calculation can be modified by the usage of this muscle (Ibáñez-Gimeno et al., 2014a; Publication 3.2). The vertical component of the force vector ($\vec{F}_p$) indicates that an important part of pronator teres force is employed to compress the radius lengthwise towards the capitulum of the humerus (Ibáñez-Gimeno et al., 2014a; see Fig. 1 in Publication 3.2). This compression may play an important role in the enhancement of the curvature of the radius bone, especially in pronated positions of the forearm, where this compressive effect is higher (Ibáñez-Gimeno et al., 2014a; Publication 3.2). The increase of pronator teres compressive component may partially compensate the reflex inhibition of the biceps brachii muscle during forearm pronation (Basmajian and Latif, 1957; Naito et al., 1991; Latarjet et al., 2004) by assisting elbow flexion and stabilizing the joint (Ibáñez-Gimeno et al., 2014a; Publication 3.2). The curvature of the radius is also enhanced by the radial component of pronator teres force vector ($\vec{F}_r$) in pronated positions of the forearm, especially in elbow flexion (Ibáñez-Gimeno et al., 2014a; see Fig. 3 in Publication 3.2). This is in agreement with a previous study that showed that the entheseal development of pronator teres is correlated to the degree of lateral curvature of the diaphysis of the radius (Galtés et al., 2009b), suggesting that the muscular loading exerted on the apex of the radial curvature by pronator teres is a mechanical stimulus for diaphyseal bowing (Galtés et al., 2009b).

The effect of the force components on radial bowing enhancement is also influenced by the skeletal structure. The increase of the curvature of the radius bone causes $\vec{F}_r$ to have a lower effect on the enhancement of radial bowing. Conversely, a more medially projected medial epicondyle and a more proximally located radial enthesis of pronator teres cause this component to have a greater effect on radial bowing (Ibáñez-Gimeno et al., 2014a; Publication 3.2).

The plastic changes undergone by the upper limb skeleton as a result of pronator teres activity may occur because of a continued or prolonged use of the upper limb in positions where E_{rot} is low and forces are not equilibrated, e.g. extreme pronation in elbow flexion (Ibáñez-Gimeno et al., 2014a; Publication 3.2). A change in the structure, such as an increase of radial curvature or a reorientation of the medial epicondyle of the humerus, can entail an adjustment to overcome these unfavorable conditions, i.e. these changes lead to an increase of E_{rot} and a better equilibrium of forces in these previously unfavorable positions (Ibáñez-Gimeno et al., 2014a; Publication 3.2).

Although a relationship between pronator teres entheseal development and epicondylar orientation has not been observed, the results suggest that the latter can indeed be modified by muscular loadings (Ibáñez-Gimeno et al., 2013b; Publication 3.4). A simple observation of the upper limb positioning shows that a habitual and continued contraction of pronator teres in full elbow flexion may reorient the epicondyle towards a more proximal position, which would enhance E_{rot} precisely in elbow flexion. Conversely, it can be hypothesized that if the continued usage took place in full elbow extension, this reorientation would occur distally, which would enhance E_{rot} in elbow extension (Ibáñez-Gimeno et al., 2014a; Publication 3.2).

4.2.2. The effect of overall muscular activity of the upper limb on skeletal structure

The orientation of the medial epicondyle is here reported as a characteristic correlated with entheseal development of elbow flexors and extensors and hand and wrist flexors in humans (Ibáñez-Gimeno et al., 2013b; Publication 3.4). It is thus probably affected by mechanical loadings derived from muscular activity, which suggests its, in some degree, dependence on activity (Ibáñez-Gimeno et al., 2013b; Publication 3.4). The retroflexion of the medial epicondyle can be stimulated by elbow flexion, whereas elbow extension and hand and wrist flexion can enhance the orientation of the epicondyle towards a more proximal position (Ibáñez-Gimeno et al., 2013b; Publication 3.4). These (elbow flexion-extension and hand and wrist flexion) are essential movements required during the human reach-and-grasp task (Lan and Baker, 2004). An increase of epicondylar retroflexion and a proximal reorientation of the epicondyle cause a shift of the forearm positions where E_{rot} is maximal towards pronation in elbow extension and towards supination in flexion. These shifts lead to an improvement of the rotational capacity precisely during the reach-and-grasp task.

