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Titre

Morphological analysis of the proximal humerus of fossil *Theropithecus brumpti* by using 3D reconstructed models. For a functional interpretation of quadrupedal locomotion.

Candidat

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Abstract

There are two extinct lineages within *Theropithecus* represented by the species *Theropithecus oswaldi* and *Theropithecus brumpti*. *T. brumpti* is only found at sites in Kenya and Ethiopia: Lake Turkana basin, Nachukui Formation of West Turkana ,the Koobi Fora Formation of east Turkana and lake Baringo in the Kenya rift valley and the Omo Shungura Formation in Ethiopia. The objective of my study was to initiate a functional anatomical study of fossil quadrupedal primates based on segmented 3D images of *Theropithecus* with the bone anatomy related to muscle attachment and its significance for quadrupedal locomotion. The study was made on 3D reconstructed models of humerus of Papio anubis. Morphological features observed on the 3D models of the proximal humerus of *Theropithecus oswaldi* and *Theropithecus brumpti* were compared to the available knowledge on papionine. The comparison shows many morphological and functional similarity between both taxa, both largely adapted to arboreal and terrestrial quadrupedalism.

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Chapter 1

1. Introduction

1.1 Context of the research

Pliocene and Pleistocene deposits of Africa hold a well-preserved fossil record of primates. Among them is the Cercopithecinae, a subfamily of cercopithecid monkeys that started to diversify in the Plio-Pleistocene and nowadays is still abundant and taxonomically diverse (G. Eck, 1977a; Iwamoto et al., 1996). Within this subfamily, *Theropithecus*, there is fossils evidence of a large-bodied monkey which presents unusual craniodental characteristics, including high crowned molar teeth characterized by complex enamel folding, pinched and columnar cusps (E Delson et al., 1993; N G Jablonski et al., 2008; Szalay & Delson, 2013) , and also because its occurrence often overlaps with that of hominins in eastern African fossil sites (Foley, 1993).

The earliest appearance of the genus *Theropithecus* in the fossil record dates to 4 Ma (Eric Delson, 1993; N G Jablonski & Frost, 2010; N. G. Jablonski, 1993). *Theropithecus* is well-represented in eastern Africa at sites such as Tugen Hills' sequence (Gilbert et al., 2011), Koobi Fora(Nina G. Jablonski et al., 2002) , Lonyumun (Leakey, 1993), and Shungura (G G Eck, 1987). Today the extant species, *T. gelada* is only found in the highlands of Ethiopia (Belay & Mori, 2006; Iwamoto, 1993; Jolly & CJ, 1972) and is thought to be a distant evolutionary relation of the extinct *Theropithecus* species rather than a descendant (Jablonski, 1993; Szalay & Delson, 2013).

There are two extinct lineages within *Theropithecus* represented by the species *Theropithecus oswaldi* and *Theropithecus brumpti*, as well as one extant lineage consisting of the extant species, *T. gelada* (Leakey, 1993) . Of the two extinct species lineages, *T. oswaldi* had a notably broader geographic range than *T. brumpti*, with some fossils of this species having been recovered at Pleistocene deposits in Spain, Israel and India in addition to their record in eastern and southern Africa (Belmaker, 2010; Dechow & Singer, 1984; Eric Delson, 1993; Ferràndez-Cañadell et al., 2014; Freedman, 1957; Gibert et al., 1995; Gupta & Sahni , 1981; Pickford, 1993). In contrast to *T. oswaldi*, *T. brumpti* is only found at sites in Kenya and Ethiopia: Lake Turkana basin, Nachukui Formation of West Turkana ,the Koobi Fora Formation of east Turkana and lake

Baringo in the Kenya rift valley and the Omo Shungura Formation in Ethiopia (G. Eck, 1977a; G G Eck & Jablonski, 1987; Gilbert et al., 2011; Nina G. Jablonski et al., 2002).

The evolutionary relationship between the two extinct lineages (*T. oswaldi* and *T. brumpti*) is only partly understood. In the Koobi Fora Formation, *T. oswaldi* replaces *T. brumpti* after 2 Ma as the most common *cercopithecid* (Leakey, 1993). However, in Ethiopia the two species simultaneously appear together in the Shungura Formation in the Omo around 2.4 to 2 Ma (G G Eck & Jablonski, 1987) , although *T. brumpti* is the more abundant (G. Eck, 1977a).

These different patterns of occurrence have allowed for a range of interpretations about *Theropithecus*' evolutionary history, habitat preference, and locomotion (Elton, 2002). In the Shungura Formation , *T. brumpti* occupied biogeographic range similar to those of cercopithecids, bovids, suids and hominins that have been attributed to several taxa, including colobines, *Papio Paranthropus aethiopicus*, *Australopithecus* and early *Homo* (Alemseged, 2003; Boisserie et al., 2010; Guthrie, 2011; Suwa et al., 1996). Additionally, previous research by (G. Eck, 1977a) Eck and (Foley, 1993) suggest that *T. brumpti*'s locomotor behavior is also potentially important for paleoenvironmental reconstructions because this species may have been particularly reliant on riverine gallery forest habitat (Behrensmeyer et al., 1997; Cardini & Elton, 2007; G G Eck & Jablonski, 1987; Feibel et al., 1991; Gilbert et al., 2011; Nina G. Jablonski et al., 2002).

The locomotion of the extinct *Theropithecus* species has been discerned through comparative anatomy of postcranial bones. Although locomotor inferences have been made for more than 40 years (e.g., Jolly & CJ, 1972; Rose, 1974 ; as reviewed in Krentz, 1993a), there is no clear consensus on the locomotory repertoire of fossil *Theropithecus*. This uncertainty about the locomotory behavior may be due to the fact that postcranial fossils that are certain to represent *Theropithecus* have, for a long time, been limited in number (Krentz, 1993).

One of the earliest interpretations of *Theropithecus* locomotion based on skeletal anatomy and metrical comparisons with extant species was done by Jolly (1972). Jolly examined postcranial bones of *T. oswaldi* from Olduvai, Kanjera and Olorgesailie sites. He concluded that *T. oswaldi* was a terrestrial quadruped much like modern *T. gelada*. More recently, Elton (2002), argued that *T. oswaldi* probably utilized arboreal substrates in a manner similar to modern baboons.

Turning to *T. brumpti*, previous research reported a mix of both arboreal and terrestrial features (Ciochon, 1993; Krentz, 1993; Jablonski et al., 2002, 2008). Anatomical features of *T.*

brumpti thought to provide the most insight to locomotory variation have been reviewed by Krentz (1993: table 14.1(a) p. 388-397) and include traits observed in different parts of the postcranial skeleton, such as the long bones, though morphological variation of the hindlimb of Cercopithecoids is less straightforward (Krentz, 1993a).

Quadrupedal primates show variations in scapular morphology. for instance the shape and orientation of the glenoid fossa used to distinguish arboreal monkeys from terrestrial ones (Ashton & Oxnard, 1964; Birchette JR, 1982; Kimes et al., 1981; Roberts, 1974) . Within the forelimb, the articulation between proximal humerus and glenoid cavity of the scapula form glenohumeral joint (S G Larson, 1993; Susan G Larson & Stern Jr, 2013; Potau et al., 2009) . This joint is involved in arm movement, which includes flexion and extension to abduction and adduction, and axial rotation(Arias-Martorell et al., 2015; Susan G Larson & Stern Jr, 2013; Rose, 1989). *T.brumpti* presents a features specially in the proximal humerus which emphasize great flexibility at the glenohumeral joint (Nina G. Jablonski et al., 2002; Krentz, 1993b).

Moreover the partial skeleton of *T.brumpti* (KNM-WT 39368) from Nuchkui documented exceptional scapular morphology, which is represented by a large size of the axillary gutter. This exception indicates that *T. brumpti* possesses a forelimb that is more flexible at the shoulder joint (Nina G. Jablonski et al., 2002) .The proximal humerus is the particular informative bone in terms of providing enlightenment in to the locomotor habits of *T.brumpti*. The most important features of the proximal humerus that are considered by (Krentz, 1993a) and (Nina G. Jablonski et al., 2002), are the greater tubercles of the humerus that lie below the level of the head, the insertion on m. infraspinatus is deep , insertion for *M. teres minor* is distinct, insertion for coracobrachialis is pronounced, a ridge appears on the medial border of the humeral shaft indicate, *T. brumpti* was also more arboreal than modern *Theropithecus*, *Papio* and *T. oswaldi*.

The conclusion that *T. brumpti* had an emphasis on arboreality is not reached by all investigators. For example,(Guthrie, 2011) argues that the femur of female *T. brumpti* indicates terrestrial quadruped locomotion. Part of the conflicting results may well result from the various studies exploring the forelimb versus the hindlimb. The discordance between studies may also result from the very small sample sizes included in these analyses, as Nina G. Jablonski et al., 2002 analyzed one skeleton of a male, and Gilbert et al., 2011 studied one female.

In my research presented here, I contribute to this debate by extending the size of the study sample significantly. I focus on the proximal humerus of *T. brumpti* from the Omo Formation sequence, which is one of the most completed Plio-Pleistocene deposits consisting of the Mursi, Usno and Shungura Members (Boisserie et al., 2008). The Shungura Formation located in the southwestern Ethiopia preserve a large sample of cercopithecids fossil, the genus *Theropithecus* was dominant in all Members and it represented by nearly 1500 specimens (G. Eck, 1977a). Furthermore (Boisserie et al., 2008), report that cercopithecids are the most ample taxon in the OGRE new collection from Member B,C,D and G.

In this collection, *Theropithecus* specimens are an abundant genus represented by isolated teeth, subcomplete crania, mandibles and postcranial bones (Boisserie et al., 2008). Between 1967-1974 field season, around 6000 Cercopithecoid fossils are recovered from the above three deposit (G. Eck, 1977a). These sediments have yielded 43 specimens of *Theropithecus* humeri for which the proximal part is preserved. This large sample enables us to explore the humeral component of the shoulder gridle of *T.brumpti* to investigate morphometric affinities of the locomotor system and make locomotor inferences from morphofunctional view.

Nina G. Jablonski et al., 2002 make the case that the forelimb is a particularly useful anatomic region for primate morphofunctional studies, as it is widely recognized in cercopithecoids as being more informative of modes of locomotion and manipulation than the hindlimbs, which function mainly to provide propulsive thrust in locomotion (Nina G. Jablonski et al., 2002). Following this argument, I focus exclusively on the forelimb.

1.2 *Theropithecus* at the Omo Formation

A total of 184 postcranial specimens of *Theropithecus*, which were all recovered from all members of the Shungura Formation except the Basal Member have produced specimens of the genus (E Delson et al., 1993; G. Eck, 1977a; G G Eck & Jablonski, 1987). From these 43 are listed as humerus (see table1). The Shungura *Theropithecus* fossil classified as T. brumpti, T. oswaldi. Twenty three of them are the humerus of *Theropithecus brumpti* occurs from Member C to G of Shungura Formation and thus differ in anatomical parts, which are two complete were recovered from Member C , twelve proximal part were recovered from Member C,F and G and nine distal part were recovered from Member C, D , E and F . The proximal part of humerus is the most recovered part represented by 12(52%) of the sample (E Delson et al., 1993). The most complete specimens are listed below.

Table 1. ***Theropithecus* humerus From Shungura Formation**

	Accession number	**Anatomy**	**Locality**	**Reference**
Theropithecus brumpti	L18-20	Male Lt humerus distal Fragment	C	(Delson et al., 1993)
	L32-155g	Male Lt humerus distal fragment and proximal end with 1/4 of shaft	C	
	L32-159J	?Female Lt humerus proximal fragment	C	
	L32-159k	Male Lt humerus proximal fragment plus 1/2 of shaft	C	
	L55-48	Male Lt humerus proximal fragment	C	
	L69-3	Male Rt humerus proximal fragment and 1/3 of shaft	C	
	L70-7	Male Lt humerus complete	C	
	L143-45	Female Lt humerus distal fragment	C	
	L161-43	Female Lt humerus distal fragment and 1/3 of the shaft	D	
	L292-8	Male Lt humerus distal fragment with distal shaft	C	
	L304-9	?Female Rt humerus proximal fragment	C	
	L434-8	Female Lt humerus proximal fragment and 1/4 of the shaft	G	
	L886-15	Female Lt humerus distal fragment and 1/3 of the shaft	C	
	L899-1	Male Lt humerus proximal fragment and 1/2 of the shaft	C	
	OMO 18-67-28	Male Lt humerus proximal fragment and 1/2 of the shaft	C	
	OMO 18-67-40	Male Lt humerus proximal fragment - and 1/3 of the shaft	C	
	OMO 18-68-2281	Male Lt humerus proximal fragment and 2/3 of the shaft	C	