Besides radial curvature and the orientation of the medial epicondyle, the plasticity of other structural parameters that influence E_{rot} is probably not remarkable. For instance, although the distal attachment site of pronator teres can be more or less laterally located, depending on the degree of curvature of the radius, the proximodistal location of this enthesis will most likely not be modified by mechanical loadings or activity. Nevertheless, the distance between both entheses is slightly influenced by activity, as it is affected by the radial curvature and the orientation of the medial epicondyle. The carrying angle of the elbow and the medial projection of the medial epicondyle have never been considered as plastic either, but further research is warranted to address this issue.

The abovementioned effect of entheseal development on epicondylar orientation and radial curvature may also be observed for other upper limb structural and biomechanical characteristics whose development is greatly influenced by activity (Ruff, 2000; Galtés et al., 2006; Shaw and Stock, 2009a; Niinimäki, 2012; Henderson et al., 2013a). Our results indicate that there is a covariance between the development of the upper limb entheseal changes, the cross-sectional properties of the humerus and the shape of the humeral diaphysis in humans (Ibáñez-Gimeno et al., 2013a; Publication 3.5).

The entheses of the muscles that cross the shoulder are more developed in individuals with greater diaphyseal rigidities, especially bending rigidity. Some of these entheses (especially of teres major, pectoralis major and deltoid) are also more developed in individuals with mediolaterally flatter and anteroposteriorly broader mid-proximal diaphyses. This is precisely the diaphyseal shape that individuals with high diaphyseal rigidities present (Ibáñez-Gimeno et al., 2013a; Publication 3.5). Therefore, muscles involved in the motion of the shoulder probably cause a significant bending loading on the humeral shaft, which responds increasing its rigidity to adjust to these mechanical requirements. The mid-proximal diaphysis probably broadens its anteroposterior width in order to increase the distance between muscular insertion sites for arm rotators and the rotational axis of the arm, which would improve the ability of these muscles to perform rotational movements (Ibáñez-Gimeno et al., 2013a; Publication 3.5). Entheses of muscles that do not cross the shoulder and the shape of the mid-distal diaphysis and the midshaft do not show significant covariances between them or with diaphyseal rigidity (Ibáñez-Gimeno et al., 2013a; Publication 3.5). Therefore, the mid-proximal diaphysis is probably more affected by activity and should be analyzed when aiming to reconstruct activity patterns from ancient remains.

4.3. STRUCTURAL AND BIOMECHANICAL CHARACTERISTICS APPLIED TO FUNCTIONAL INFERENCE

The results showed that the forearm positions where E_{rot} is maximal for each elbow angle are intimately related to the locomotor mode. Moreover, the functional plasticity of several characteristics related to E_{rot} calculation and of other skeletal features was assessed. In this section, the positions of maximum E_{rot} and other activity-related parameters will be used to infer functional aspects from skeletal remains. In this regard, here we deduce certain aspects of the activity patterns of archaeological populations and of the locomotor mode of fossil specimens.

4.3.1. Deducing activity patterns in Point Hope populations

Cross-sectional properties of the humeral diaphysis and E_{rot} were used to assess differences between sexes in activity patterns in Ipiutak (100BCE-500CE) and Tigara (1200-1700CE), two populations from Point Hope, Alaska (Ibáñez-Gimeno et al., in press; Publication 3.6). The results indicate the existence of a marked sexual dimorphism related to activity in Tigara. The sexual differences observed for humeral cross-sectional properties in this population are almost exclusively restricted to the torsional rigidity and the total subperiosteal area, being both of them greater among males, which indicates the existence of greater relative activity levels in males than in females (Shaw and Stock, 2009a). These differences are probably associated to hunting activities, which would be exclusively performed by males. This is indeed in agreement with observations of the Tigara population in the nineteenth century, where female hunters were extremely rare (Rainey, 1947), as well as with a study of entheseal changes in Tigara, which were in general more developed among males (Steen, 2003). Moreover, the results obtained for the Tigara population are consistent with previous analyses on forager populations that presented a marked sexual dimorphism in the upper limb cross-sectional properties, due to the fact that in these populations males were involved in more physically demanding tasks than females (Ruff, 1987; Stock and Pfeiffer, 2004; Marchi et al., 2006; Sparacello and Marchi, 2008). Nevertheless, the results fail to find sexual differences in the diaphyseal shape, and so a clear distinction of the muscles most commonly used by each gender cannot be established.

Concerning the analysis of E_{rot}, sexual differences in the positions in the pronation-supination range where E_{rot} is maximal were found in Tigara (Ibáñez-Gimeno et al., in press; Publication 3.6). In this regard, females present a gain of E_{rot} with respect to males in those elbow and forearm positions where manipulative activities are usually performed, i.e. elbow flexion and forearm supination (Kapandji, 2002; Lan and Baker, 2004; Ibáñez-Gimeno et al., 2012, 2013b, 2014a, b; Publications 3.1, 3.2, 3.3 and 3.4). This is due to the fact that females present a more proximally oriented humeral medial epicondyle than males. Females were thus probably specialized in manipulative activities, as it occurred in the modern communities of Tigara village in the nineteenth century (Rainey, 1947; Larsen and Rainey, 1948). The habitual involvement in these activities may have modified the orientation of the humeral medial epicondyle (Ibáñez-Gimeno et al., 2013b, 2014a; Publications 3.2 and 3.4).

In Ipiutak, most variables were not statistically different between sexes, although this could be due to the low sample size or a weak representativeness of the sample. In this population, sexual differences in cross-sectional properties were only found for few shape indices and the total subperiosteal area in the mid-proximal diaphysis (Ibáñez-Gimeno et al., in press; Publication 3.6). Although, these differences may be indicating a differentiated recruitment of muscles and differences in the orientation of the biomechanical loading, the general lack of differences in cross-sectional properties and in the positions in the pronation-supination where E_{rot} is maximal suggests a lower activity-related sexual dimorphism in Ipiutak when compared to Tigara. This is in agreement with previous analyses that concluded that health indicators were similar between sexes in Ipiutak and that in Tigara males presented a higher prevalence of lumbar arthritis and females displayed more dental pathologies and alterations associated to the use of teeth for manufacturing (Giardini and Eggers, 2002; Madimenos, 2005). The current results are also consistent with the fact that, in the upper limb, sexual differences for entheseal changes are more marked in Tigara than in Ipiutak (Steen, 2003). Nevertheless, the small sample size imposes limitations in the interpretation of the results, and so they should be considered prudently.

4.3.2. Reconstructing locomotion in fossil hominids

Forearm rotational efficiency (E_{rot}) was calculated in AL 288-1 (Lucy, *Australopithecus afarensis*) and the results were compared with a large sample of extant hominoid taxa (Ibáñez-Gimeno et al., in prep.; Publication 3.7). As abovementioned, the positions in the pronation-supination range where E_{rot} is maximal for each elbow angle are associated with the locomotor mode of each extant taxon, and so the comparative study focused on these values. The positions of the maximums in AL 288-1 are virtually identical to those of *Pongo* spp. throughout the entire flexion-extension range. They are also similar to the positions of the maximums in *P. troglogytes* and *G. gorilla gorilla*, but only in elbow angles close to full flexion (Ibáñez-Gimeno et al., in prep.; Publication 3.7). These resemblances are due to the fact that the positions of maximum E_{rot} are almost exclusively determined by the orientation of the epicondyle (Ibáñez-Gimeno et al., 2012, 2013b, 2014a, b; Publications 3.1, 3.2, 3.3 and 3.4). The proximodistal orientation of AL 288-1's humeral epicondyle is similar to *Pongo* spp., *P. troglodytes* and *G. gorilla gorilla*, whereas its retroflexion is more similar to *Pongo* spp. than to any other extant hominoid taxa (Ibáñez-Gimeno et al., in prep.; Publication 3.7).

In elbow flexion, AL 288-1, *Pongo* spp., *P. troglodytes* and *G. gorilla gorilla* present their maximum E_{rot} greatly shifted to supination, which causes pronator teres capacity to rotate the forearm to be greater in those positions essential during climbing, i.e. flexion of the elbow with the forearm supinated (Sarmiento, 1987, 1988; Stern and Larson, 2001; Ibáñez-Gimeno et al., 2014b; Publication 3.3).