	OMO 58-68-2225	Female Rt humerus distal fragment and 1/2 of the shaft	F	
	OMO 75 N-7-G205	Female Lt humerus proximal fragment	G	
	OMO 130-73-1894	Male Lt humerus proximal fragment and 1/3 of the shaft, distal fragment and 1/2 of the shaft	F	
	OMO 145-72-7	Female Lt humerus distal fragment	E	
	OMO 158-73-410	Male Lt humerus Complete	C	
	OMO 165-73-608	Female Lt humerus distal fragment	C	
Theropithecus oswaldi	L28-130	Female Lt humerus distal fragment and 2/3 of the shaft	E	(Delson et al., 1993)
	L74-32a	Female Rt humerus distal fragment and 2/3 of the shaft	G	
	L74-32b	Female Rt humerus proximal fragment and 1/3 of the shaft	G	
	LI78-6	Male Rt humerus proximal fragment and 1/3 of the shaft	E	
	L238-257	Female Lt humerus proximal fragment and 1/3 of the shaft	F	
	L867-13	Male Rt humerus shaft	F	
	OMO 33-69-404	Female Lt humerus proximal fragment and 1/4 of the shaft	F	
	OMO 47-73-1474	Female Lt humerus distal fragment and 1/3 of the shaft	G	
	OMO 75 N-7-G201	Male Rt humerus distal fragment and 1/2 of the shaft	G	
	OMO 75 N-7-G203	Female Lt humerus distal fragment	G	
	OMO 75 N 71 688	Male Rt humerus proximal fragment and 1/3 of the shaft	G	

	OMO 75 N-71-692	Male Lt humerus distal fragment and 1/3 of the shaft	G	
	OMO 75 N-71-693	Male Lt humerus proximal fragment	G	
	OMO 75 S-69-461	Male Rt humerus proximal fragment and 1/3 of the shaft	G	
	OMO 92-73-984	Female Lt humerus distal fragment and 1/3 of the shaft	E	
	OMO 233-73-4554	Female Lt humerus distal fragment and 1/3 of the shaft	G	
Theropithecus ssp. *Indent.*	L304-10	Lt humerus proximal fragment	C	(Delson et al., 1993)
	OMO 75 N-7-202	Lt humerus proximal fragment	G	
	OMO 199-73-1273	Rt humerus proximal fragment	F	
	OMO 199-73-1421	Lt humerus distal fragment	F	

1.3 Aims of the research

My research focuses on the proximal humerus of *Theropithecus brumpti* of Omo. I will conduct quantitative analysis of the shape of proximal humerus we will use three dimensional (3D) images for the morphological description and metrics data collection . Correspondingly we will comparing this data to the fossil specimens of *Theropithecus oswaldi* from Omo Shungura Formation and pictures of comparative extant material of *papionins* . To test arboreal and terrestrial locomotion of *Theropithecus brumpti* at the functional and paleoenvironmental point of view based on two complete and nine proximal part of the humerus of *T. brumpti* and *T. oswaldi* that recovered from the Shungura Formation.

Chapter 2

2. Background and literature review

1.4 Location of the project area and geological setting

Theropithecus specimen recovered from all Member of Suhungura Formation except the basal Member and Member K (G. Eck, 1977a; G G Eck & Jablonski, 1987; Gerald G Eck & Jablonski, 1984). Based on cranial evidence, during 2.9 to 0.9 m.y, two species of *Theropithecus* inhabited the lower Omo Basin. These are *T. oswaldi* and *T. brumpti* , (G. Eck, 1977b). *T. brumpti* from the Shungura Formation is one of the largest and best preserved fossil specimen (Eric Delson, 1993; G G Eck, 1987; Krentz, 1993a).

The Shungura Formation is located in the Lower Omo Basin, which is the northerly continuation of the Turkana basin into Ethiopia. The Plio-Pleistocene deposits of the lower Omo Valley are divided into three geological formations: the Shungura, Usno, and Mursi Formations (Figure 1). Radiometric ages indicate that the Formation covers a time span from 3.6 to 1.16 Ma (Feibel et al., 1989). Different sedimentary cycles of the Formation are grouped into 12 members (Basal, A, B, C, D, E, F, G, H, J, K and L), each commencing by a volcanic tuff designated by the same letter figure 1. the lowermost sediments constitute the Basal Member (Alemseged, 2003; Bobe et al., 2002;).

Member A to Member L, based on widespread volcanic tuffs that underlie each member: Member A has 4 units, Member B has 12, Member C has 9, Members D, E, and F have 5 each, Member G has 29, Members H and J have 7 each, Member K has 4, and Member L has 9 units(From Heinzelin & Haesaerts, 1983). According to (Boisserie et al., 2008) cercopithecids are the most abundant taxon in Member B, C ,D and G Fig 2,. Genus *Theropithecus* are the abundant fossil represented by numerous isolated teeth but also sub complete crania, mandibles, and postcranial bones.

The available evidence suggest that the geologically most oldest *T. brumti* comes from unit B-10 (2.95m.y) , unit C-6 (2.7m.y) and the youngest come from unit G-12 (2.0 m.y), (G G Eck & Jablonski, 1987).

G G Eck & Jablonski, 1987 has shown that the distribution of arboreal taxa in the Shungura Formation in the area of each member. These spectra suggest that arboreal taxa were more common in the Members, B and C become for less common in Member E and F and recover slightly frequency in the lower Member G. these evidence show that the habitat preference of *T. brumpti* was riverine forest wood land plant communities.

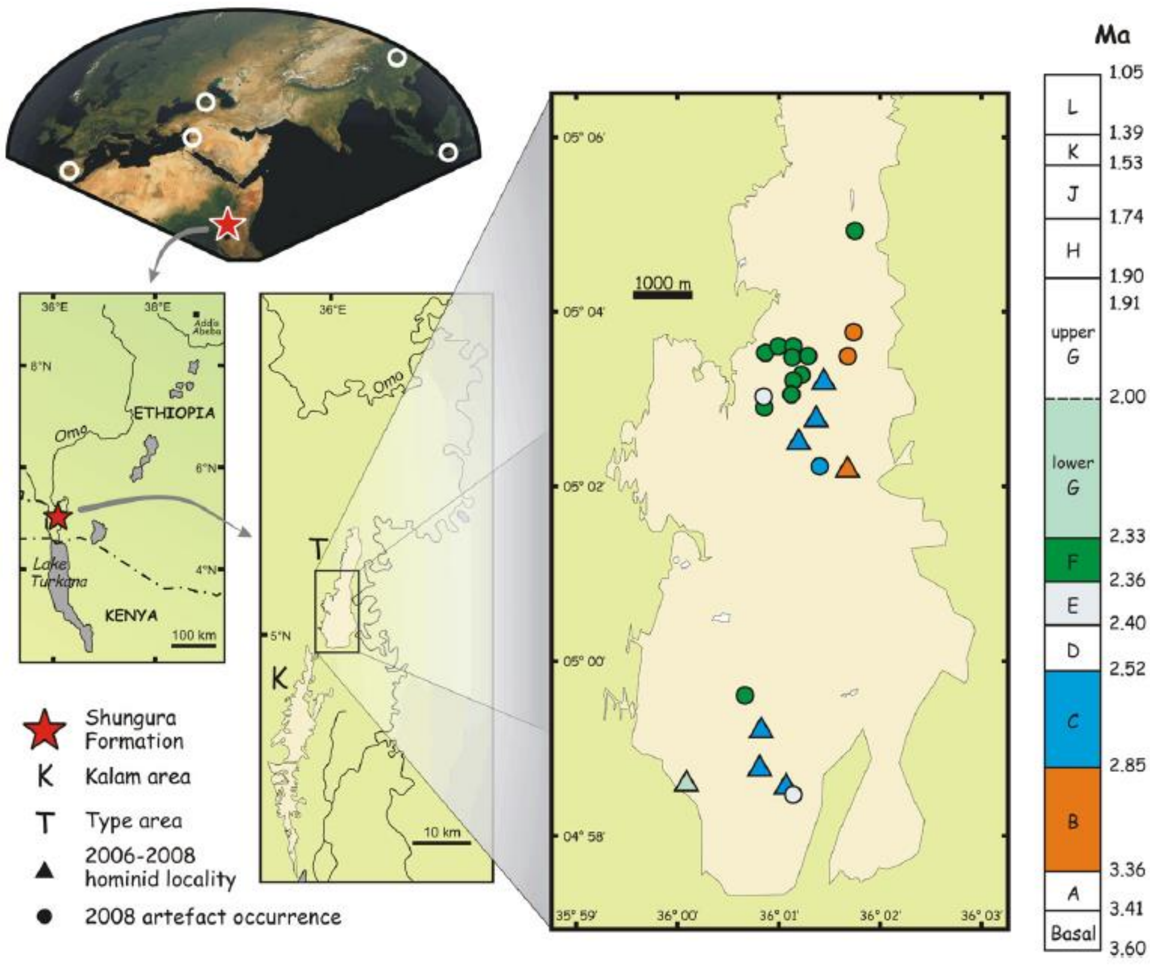


Figure 1. Geographic and chronostratigraphic location of 2006–2008 paleoanthropological discoveries by the Omo Group Research Expedition in the Shungura Formation, Lower Omo Valley, Ethiopia. Empty circles on the satellite view of Eurasia (upper left) indicate areas bearing some of the most critical evidence for earliest human dispersals outside Africa. General chronostratigraphic column of the Shungura Formation (extreme right) is 766 m high. Source: (Boisserie et al., 2010).

1.5 Evolutionary Success of *Theropithecus*

Theropithecus is one of the best known of fossil primate taxa, being recognized from thousands of specimens from sites in northern, eastern and southern Africa from the middle Pliocene through most of the Late Pleistocene. *Theropithecus* are most closely related to baboons of genus *Papio*. Both have common ancestor and they diverging form the common ancestor of *Mandrillus* and *Cercocebus* probably in the early Pliocene (Disotell, 2000). Eric Delson, (1993) describes the representative of fossil *Theropithecus* has recorded by two distinct lineages by the species of *T. oswaldi* and *T. brumpti*. They distinguished taxonomically as the subgenera *T. (Theropithecus)* and *T.(Omopithecus).*

Delson, 1993; Gibert et al., 1995 on Pleistocene-aged the most widespread species of the genus, has *T. oswaldi*. It is recognized from sites outside of Africa, in India and Spain . *T. brumpti* was more localized in its spatial distribution, being recognized only from Pliocene-aged sites of the Shungura Formation of the Omo Ethiopia and the Lake Turkana Basin, Kenya. *T. brumpti* has been interpreted as occupying a riverine gallery forest habitat (G G Eck & Jablonski, 1987), while *T. oswaldi* is associated with more open habitats(G G Eck, 1987).

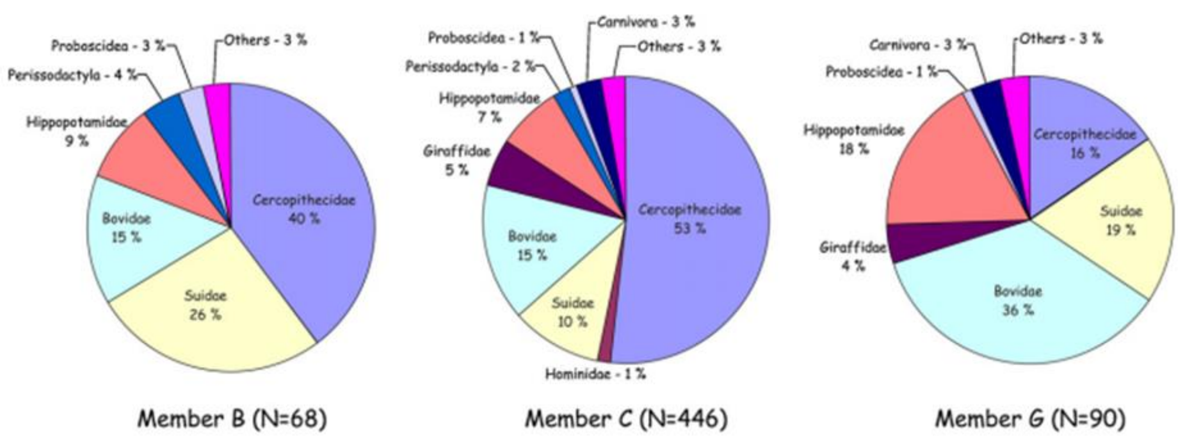


Figure 2. 2006–2007 specimen distribution by higher rank taxa in Members B, C, and G. Source: (Boisserie et al., 2008).

1.6 Anatomy of the Humerus

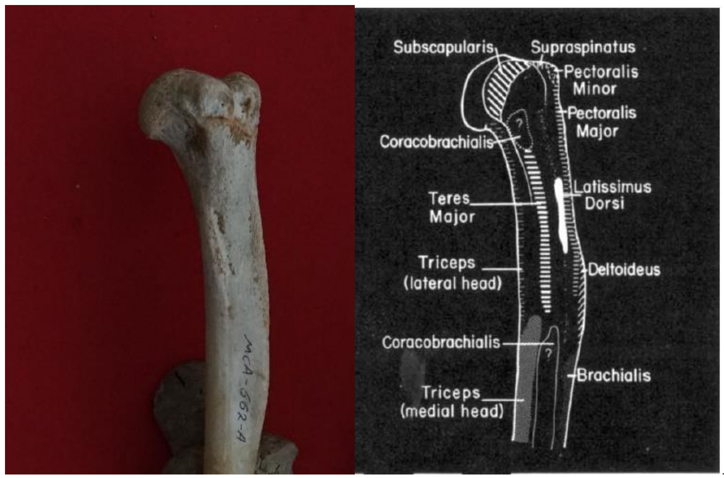
Musculoskeletal system is one of the important systems in primate locomotor behavior. The proximal part of humerus is the component of glenohumeral joint. The anatomy of the proximal part shows two structures that determine functionality : the articular surface of the humerus, and the major and minor tubercles, which serve the origin and insertion site of Several muscles that are involved in producing abduction , adduction, flexion, extension, lateral and medial rotation of shoulder, one of the key muscles group is the rotator cuff (Arias-Martorell et al., 2015), which consists of four muscles: the subscapularis, the supraspinatus, the infraspinatus and teres minor. These four muscles rotate the humerus, the infraspinatus and teres minor muscles rotate the humerus laterally while the subscapularis with the teres major rotates the humerus medial (Arias-Martorell et al., 2015; Ashton & Oxnard, 1964).