As the elbow extends, the positions of the maximum E_{rot} in AL 288-1 shift towards pronation, reaching less pronated positions in full elbow extension than knuckle-walker taxa, which supports the accepted idea of lack of knuckle-walking in *Au. afarensis* (Kimbel et al., 1994; Drapeau et al., 2005; Kimbel and Delezene, 2009). Overall, the similarity of the maximum positions for AL 288-1 with arboreal extant hominoids (*Pongo* spp. throughout the entire flexion-extension range and *P. troglodytes* and *G. gorilla gorilla* in elbow flexion) indicates that the upper limb skeleton of AL 288-1 was probably still adapted to arboreal locomotion.

The comparison of the results obtained for AL 288-1 with *H. sapiens* is also of interest, as they display different values throughout the entire flexion-extension range. *Homo sapiens* present their maximum E_{rot} in elbow flexion in less supinated positions than AL 288-1, probably because the former required the use of the precision grip, which is commonly used for manipulative behaviors. Positions of the maximums during elbow flexion closer to the neutral position of the forearm would be advantageous for modern humans, because this is the position in which the precision grip is enhanced (Kapandji, 2002; Ibáñez-Gimeno et al., 2012; Publication 3.1). In positions close to elbow extension, AL 288-1 does not present its maximums in greatly pronated position probably because that is not useful for arboreal locomotion (Ibáñez-

Gimeno et al., 2014b; Publication 3.3). *Homo sapiens* do display their maximums in elbow extension in more pronated positions of the forearm, which is favorable during the reach-and-grasp task, where humans use their prone hand to grab objects that are far from the body (Kapandji, 2002).

These changes shown by *H. sapiens* may therefore have occurred in the human lineage due to the requirements related to the increasing manipulative capacities. Although *Au. afarensis* was probably capable of enhanced manipulation (Alba et al., 2003; Almécija and Alba, 2014), the results indicate that concerning pronator teres rotational efficiency, these capabilities were far from those observed in modern humans.

4.4. FUTURE LINES OF RESEARCH

The biomechanical analysis of the upper limb in extant and fossil hominoids has enabled to make functional inferences from skeletal remains. Nevertheless, our findings lead to new lines of research and some new unanswered questions.

Forearm rotational efficiency (E_{rot}) can only be calculated when the humerus, radius and ulna are complete and well-conserved. In order to assess E_{rot}, the long axis has to be represented in the three-dimensional image of the humerus, which requires the humerus to be complete. For the assessment of the orientation of the medial epicondyle, its apex has to be determined, and so the surface of this structure, which is often eroded, must be in perfect state. Several measures of the radius and ulna are also used, including lengths and epiphyseal widths, and so fragmented bones, as well as bones cracked or damaged in specific areas, cannot be analyzed. As all these conditions are not frequent in fossil remains, this analysis has only been performed on AL 288-1 (Ibáñez-Gimeno et al., in prep.; Publication 3.7). Nevertheless, the study of other specimens, such as MH2 (*Australopithecus sediba*; Churchill et al., 2013), with a well-conserved upper limb, would shed some light on the evolutionary pathway of E_{rot} in the hominid lineage.

The positions in the pronation-supination range where E_{rot} is maximal, as mentioned afore, basically depend on the orientation of the medial epicondyle. The current biomechanical model uses angle φ, which can be used as a proxy for epicondylar orientation and which can only be calculated in complete humeri (it depends, for instance, on the humeral axis, which can only be represented when the humerus is complete). Nevertheless, proxies for the proximodistal and anteroposterior orientation of the epicondyle calculated using only the distal epiphysis could be defined. These proxies should be highly correlated with angles φ (90°) and φ (180°), and so they would enable to assess the positions in the pronation-supination range where E_{rot} is maximal in fragmentary fossil specimens of the hominoid lineage, such as KNM-KP 271 (*Australopithecus anamensis*; Ward et al., 2001), AL 137-48a (*Au. afarensis*; Johanson et al., 1982), RUD 53 (*Hispanopithecus hungaricus*; Morbeck, 1983; Alba et al., 2011) and KNM-FT 2751 (*Kenyapithecus wickeri*; Andrews and Walker, 1976; Alba et al., 2011).

Although E_{rot} has already been widely studied in extant hominoids, the biomechanical model may be applied to other primate taxa. The locomotor repertoires in nonhominoid primates are diverse and present important differences with those of hominoids (Fleagle, 1988; Stern and Larson, 2001; Sarmiento, 2002). While hominoids are orthograde, and so they display an upright position of the trunk during locomotion and their limbs swing in opposition to one another for balance, the rest of primates are pronograde, and so their trunk remains parallel to the subtract and the upper limbs are ventrally located (Fleagle, 1988; Aiello and Dean, 1990; Gebo, 2010). These basic dissimilarities may entail important differences in how functional advantages associated to E_{rot} are achieved. Moreover, upper limb skeletal structure displays a wide range of variation when all primates are considered, and some aspects of the biomechanical model, such as the assessment of some anatomical points, should be adapted if applied to other taxa. The application of the biomechanical model to nonprimate taxa would also be of great interest. Previous studies demonstrated a relationship between the shape of the distal humeral diaphysis and the pronation-supination abilities in musteloid carnivores (Fabre et al., 2013a, 2013b). The current biomechanical model could contribute to get further information on the importance of pronator teres mechanics in the locomotion of these and other taxa.

Besides pronator teres, the humeral medial epicondyle is the attachment site of the internal lateral ligament and the common tendon of origin of some of the flexor muscles of the forearm (Gray, 2010). Although the contribution of pronator teres to defining the epicondylar orientation is major, the analysis of these other muscles, of their influence on the medial epicondyle and of their relationship to pronator teres biomechanics would be of interest. These muscles also play an important role in manipulative behaviors, and parameters such as precision in grasping and manipulating objects may be also affected by them. Analyses involving the skeletal structure of the wrist and hand and its relationship with the different types of grips employed in manipulation would provide information on the evolution of manipulative capacities. In this regard, the association between the axes of the forearm and of the hand during grasping and its relevance to the precision of the motion should be further investigated.

Concerning the analyses employing skeletal markers of activity, it has to be taken into account that the use of entheseal changes to determine the level of plasticity of skeletal features has limitations, as there are many aspects about entheses still poorly understood that require further investigation. For instance, many researchers state that entheseal changes are not as good indicators of activity as previously thought (e.g. Villotte et al., 2010; Niinimäki and Baiges Soto, 2013; Villotte and Knüsel, 2013; Rabey et al., 2015). A lack of understanding of entheseal development has led to oversimplified conclusions of activity patterns in ancient populations, probably because the complex etiology of attachment sites has not been fully explored (Alves Cardoso and Henderson, 2010; Villotte et al., 2010; Henderson, 2013; Henderson and Alves Cardoso, 2013; Henderson et al., 2013b; Niinimäki and Baiges Soto, 2013; Villotte, 2013; Villotte and Knüsel, 2013; Rabey et al., 2015). The correlation between the orientation of the humeral medial epicondyle and the entheseal development of elbow flexors and extensors and of hand and wrist flexors observed in the current thesis (Ibáñez-Gimeno et al., 2013b; Publication 3.4) may be a result of a complex relationship triggered by a multifactorial etiology, which should be further investigated. Therefore, studies exploring the bases of entheseal development, rather than analyses inferring activity patterns from entheseal changes, are required. Analyses similar to those performed in this dissertation are useful to get further insight into the relationship between entheses and function, as they relate these changes with other characteristics in direct association with activity.

Together with the limitations that the use of entheseal changes imposes, certain methodological aspects involving the assessment of cross-sectional properties and the analysis of diaphyseal shape in specific sections of the diaphysis need to be mentioned. The skeletal remains need to be in a great degree of conservation for this kind of analyses. The cortical surface has to be well-conserved, because degradation would cause shape and biomechanical properties to be inaccurately assessed. Moreover, great precision needs to be guaranteed when determining what part of the diaphysis is being studied. In this regard, only complete bones can be used. Otherwise, the specific section under study cannot be established with precision, which may affect the reliability and reproducibility of the results. These considerations impose limitations, especially in the possibility of analyzing large sample sizes.

Therefore, research focused on overcoming these limitations, such as methods to infer total lengths from long bone fragments, would be extremely useful.

Because of these limitations, only sexual dimorphism has been explored in Tigara and Ipiutak populations (Ibáñez-Gimeno et al., in press; Publication 3.6). Future analyses should intend to explore other activity-related aspects, such as bilateral asymmetry, the effect of age and interpopulation differences. Nevertheless, other activity-dependent variables should be used for these purposes, as conservation and preservation are far from optimal for the assessment of cross-sectional properties and E_{rot} in a large set of individuals in these populations.