Furthermore electromyography studies of the primate muscle describes four distinct but interrelated groups of muscles. The first group contain muscle that pass from the trunk to the humerus and retract the forelimb. Muscle that work in this group consist pectoralis major, pectoralis minor, pectoralis abdominalis and latissimus dorsi muscle closely associated with muscle terse major. The second, third and fourth groups includes muscles that raise the forelimb, stabilize the shoulder joint and shoulder gridle (Fig , 3).

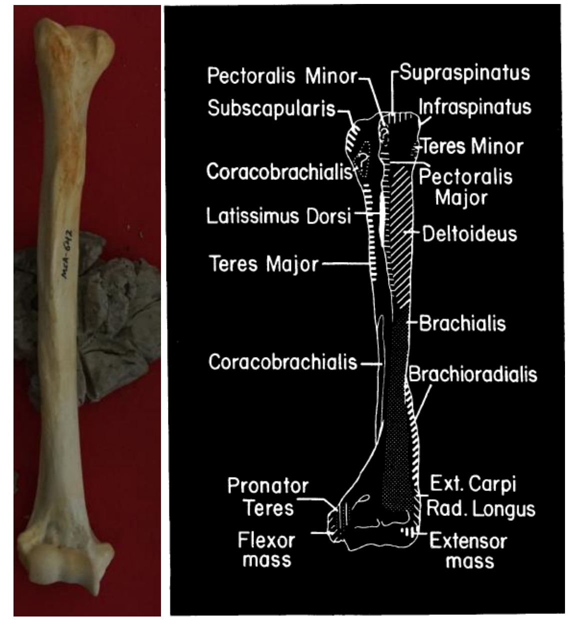
Table 2. **Morphological characterstics on the proximal humerus are described for their appearance in *Theropithecus brumpti*.**

Morphological characters of Proximal Humerus				
Characters	Function	Behaviour		References
		Arboreal	Terrestrial	
Shape and size of the greater tubercle	Attachment site for the rottater cuffe muscle (subscapularis, supraspinatus, infraspinatus and teres minor). They support stability around the glenohumeral joint by providing skeletal support.	Small greater tubercle lie below humeral head.	Large ,anteriorly placed and proximally extended greater tubercle.	Savage,1957;Napier& Davis,1959;Jolly, 1967; Fleagle & Simons, 1982; Krenze 1993
Insertion of muscle supraspinatus, in the proximal surface of the greater tubercle.	Stabilizes the shoulder joint, Protractor or flexor of humerus, elevator of forearm against gravity.	Well defined insertion on the superior greater tuberosity.	Not marked insertion on the superior greater tuberosity.	Larson & Stern, 1989; Fleagle & Simons, 1982 ; Ciochon, 1986
Insertion of muscle infraspinatuntus on the later suface of greater tubercle.	Stabilizes the shoulder joint, and lateral rotator of the humerus.	Have large infraspinatus muscle. On the lateral surface of the greater tubercle a deep concave shape are formed.	Relatively small infraspinatus muscle. No preservation of deep concavity on the lateral surface of greater tubercle.	Maire, 1972; Fleagle & Simons, 1982 ; Krenze 1993; Jablonski, 2002,2008 .

Insertion of muscle teres minor inferior to greater tubercle	Lateral rotator of humerus	Longitudinal depression show on the lateral surface of greater tubercle. Have large teres minor muscle	No longitudinal depression. Relatively small teres minor muscle .	Maire, 1972; Fleagle & Simons, 1982 ; Krenze 1993; Jablonski, 2002,2008 .
Insertion of muscle coracobrachialis profundus inferior to the lesser tubercle.	Medial rotator of the humerus.	Depression can be seen inferior to the lesser tubercle.	No depression	Ashton & Oxnard, 1963; Maire, 1972; Krenze 1993
width and shape of intertubercular or bicipital groove.	keep the tendon of biceps brachii	Narrow and deep intertubercular or bicipital groove.	Wide and superficial intertubercular or bicipital groove.	Ashton & Oxnard, 1963; Fleagle & Simons, 1982; Krenze 1993



A



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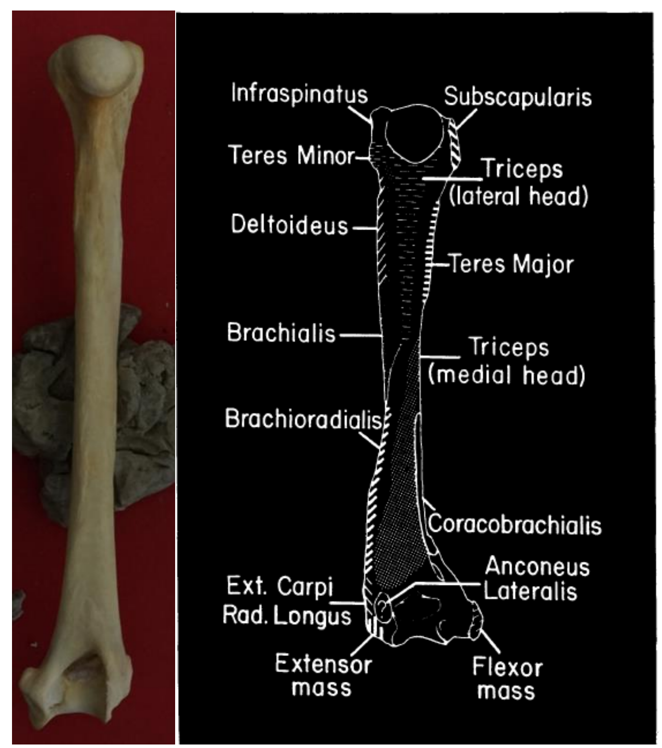


C

Figure 3. A, Medial View, B, Anterior view and C, Posterior view of the humerus of Theropithecus gelada and Aegptopithecus Zeuxis with schematic reconstruction of the muscle attachments area based on preserved scars, (Fleagle & Simons, 1982) T. gelada pictures from OMO Group research expedition.

1.7 Material and Method

All *Theropithecus* fossil used in this analysis were recovered from Plio- Pleistocen deposits of the Shungura Formation in the Omo, Ethiopia. This analysis relies on two types of data collected from humeri: linear measurements and qualitative assessment of morphological features. These data were collected from 10 *Theropithecus* humeri from the Shungura Formation in the Omo, Ethiopia and one *Theropithecus* from Olduvai Tanzania (Table 3). For the taxonomy of specimens that are not associated with craniodental material , we use hypothesis used by earlier studies (Eric Delson, 1993; Krentz, 1993a).

1.8 Data collection

The description of forelimb of *T. brumti* and its comparison with extant *papionins* following standard paleontological visual observation and anatomical diagnosis is done by following E Delson et al., 1993; Fleagle & Simons, 1982; Guthrie, 2011; N G Jablonski et al., 2008; Nina G. Jablonski et al., 2002; Jolly & CJ, 1972 with additional observation. This observation helps to develop qualitative studies together with non-metric assessment of functional morphology and linear measurement. Linear Measurement (table 4 and 5) were taken with MeshLab 2020.12-windows on the fossil specimen and entered directly into a Microsoft Excel and SPSS.

Humeri from modern taxa were also included in this analysis. Modern *papionins* specimens for comparison included 15 from HoBiS, 3D collection of the Musee de L'Homme (A. Perrier & G. Berillon). Additionally, morphological features were assessed from photographs of 17 total modern *Theropithcus gelada*, *12 M_fascicularis,* 14*M_mulatta , 5 M_nemestrina* , 4 M nigra , 3 *M_radiata* , 4 *M_sinica* , 5 *M_sylvanus* , 1 *M_thibetana* , 5 *M_leucophaeus* , 6 *M_sphinx , 8 P_anubis* , 3 *P_cynocephalus* , 11 *P_hamadryas* , 4 *P_papio* , 1 *P_ursinus, which* are part of the collection at the National Museum of Ethiopia, Addis Ababa, MNHN Paris and *Zurich Anthropological Institute.*

Table 3. **Theropithecus specimens included in this analysis from the Shungura Formation of the Omo.**

Shungura Formation Member	Estimated Geological Age Range1	Specimen Numbers	Anatomical[a] element	Side	Period	Species	Museum[b]	Reference
Member G lower	2.33 – 1.90 Ma	OMO75n_7_c 205	PH	Left	Pleistocene	*Theropithecus oswaldi*	ARCCH	(Delson et al., 1993)
Member E	2.40 - 2.36 Ma	L178_6	PH	Right	Pleistocene	*Theropithecus oswaldi*	ARCCH	(Delson et al., 1993)
Member C	2.85 - 2.52Ma	L 70 _7	CH	Left	Plio-Pleistocene	*Theropithecus brumpti*	ARCCH	(Delson et al., 1993)
		L 899 _ 1	PH	Left	Plio-Pleistocene	*Theropithecus brumpti*	ARCCH	(Delson et al., 1993)
		OMO 18 _ 1968 – 2281	PH	Left	Plio-Pleistocene	*Theropithecus brumpti*	ARCCH	(Delson et al., 1993)
		L30_100001	PH	Left	Plio-Pleistocene	*Theropithecus brumpti*	ARCCH	(Delson et al., 1993)
Member B	3.36 - 2.85Ma	L336_2	PH	Left	Plio-Pleistocene	*Theropithecus brumpti*	ARCCH	(Delson et al., 1993)
		OMOVE3_10006	PH	Left	Plio-Pleistocene	*Theropithecus brumpti*	ARCCH	(Delson et al., 1993)
		OMO755_69_461	PH	Right	Plio-Pleistocene	*Theropithecus oswaldi*	ARCCH	(Delson et al., 1993)
		OMO 75N _71 _688	PH	Right	Plio-Pleistocene	*Theropithecus oswaldi*	ARCCH	(Delson et al., 1993)
Olduvai		MCK II 67_500	CH	Left	Pleistocene	*Theropithecus oswaldi*	Tanzania	(Delson et al., 1993)

[a]PH : proximal humerus CH : complete humerus

[b]ARCCH   authority for conservation of cultural heritage

[1]Geological age ranges are from (Heinzelin, 1983)

1.9 Description of Measurements and Statistical Methods

Eleven linear measurements are taken from the literature. Table 4 and 5 gives the description of each measurement (fig 4).

Table 5, gives a description of five simple ratios to reflect shape the functional length over which muscle work, in addition to reduce the effects of differences in proportions among individual and species. These indices are either standard postcranial indices or thought to have functional significance to this analysis(E Delson et al., 1993; Fleagle & Simons, 1982; Guthrie, 2011; N G Jablonski et al., 2008; Nina G. Jablonski et al., 2002; Jolly & CJ, 1972) Furthermore some indices, will take from literatures based on their significancy.

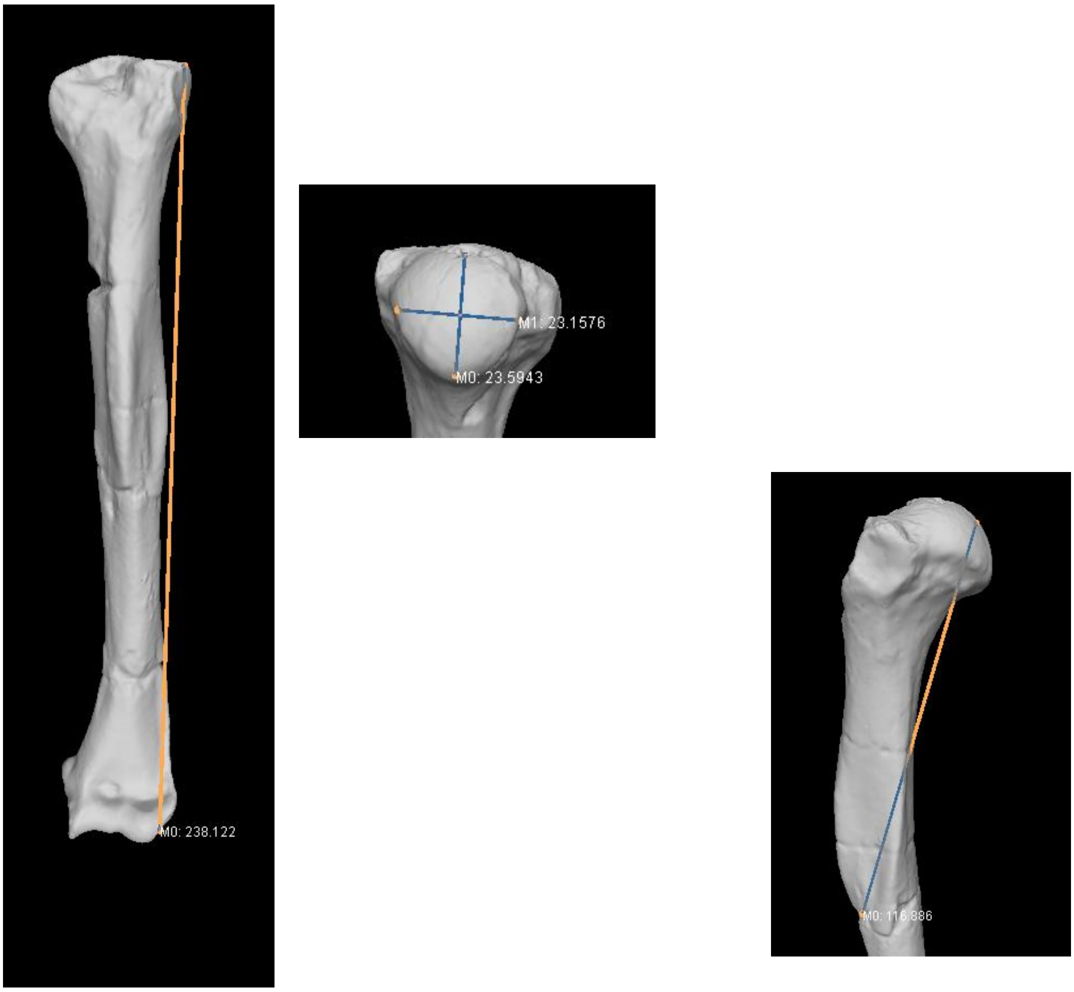


Figure 4.   Main measurement drawing on 3D surface model.

1.10 Measurements:

Table 4. **Humerus measurements:**

Measurement	Description	Reference
Humerus length 1	Head-Capitulum	Fleagle & Simons, 1982;Ciochon, 1993 ; Elton, 2002
Humerus length 2	Greater tuberosity-capitulum	Fleagle & Simons, 1982;Ciochon, 1993 ; Elton, 2002
Humeral length 3	Distal extension of deltoid tuberosity(V) to humeral head	Fleagle & Simons, 1982;Guthrie, 2011
Bituberosity width	Greater tuberosity to lesser tuberosity	Fleagle & Simons, 1982;Ciochon, 1993 ; Elton, 2002
Anteroposterior head diameter	Maximum diameter of the humeral head in the anteroposterior plane	Fleagle & Simons, 1982;Ciochon, 1993 ; Elton, 2002
Mediolateral head diameter	Maximum diameter of the humeral head in the medio lateral plane.	Fleagle & Simons, 1982;Ciochon, 1993 ; Elton, 2002
Bicipital groove width	Minimum width of the bicipital groove at its center	Fleagle & Simons, 1982;Ciochon, 1993 ; Elton, 2002
Bicipital groove depth	Maximum width of the bicipital groove at its center	Fleagle & Simons, 1982;Ciochon, 1993 ; Elton, 2002
Greater tubercle maximum width	Maximum anteroposterior width of the greater tubercle	Fleagle & Simons, 1982;Ciochon, 1993 ; Elton, 2002
Lesser Tubercle maximum width	Maximum anteroposterior width of the lesser tubercle	Fleagle & Simons, 1982;Ciochon, 1993 ; Elton, 2002
Biepicondylar width	Maximum width across the distal humerus between the epicondyles	Fleagle & Simons, 1982;Ciochon, 1993 ; Elton, 2002

Table 5. **Proximal humerus indices used in the study**

Humerus		Reference
Humeral head shape	Humeral Head Width/Length*100	Fleagle & Simons, 1982; Elton, 2002; Guthrie, 2011
Biciptal Groove width	Biciptal Groove Width*100/Mediolateral Head Diameter	Fleagle & Simons, 1982; Elton, 2002;
Graeter tubercle size	Greater Tubercle Maximum Width*100/Anteroposterior Head Diameter	Fleagle & Simons, 1982; Elton, 2002;
Leaser tubercle size	Lesser tubercle maximum width* 100/Anteroposterior Head Diameter	Fleagle & Simons, 1982; Elton, 2002;
Delto- pectoral crest length	Humeral length 3/Maximum Humeral Length *100	Fleagle & Simons, 1982;Guthrie, 2011

Chapter 3

3. Comparative morphological description of the fossil specimens

1.11 Description of Fossils *Theropithecus brumpti*

L 70 -7 (*T. brumpti*), which is approximately a complete humerus except some crushing and depression around the anterior surface of the head, medial and lateral lip of intertubercular grooves (fig 5). The anterior and medial borders of the greater and lesser tuberosity are eroded away. Nevertheless the morphology of the tuberosities and associated crests is still informative. Moreover in the medial border, anterior surface and the lateral supracondylar rig of the shaft there is present depression and crack due to crush.

The head of the humerus in L 70 -7 is relatively narrow. The maximum linear head length in L70-7 is 24.4 mm and the maximum estimated width is 25.41 (Table 6). The head L70-7 humerus is to some extent elongated mediolaterally than anterioposteriorly dimension. which differs slightly from other terrestrial papionins such as *Papio anubis*. Moreover the width/ head length index of this fossil indicates that 104.13, which is similar to that seen in many extant forest arboreal (Elton 2002).

Greater tuberosity is a little crushed the ventral surface but it is clear that the greater tuberosity is not projecting above the humeral head. The greater tuberosity is approximately 14.85mm in width and the insertion of *M. supraspinatus* on its superior aspect is marked by a well-defined facet (fig. 5). A large, facet for the insertion of *M. infraspinatus* is well demarcated on the lateral surface of the tuberosity. Inferior to the greater tubercle there is a distinct and elongated depression for the insertion of muscle *teres minor*.

The lesser tuberosity lies bellow the humeral head. The attachment of *M. subscapularis* is marked on its medial surface. The anterior surface of the tuberosity a little crushed therefore it can’t forms the medial lip of the intertubercular groove.

The deltopectoral crest begins at the medial margin of the greater tuberosity, which is a continuation of the lateral lip of the intertubercular groove, is very strongly developed, and form concave shape, which is extends down the anterior surface of the shaft approximately to the midpoint (fig 5) .

A

B

C

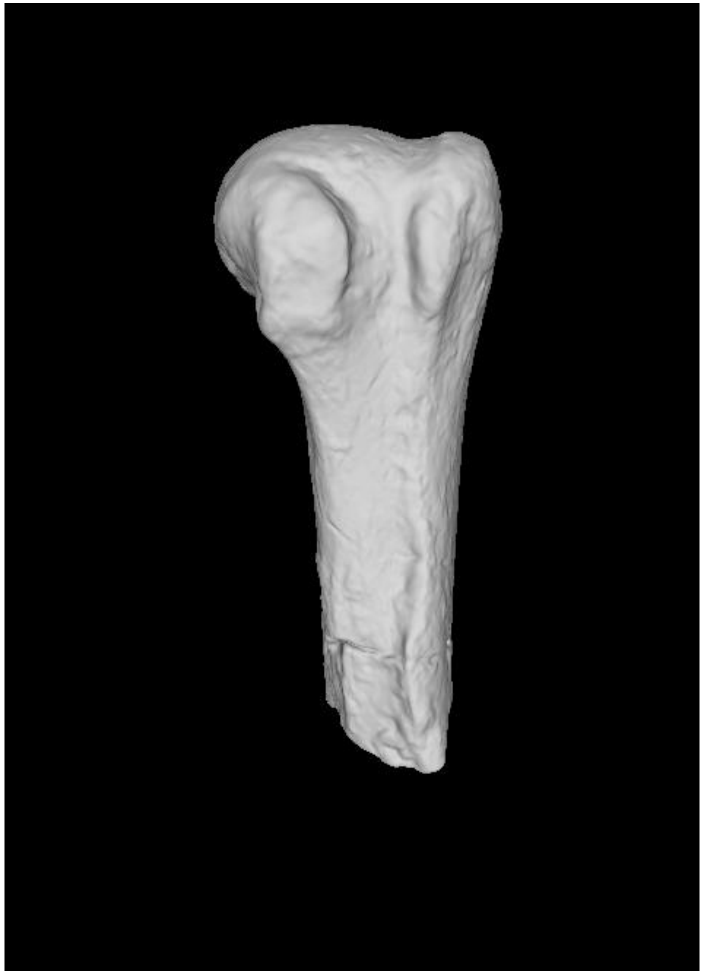
D

Figure 5. The Left humerus, L70-7 ; (A) Anterior view ; (B) posterior view; (C) Medial view; (D) lateral view.

L 899 _ 1 ; (*T. brumpti*) proximal left humerus with ½ of the shaft, greater tubercle, lesser tubercle , head and bicipital groove preserved. comparing with L70_7 the humerus head of L 899 _ 1 is relatively broad. The maximum linear head length in L 899 _ 1 is 25.77 mm and the maximum estimated width is 25.99 (Table 6). The head L 899 _ 1 humerus is to some extent elongated mediolaterally than anterioposteriorly dimension. which differs slightly from other terrestrial papionins. Additionally the humeral head shape index of this fossil directs that 100.85, which is similar to that seen in many extant forest arboreal (Elton 2002).

Greater tuberosity is a little crushed the ventral surface but it is clear that the greater tuberosity is not projecting above the humeral head. The greater tuberosity is broad, extend superiorly the level of the humeral head. The maximum width of this tuberosity is 31.30 (Table 6) and a large, facet for the insertion of *M. infraspinatus* is well demarcated on the lateral surface of the tuberosity (fig.6) , the insertion of *M. supraspinatus* on its superior aspect is marked by small facet. Inferior to the greater tubercle there is a distinct and elongated depression for the insertion of muscle *teres minor*.

The lesser tuberosity lies almost the same level to the humeral head (fig 6). The attachment of *M. subscapularis* is marked on its medial surface also this tuberosity width is about 23. 88 mm. The anterior surface of this tuberosity forms the medial lip of the intertubercular groove. The groove is narrow and deep, and remains well defined below the surgical neck.



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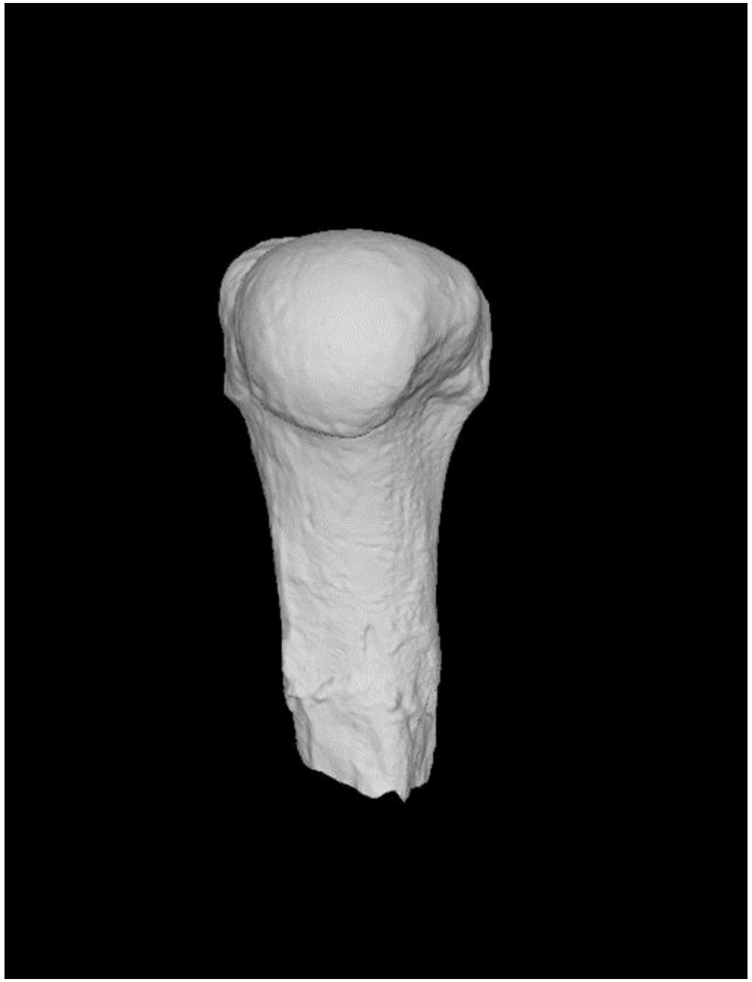