5. CONCLUSIONS

As many truths as men. Occasionally, I glimpse a truer Truth, hiding in imperfect simulacrums of itself, but as I approach, it bestirs itself and moves deeper into the thorny swamp of dissent.

David Mitchell
Cloud Atlas

1. The differences in the positions in the pronation-supination range where E_{rot} is maximal for each elbow angle observed among extant hominoid taxa reflect adaptations to locomotor specializations. *Gorilla* spp. and *P. troglodytes* are the taxa with maximum E_{rot} in elbow extension located in the most pronated positions of the forearm, which is associated to their habitual engagement in knuckle-walking. Maximum E_{rot} in elbow flexion is in more supinated positions in *Pongo* spp. and *P. troglodytes*, which is associated to their habitual engagement in arboreal locomotion. In flexion, *Gorilla gorilla gorilla* display maximum E_{rot} in more supinated positions than *G. beringei* because the former is more arboreal and the latter is essentially terrestrial. In Hylobatidae, maximum E_{rot} is close to the forearm neutral position throughout the flexion-extension range, which is related to their engagement in true brachiation. Maximum E_{rot} in *H. sapiens* is located in between arboreal and terrestrial hominoids, which is associated to their upper limbs being free from locomotor demands and to an enhancement of the manipulative capacities.

2. The differences in the position in the pronation-supination range where E_{rot} is maximal among taxa are due to differences in the orientation of the humeral medial epicondyle. In elbow extension, a greater retroflexion of the humeral medial epicondyle causes maximum E_{rot} to be located in more pronated positions of the forearm. In elbow flexion, a medial epicondyle of the humerus more proximally oriented causes maximum E_{rot} to be located in a more supinated position of the forearm.
3. Forearm rotational efficiency (E_{rot}) increases as the radial curvature and the medial projection of the humeral medial epicondyle increase, as the radial insertion site of pronator teres is more proximally located and as the carrying angle of the elbow decreases. This accounts for maximum E_{rot} values being the highest in *Gorilla* spp., followed by *P. troglodytes*, *Pongo* spp. and *H. sapiens*, and the lowest in Hylobatidae. The value of E_{rot} is therefore dependent on the absolute upper limb size.
4. Some skeletal structures involved in E_{rot} calculation are plastic and can be modified by the usage of pronator teres, among other factors. These modifications occur when the upper limb is used in positions with low E_{rot} values or that entail a lack of equilibrium of forces in order to adjust and overcome these unfavorable conditions. In this regard, the radius is more easily bowed by pronator teres activity when its curvature is low, when the medial projection of the humeral medial epicondyle is high and when the radial insertion site of pronator teres is more proximally located.
5. The orientation of the medial epicondyle of the humerus is also probably plastic and modifiable by activity in humans. An increase of the retroflexion and a proximal reorientation of the epicondyle, which lead to an increase of the manipulative capacities, are correlated to the development of the entheseal changes of elbow flexors and extensors and of hand and wrist flexors.

6. Upper limb skeletal features related to activity covariate among them. Humeri with greater rigidities present more developed entheseal changes of those muscles that cross the shoulder. The entheseal changes of the muscles that participate in the rotation of the arm are more developed in those individuals that have a midproximal humeral diaphysis with an anteroposteriorly broad shape, which in turn have greater diaphyseal rigidities. This indicates that the mid-proximal diaphysis may be used to assess the overall level of proximal upper-limb mechanical loading.
7. The differences in the cross-sectional properties between sexes in Tigara foragers indicate that males were involved in more physically demanding tasks, probably associated to hunting activities. The differences in the forearm positions in the pronation-supination range where E_{rot} is maximal suggest that Tigara females were more frequently involved in manipulative tasks than males. Ipiutak individuals displayed few activity-related sexual differences in these parameters, which is consistent with a lower degree of division of labor, although interpretations should be carefully considered given the small sample size.
8. The similarities in the positions in the pronation-supination range where E_{rot} is maximal between AL288-1 and *Pongo* spp. throughout the entire flexion-extension range, as well as the similarities for these positions between AL 288-1 and *P. troglodytes* and *G. gorilla* in elbow flexion, suggest that the upper limb of *Australopithecus afarensis* was probably still adapted to arboreal locomotion. The differences observed in *H. sapiens* with respect to AL 288-1 probably arose as a result of the requirements related to the increasing manipulative capacities.