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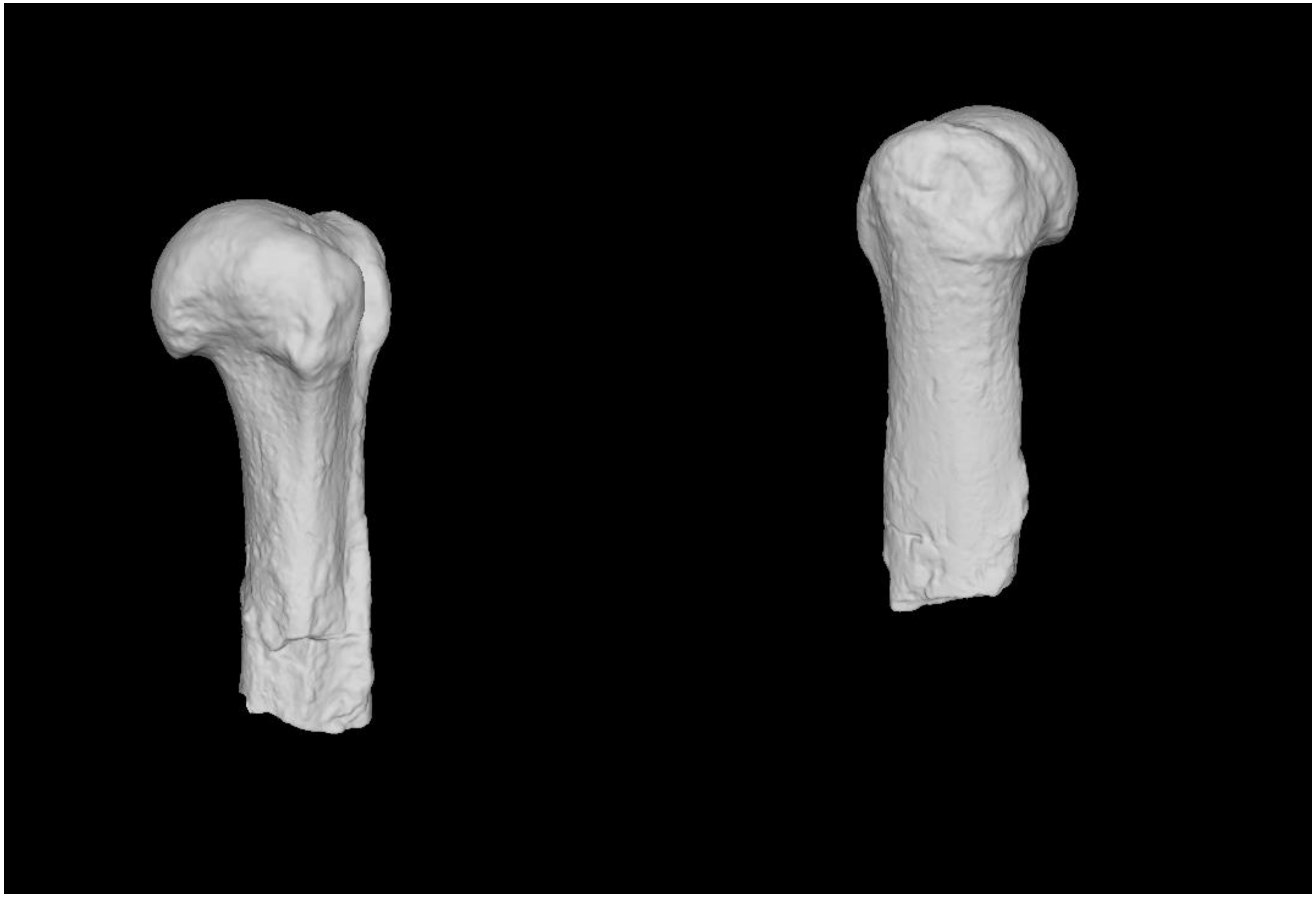


C D

Figure 6. The Left humerus, L 899 _ 1 ; (A) Anterior view ; (B) posterior view; (C) Medial view; (D) lateral view.

OMO 18 – 1968 – 2281 is *T. brumpti* left humerus, which is recovered from locality C represented by proximal fragment with 2/3 of the shaft (Table 2). This fossil exhibit all Proximal humerus characteristics of *Theropithecus brumpti* that stated in the earlier study of this species. The arrangement of the humeral tuberosities in OMO 18 – 1968 – 2281 most resembles that in living primate such as *Mandrillus.*

The greater tuberosity does not project above the level of the articular surface(fig. 7).The maximum anteroposterior width of the greater tubercle is 33.16 mm. the insertion of *M. supraspinatus* on its superior aspect is marked. A large, facet for the insertion of *M. infraspinatus* is well demarcated on the lateral surface of the tuberosity. Inferior to the greater tubercle there is a distinct and elongated depression for the insertion of muscle *teres minor*.

The maximum anteroposterior width of the lesser tubercle is 22.2 (Table 6) and the attachment of *M. subscapularis* is marked on its medial surface (fig. 7). Anteromedial surface of humerus distal to crest of lesser tubercle there is well-marked depression for the insertion of *M. coracobrachialis*. The anterior surface of the tuberosity forms the medial lip of the intertubercular groove.

The deltopectoral crest begins at the medial margin of the greater tuberosity, which is a continuation of the lateral lip of the intertubercular groove, is very strongly developed, and form concave shape, which is extends down the anterior surface of the shaft approximately to the midpoint (fig) .

The humeral head of in OMO 18 – 1968 – 2281 is narrow. The maximum linear head length is 29. 59 mm and the maximum estimated width is 31.28 (Table 6). The head OMO 18 – 1968 – 2281 humerus is elongated mediolaterally than anteroposterior dimension.

A

B

C

D

Figure 7. The left humerus, OMO 18 – 1968 – 2281 (A) Anterior view ; (B) posterior view; (C) Medial view; (D) lateral view.

L 336-2 (*T. brumpti*) (Fig. 8) a proximal left humerus with some part of the shaft, greater tubercle, lesser tubercle , head and bicipital groove preserved. The greater tuberosity is broad, and almost the same level of the humeral head. On the lateral surface of the greater tuberosity, a large and deep facet for the insertion of *M. infraspinatus* is well demarcated. the insertion of *M. supraspinatus* on its superior aspect is marked by two facets on the anterior and posterior surface (fig 8). Anteriorly , greater tuberosity well preserved that forms the proximal end of the lateral lip of the intertubercular groove.The maximum anteroposterior width of the greater tubercle is 25.21 mm (Table 6).

The maximum anteroposterior width of the lesser tubercle is 20.52 mm and the attachment of *M. subscapularis* is marked on its medial surface. The anterior surface of the tuberosity forms the medial lip of the intertubercular groove

The humeral head of in L 336-2 is narrow. The maximum linear head length is 27.57 mm and the maximum estimated width is 24.68 (Table 6). The head L 336-2 humerus is elongated mediolaterally with well-developed anatomical neck of humeral head.

A B

C D

Figure 8. The Left humerus, L 336-2 ; (A) Anterior view ; (B) posterior view; (C) Medial view; (D) lateral view.

L30-100001 is *T. brumpti* left humerus, which is represented by proximal fragment with 2/3 of the shaft. This fossil display similar morphology like OMO 18 – 1968 – 228. The arrangement of the humeral tuberosities and shaft is most resembles that in living primate such as *Mandrillus.*

The greater tuberosity does not project above the level of the articular surface(fig. 9).The maximum anteroposterior width of the greater tubercle is 22.08 mm. the insertion of *M. supraspinatus* on its superior aspect is marked with small facete. A large, facet for the insertion of *M. infraspinatus* is well demarcated on the lateral surface of the tuberosity. Inferior to the greater tubercle there is a distinct and elongated depression for the insertion of muscle *teres minor*.

The maximum anteroposterior width of the lesser tubercle is 15.9 and the attachment of *M. subscapularis* is marked on its medial surface. Anteromedial surface of humerus distal to crest of lesser tubercle there is well-marked depression for the insertion of *M. coracobrachialis*(fig. 9). The anterior surface of the tuberosity forms the medial lip of the intertubercular groove.

The deltopectoral crest begins at the medial margin of the greater tuberosity, which is a continuation of the lateral lip of the intertubercular groove, is very strongly developed, and form concave shape, which is extends down the anterior surface of the shaft approximately to the midpoint (fig) .

The humeral head of in L30-100001 is narrow. The maximum linear head length is 21. 57 mm and the maximum estimated width is 24.24 (Table 6). The humerus head of L30-100001 is oriented mediolaterally like OMO 18 – 1968 – 2281.

A B

Figure 9. The Left humerus, OMO 18 – 1968 – 2281 ; (A) Anterior view ; (B) posterior view; (C) Medial view; (D) lateral view.

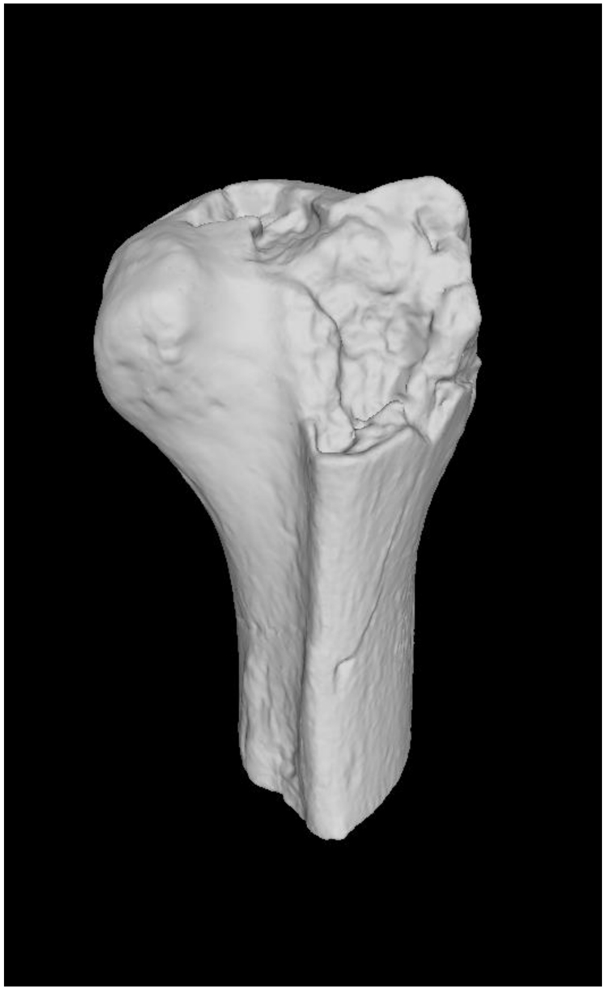
OMO VE3-10006 (*T. brumpti*), is a proximal left humerus. The anterior surface of the greater tubercle is eroded away and depression around the anterior surface of the head (fig.10). this taphonomy affect the morphology of lateral lip of intertubercular groove and superior part of the shaft.

The head of the humerus in OMO VE3-10006 is relatively narrow. The maximum linear head length in OMO VE3-10006 is 36.63 mm and the maximum estimated width is 38.61 (Table 6).The humeral head OMO VE3-10006 is to some extent elongated mediolaterally than anterioposteriorly dimension.

Greater tuberosity is a little crushed the ventral surface but it is clear that the greater tuberosity is not projecting above the humeral head. The greater tuberosity is approximately 14.85mm in width and the insertion of *M. supraspinatus* on its superior aspect is marked by a well-defined facet. A large, facet for the insertion of *M. infraspinatus* is well demarcated on the lateral surface of the tuberosity. Inferior to the greater tubercle there is a distinct and elongated depression for the insertion of muscle *teres minor*.

The lesser tuberosity lies bellow the humeral head. The attachment of *M. subscapularis* is marked on its medial surface. The anterior surface of the tuberosity a little crushed therefore it can't forms the medial lip of the intertubercular groove.

The deltopectoral crest begins at the medial margin of the greater tuberosity, which is a continuation of the lateral lip of the intertubercular groove, is very strongly developed, and form concave shape, which is extends down the anterior surface of the shaft approximately to the midpoint (fig. 10) .



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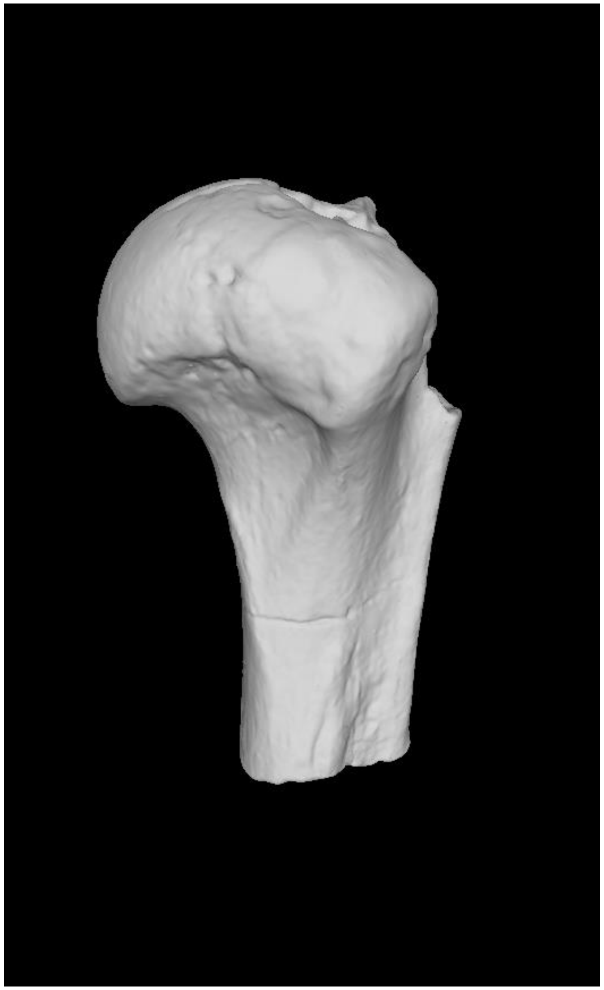
B



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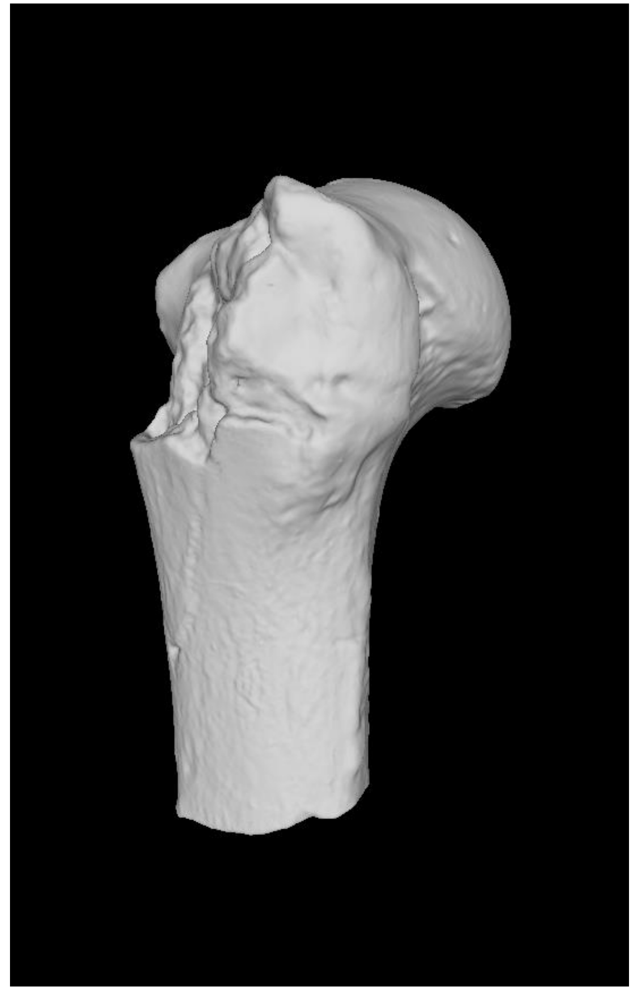


D

Figure 10. The Left humerus, OMO VE3-10006; (A) Anterior view ; (B) posterior view; (C) Medial view; (D) lateral view.

1.12 Main morphological traits of *Theropithecus brumpti*

Theropithcus brumpti proximal humerus varies on a number of characters ; greater tubercle lies below the level of the head, nearly equal size of lesser and greater tubercles, deep insertion site for *M. infraspinatus,* inferior to the greater tubercle insertion for *M. teres minor* is marked , insertion of *M. coracobrachialis* is well marked inferior to lesser tubercle, and having a concave deltoid pectoral crest morphological pattern that has functional importance in quadrupedal locomotion. A more detailed description of these characters are provided in this study for the understanding of the postural and locomotor behaviour of this species. Many of the detailed characters are listed in pages 19 to 37.

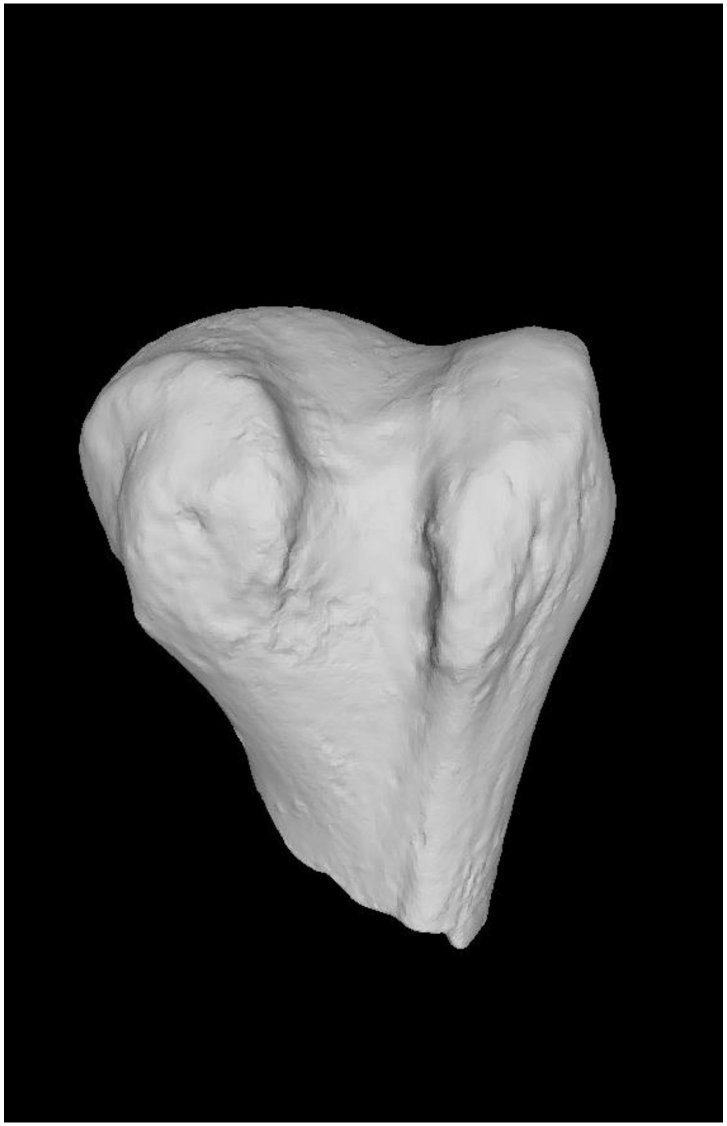
1.13 Description of Fossils *Theropithecus oswaldi*

OMO75n-7-c 205 (*T. oswaldi*), is a proximal left humerus. Inferior to lesser tubercle there is a depression, but this is not biologically relevant in this study.

OMO75n-7-c 205 (*T. oswaldi*) (fig. 11) proximal left humerus with ¼ of the shaft, greater tubercle, lesser tubercle , head and bicipital groove preserved. The greater tuberosity is broad, 26.17 mm which, extend superiorly the level of the humeral head. A large, facet for the insertion of *M. infraspinatus* is demarcated on the lateral surface of the tuberosity, the insertion of *M. supraspinatus* on its superior aspect is marked by small superficial facet. Anteriorly , greater tuberosity well preserved that forms the proximal end of the lateral lip of the intertubercular groove.

The humerus head of OMO75n-7-c 205 is wide. The maximum linear head length is 23.22 mm and the maximum estimated width is 24.36 mm (Table 7). The humeral head OMO75n-7-c 205 is to some extent elongated anteroposterior than mediolaterally.

The lesser tuberosity lies above the humeral head. The maximum anteroposterior width of the lesser tubercle is 18 mm. The attachment of *M. subscapularis* is marked on its medial surface. The anterior surface of the tuberosity forms the medial lip of the intertubercular groove. The groove is wide and shallow, and remains well defined below the surgical neck.



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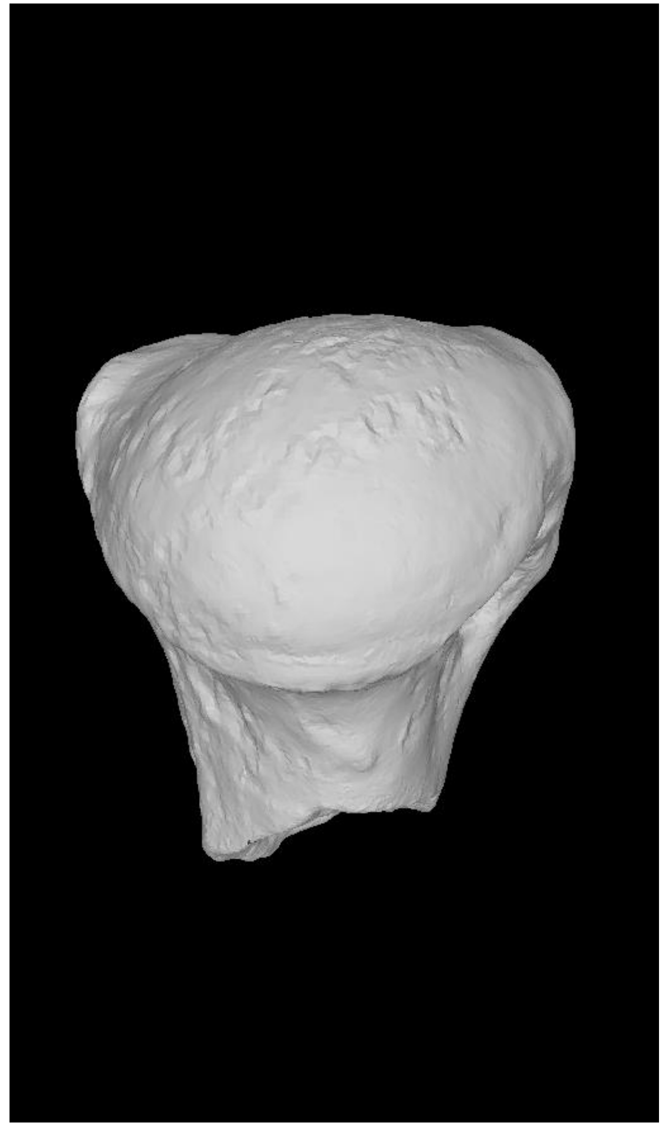

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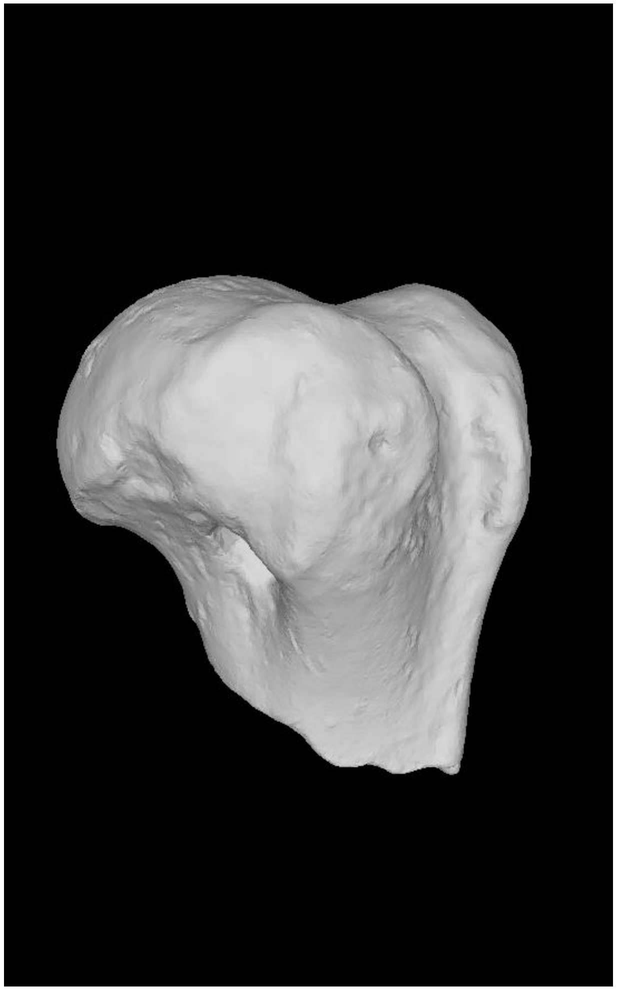

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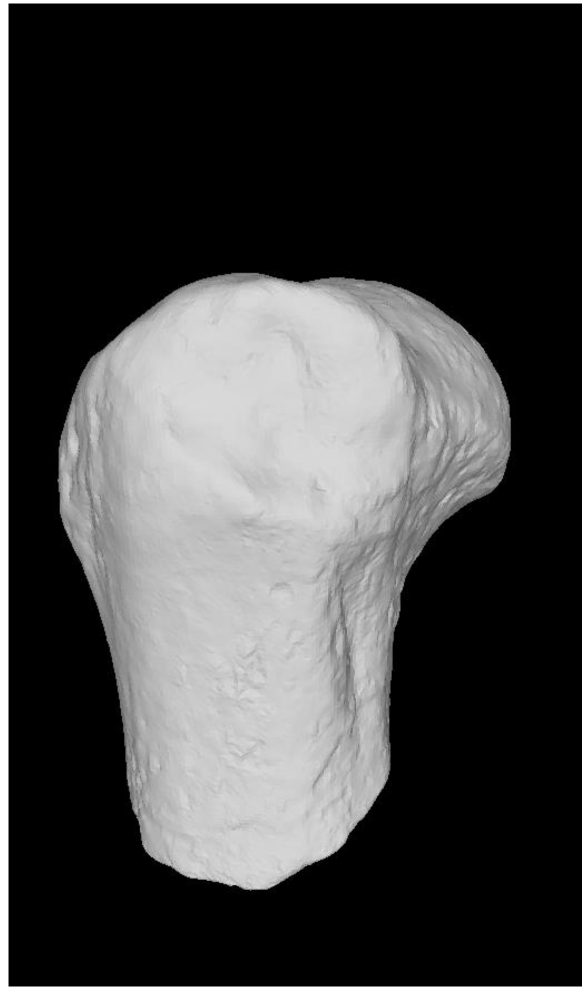


D

Figure 11. The Left humerus, OMO75n-7-c 205; (A) Anterior view ; (B) posterior view; (C) Medial view; (D) lateral view.