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If you can quote the rules, then you can obey them.

Tony Soprano

The Sopranos

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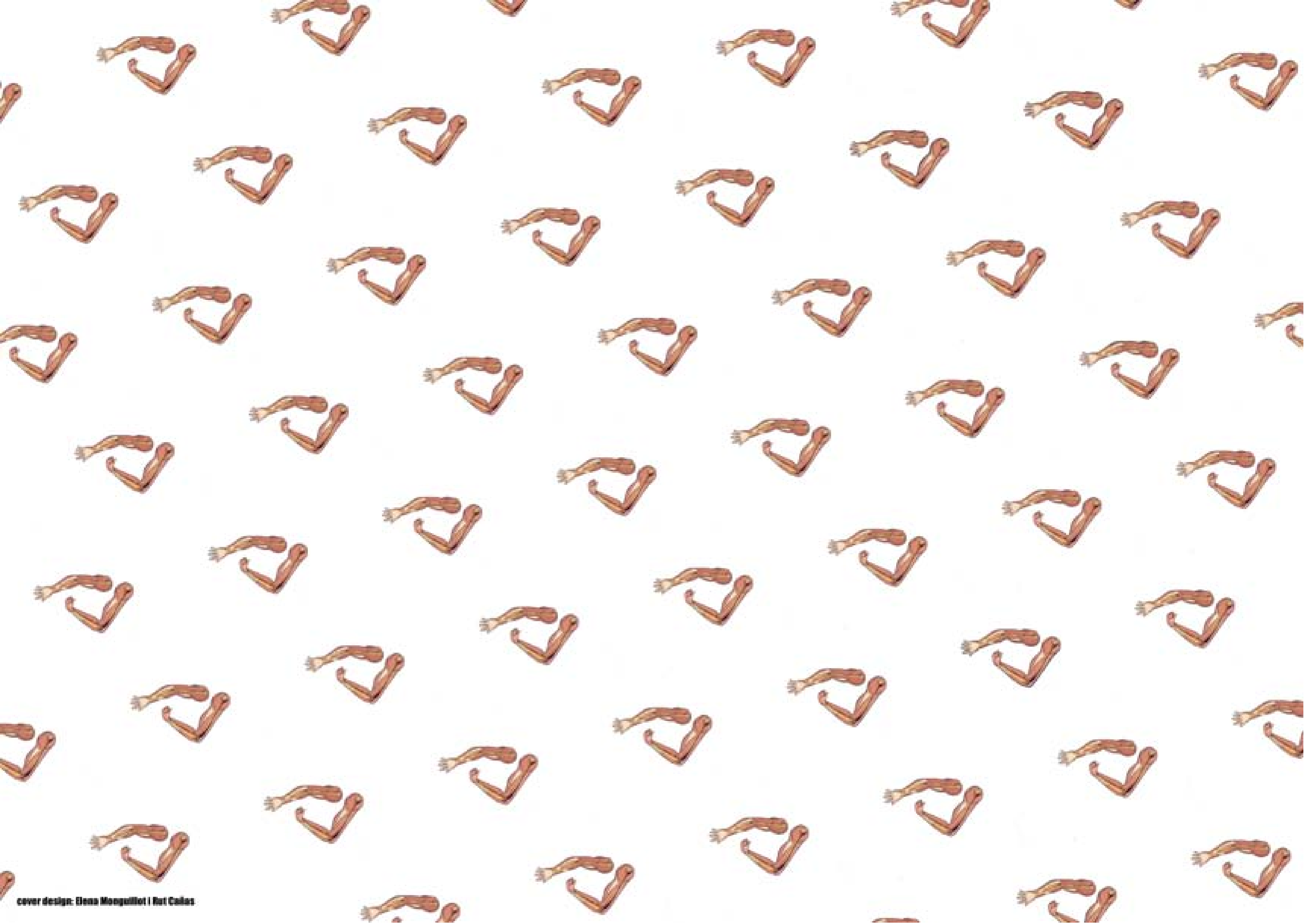

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