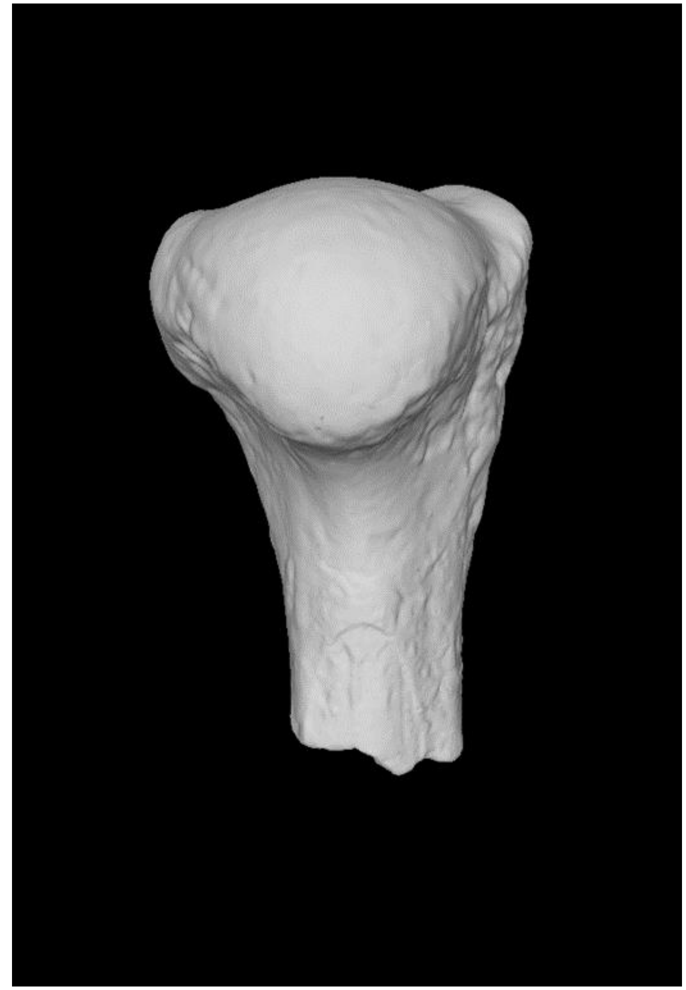
L 178-6 is *T. oswaldi* rigth humerus, which is recovered from locality E represented by proximal fragment with 1/3 of the shaft. The humeral head of in L 178-6 is relatively narrow compared with other *T. oswaldi* species. The maximum linear head length is 22.68 mm and the maximum estimated width is 26.38mm (Table 7). The head L178-6 humerus is elongated mediolaterally than anteroposterior dimension.

The greater tuberosity is proximally project above the level of humeral head (fig.12). The maximum anteroposterior width of the greater tubercle is 23.46 mm. The insertion of *M. supraspinatus* on its superior aspect is marked with small facet. The lateral surface of the tuberosity have a facet for the insertion of *M. infraspinatus*. The greater tubercles have small rugosities for the insertion of muscle *teres minor*.

The maximum anteroposterior width of the lesser tubercle is 18.39 mm and the attachment of *M. subscapularis* is marked on its anteromedial surface. The lesser tubercle of L 178-6 is posteriorly placed. The insertion of *M. coracobrachialis* is missing. The anterior surface of the tuberosity forms the medial lip of the intertubercular groove.

Like other terrestrial monkeys L 178-6 have a wide bicipital groove, which is formed by small size of the lesser tubercle. Widest groove associated with high indices are found in terrestrial monkeys. Correspondingly L 178-6 have wide groove with 24.9 mm bicipital groove which is indication of terrestrial habits.

A



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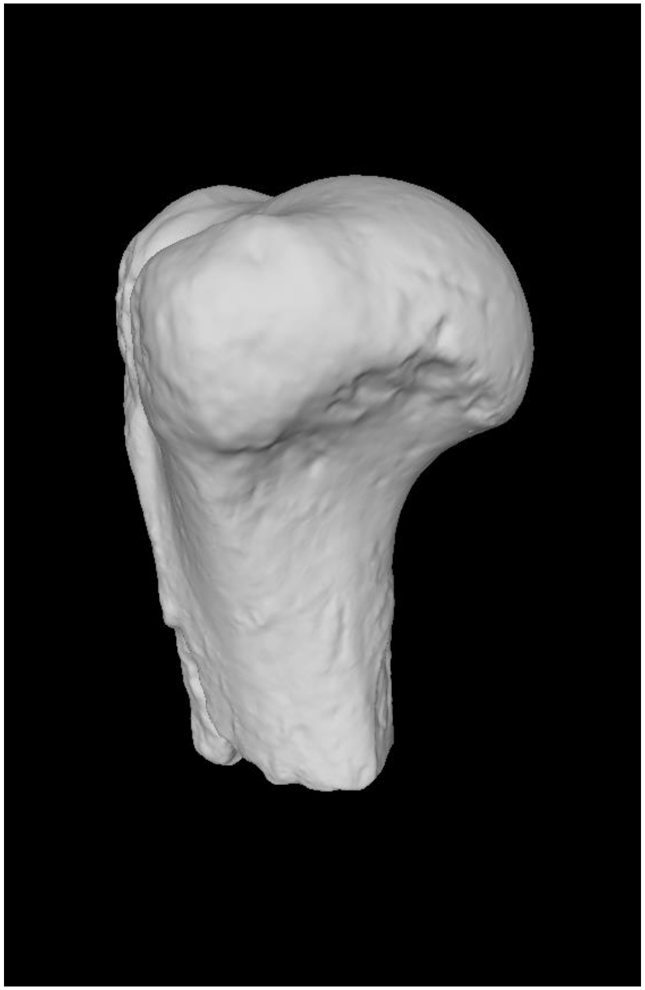

C

D

Figure 12. The right humerus, L178-6 (A) Anterior view ; (B) posterior view; (C) Medial view; (D) lateral view.

OMO_755_69_461(*T. oswaldi)* is a partial right humerus, preserving the proximal half of the shaft, although there is considerable damage, in the anteriomedian side of the greeter tubercle. It is morphologically distinct from other *T. oswaldi* specimen included in this study.

The lesser tubercle is short, small, and projects posteriorly. The anterior projection of lesser tubercle for the medial lip of inter tubercular groove. There is a triangular structure between the crest of the lesser tubercle and the crest of the grater tubercle.

The greater tuberosity is broad 24.52 mm, extend superiorly the level of the humeral head. A large, facet for the insertion of *M. infraspinatus* is well demarcated on the lateral surface of the tuberosity, the insertion of *M. supraspinatus* on its superior aspect also represent by small facet. Anteriorly , greater tuberosity is well preserved that forms the proximal end of the lateral lip of the intertubercular groove (fig 13).

The humeral head shape of OMO_755_69_461 is broad . The maximum linear head length is 28.01 mm and the maximum estimated width is 23.65 (Table 7).

Figure 13. The left humerus, OMO_755_69_461 (A) Anterior view ; (B) posterior view; (C) Medial view; (D) lateral view.

1.14 Main morphological traits of *Theropithecus oswaldi*

Theropithcus oswaldi proximal humerus distinguish from *Theropithcus brumpti* by a number of characters ; greater tubercle lies proximally the level of the humeral head, nearly small size of lesser tubercles, wide bicipital groove , insertion site for *M. infraspinatus* is not well marked like *T. brumpti ,* wide humeral head and straight deltoid pectoral crest a more detailed description of these characters provided in this study in pages 39 to 46 that have functional importance in quadrupedal locomotion and postural of this species.

Chapter 4

4. Comparative metric analysis

The shape and orientation of humeral head reflect locomotion in quadrupedal primates; arboreal cercopithecines having long humeral head in the anteroposterior direction than terrestrial cercopithecines ((Elton, 2002; Guthrie, 2011). Furthermore morphology of humeral head indicates habitat use, for instance open terrestrial species having elliptical humeral head. on the other hand forest arboreal and open mixed species having round humeral head (Elton, 2002).

The humeral head shape of *Theropithecus brumpti* index in table 6 and figure 14 indicate that *T. brumpti* is intermediate between forest arboreal and open mixed species those are identified by (Elton, 2002). Furthermore *Theropithecus oswaldi* fossils index in table 7 and figure 14 indicate that there is variation of humeral head shape morphology within the same species , which shows that *T. oswaldi* is intermediate between terrestrial and open mixed arboreal forms.

The rotator cuff muscles , which originated from the scapular fossa and attached at the greater and lesser tuberosity of the proximal humerus contribute stability and movement around the glenohumeral (Krentz, 1993a; Schmitt, 1994). Different in size and shape of the greater and lesser tuberosity reflects the function and importance of rotator cuff muscles during protraction and retraction of humerus in related to there locomotion and postural behaviors (Guthrie, 2011; Krentz, 1993b; Susan G Larson & Stern, 1987; Susan G Larson & Stern Jr, 1986; Savage, 1957).

Within considerable variation the size and shape of the grater tubercle have been related to terrestrial and arboreal quadrupedal locomotion (Fleagle & Simons, 1982). Proximal prolongation of greater tuberosity has associated with terrestrial quadrupedalism (Savage, 1957). In contrast arboreal monkey grater tubercle lies below the level of humeral head (Jolly & CJ, 1972).

The difference in greater tubercle size between *T. brumpti* and *T. oswaldi* indicated in table six, seven and figure sixteen presented that *Theropithecus brumpti* grater tubercle lies below the level of humeral head is represented by lower index 41.35 to 91.43. this data is supported previous study conducted by (Krentz, 1993a).

In contrast *Theropithecus oswaldi* have a greater tubercle that rise above the head indicating by high index that lies between 72.21 to 112.7. The exact role of this tuberosity associated with functional locomotion is well documented in table two.

Besides the high of greater tubercle the two muscle (*infraspinatus and ters minor*) that are associated with this tuberosity shows functionally and anatomically important in related to arboreal and terrestrial locomotion. The presence of a deep concave shape on the lateral surface of greater tubercle reflected the existence of large infraspinatus muscle to improve flexibility in Arboreal primates (table 2). However terrestrial primates companies a small infraspinatus muscle.

Arboreal species have a large teres minor muscle, which is important for lateral rotation of the humerus. The presence of large teres minor muscle is reflated on the proximal humerus by forming longitudinal depression (Krentz, 1993a). In general arboreal primates have large rotator cuff muscle than terrestrial one.

Inferior to the lesser tubercle there is a deep place for the insertion of *M. coracobrachialis,* which is indication of the presence of large rotator cuff muscles in arboreal primate but not terrestrial (Maier, 1972) . This difference is indicated in our metric data see table six, seven and figure fourteen and sixteen.

The shape of bicipital groove determine variations between locomotor groups. The anterior extension of the greater and lesser tuberosities determine the width of bicipital groove and muscles that inserted in this groove. Narrow groove is useful during wide range of movement like circumduction around shoulder joint (Fleagle & Simons, 1982; Krentz, 1993b). on the contrary wide bicipital groove is observed in terrestrial primates, it specifies lack of structural specialization for suspensory postures (Fleagle & Simons, 1982; Guthrie, 2011; Krentz, 1993).

Theropithecus oswaldi have a wide bicipital groove indices 29.93 (table 7) is similar to terrestrial species reported by Krentz, 1993, which includes *Papio* (29.8) and *Cercocebus*. However *Theropithecus brumpti* have low indices 14.15 (table 6)which indicates this species have a narrow bicipital groove width, which is advantageous for circumduction around shoulder joint like suspensory and brachiating primates.

Table 6. ***Theropithecus brumpti* Humerus measurement and Indices.**

	Theropithecus brumpti					
Humerus measurement / Cat. No.	L 70 -7	L 899 – 1	OMO 18 – 1968 – 2281	L 336-2	L30-100001	OMO VE3-10006
Humerus length 1	235.86					
Humerus length 2	238.36					
Humeral length 3	119.06	99.4	114.05		88.36	
Bituberosity width		15.42	18.39	13.21	20.82	
Anteroposterior head diameter	24.4	25.77	29.59	27.57	21.57	36.63
Mediolateral head diameter	25.41	25.99	31.28	24.68	24.24	38.61
Bicipital groove width		3.68	5.8	4.44	5.36	6.21
Bicipital groove depth		10.87	7.63	7.96	9.1	11.35
Greater tubercle maximum width	14.85	31.35	33.16	25.21	22.08	15.15
Lesser Tubercle maximum width	14.73	23.88	22.2	20.52	15.09	18.29
Indices of the humeri of *Theropithecus brumpti*						
Humeral head shape	104.13	100.85	105.71	89.51	112.37	105.4
Biciptal Groove width		14.15	18.54	17.99	22.11	16.08
Graeter tubercle size	60.86	121.65	112.06	91.43	102.36	41.35
Leaser tubercle size	60.36	92.66	75.02	74.42	69.95	49.93
Delto- pectoral crest length	49.94					

Table 7. ***Theropithecus oswaldi* Humerus measurement and Indices.**

Humerus measurement / Cat. No.	*Theropithecus oswaldi* OMO 75 N - 7- C 205	L 178-6	OMO 75N _71 _688	OMO_755_69_ 461	Olduvai 67- 500
Humerus length 1					256.32
Humerus length 2					268.86
Humeral length 3					138.09
Bituberosity width	16.64	15.08	15.07	19.72	29.6
Anteroposterior head diameter	23.22	22.68	26.91	28.01	44.48
Mediolateral head diameter	24.36	26.38	29.83	23.65	39.19
Bicipital groove width	6.49	6.57	8.93		11.47
Bicipital groove depth	8.64	9.52	11.4	4.94	6.45
Greater tubercle maximum width	26.17	23.46	28.47	24.52	32.12
Lesser Tubercle maximum width	18	18.89	18.02	16.95	23.31
Indices of the humeri of *Theropithecus oswaldi*					
Humeral head shape	104.9	116.31	110.85	84.43	88.1
Biciptal Groove width	26.64	24.9	29.93		29.26
Graeter tubercle size	112.7	103.43	105.79	87.54	72.21
Leaser tubercle size	77.51	83.28	66.96	60.51	52.4

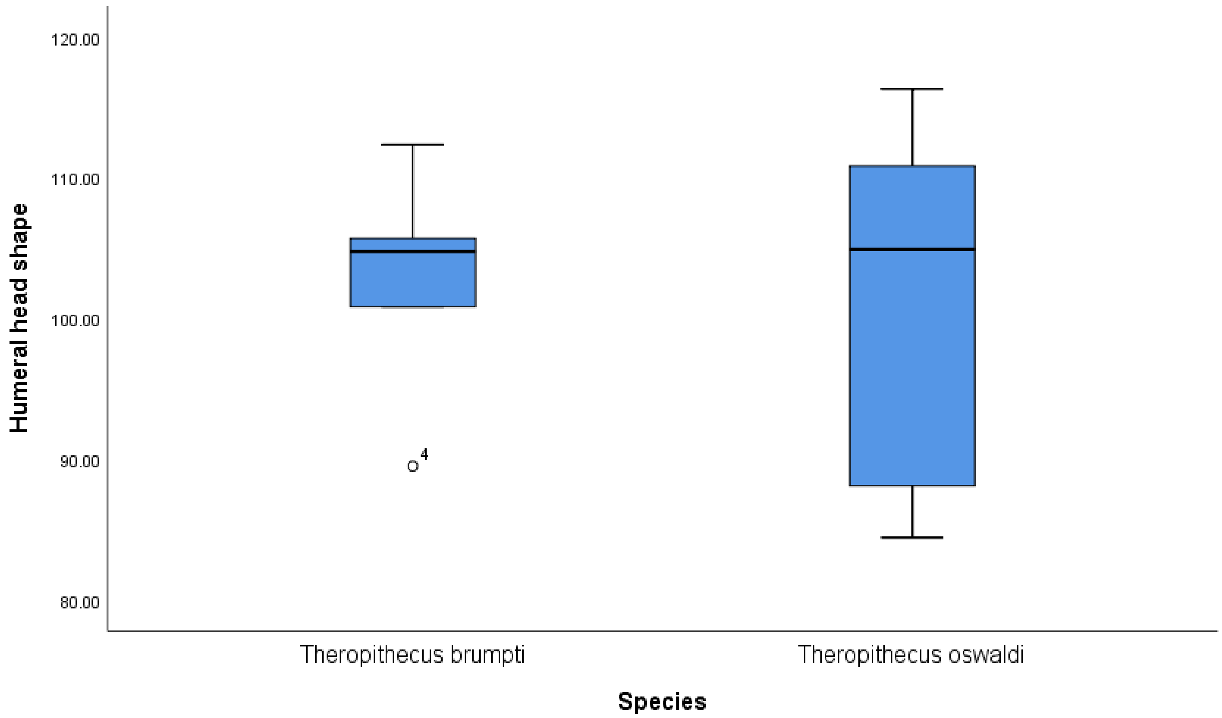

Figure 14. Humeral head shape index 1.

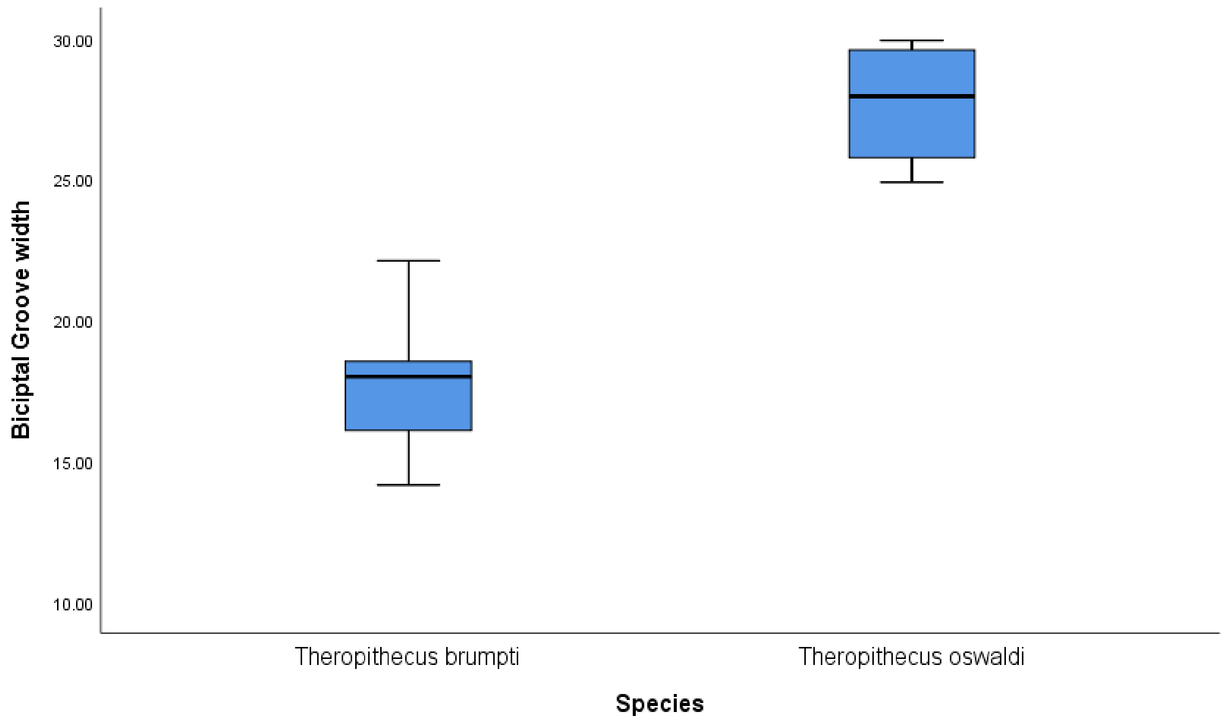

Figure 15. Bicipital grove width index 2.

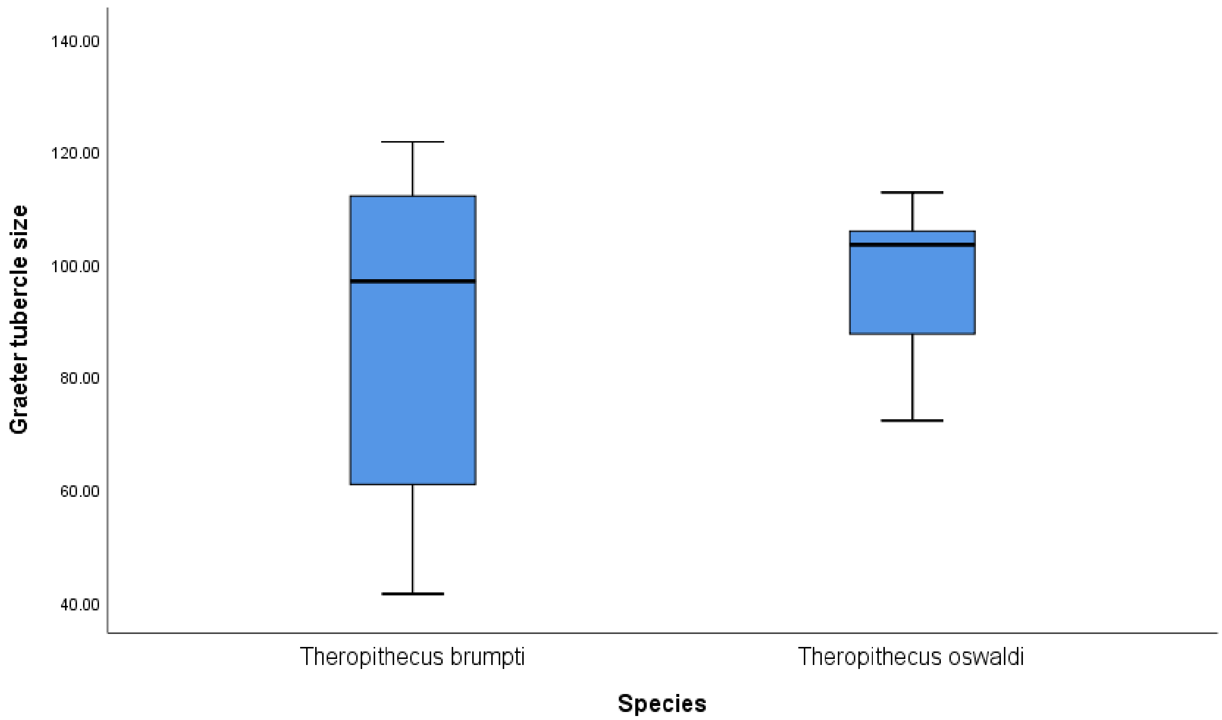

Figure 16. Greater tubercle size index 3.

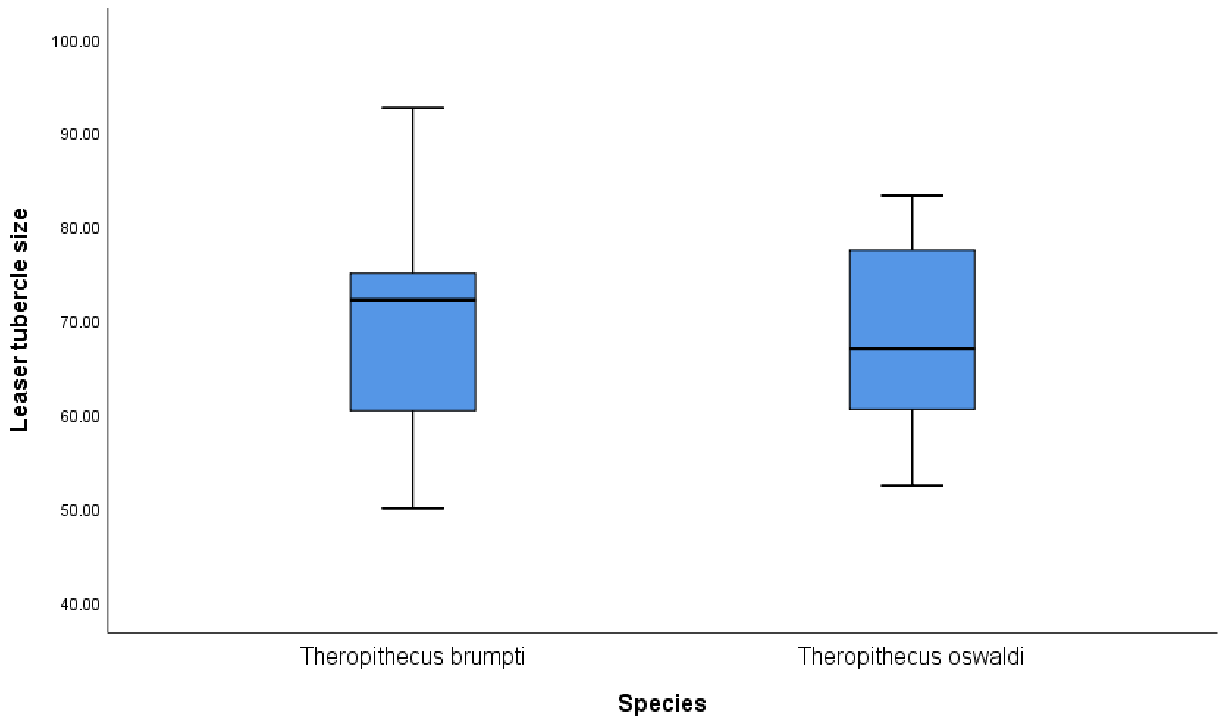

Figure 17. Lesser tubercle size index 4 .

Chapter 5

5. Conclusion

The result of this study show that *Theropithecus brumpti* exhibit differential proximal humerus morphologies, showing affinities within *Theropithecus* and *papionine*. The morphology of *T. brumpti* display distinctive combination of arboreal and terrestrial characteristics, such as a narrow bicipital grove width , greater tuberosity lies below the level of humerus , deep concave depression on the lateral surface of greater tuberosity, and the presence of longitudinal depression for the insertion of terse minor muscle are not found in *Theropithecus oswaldi*. This conclusion is parallel that of Krentz (1993), who is discovering all characteristics of postcranial morphology of *Theropithecu*s specially forelimb flexibility.

The main characteristics of *Theropithecus brumpti* proximal humerus that support it to arboreal papionine that are related to flexibility and stability of glenohumeral joint. The proximal humerus morphology of this species includes narrow bicipital groove which is related to latissimus dorsi muscle, it exhibit important function during climbing by extending, adducts , medially rotates of the humerus and raise the body towards the arm.

Furthermore more the exact role of supraspinatus muscle is debatable however the anatomy of our *T. brumpti* fossil shows the association of supraspinatus muscle with deltoid muscle begins the motion of circumduction by abducting and lifting the humerus above the head. This motion indicates that *T. brumpti* humerus show similarity with *Mandrillus* by forming flexible shoulder joint. This thesis conclude that *Theropithecus brumpti* was arboreal and terrestrial primate with flexible shoulder joint.

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