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Functional morphology of *Mesopithecus* femora (Colobinae, Primates) from China and Greece

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Functional morphology of *Mesopithecus* femora (Colobinae, Primates) from China and Greece – *Master Thesis*

Λειτουργική μορφολογία μηρών *Mesopithecus* (Colobinae, Primates) από την Κίνα και την Ελλάδα – *Μεταπτυχιακή Διπλωματική Εργασία*

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Abstract

Mesopithecus is the most widely known and geographically spread species of colobine monkeys in the Eurasia during Late Miocene and Pliocene. It appears progressively in many sites from Europe to southeast Asia and with at least three different species that vary in size. Although abundant and rather common in Europe, *Mesopithecus* is scarcely documented in Asia. Some specimens from Shuitangba, China are recently attributed to *M. pentelicus* based on research on the mandible. European *Mesopithecus* ecology has been investigated by several proxies, on the contrary, paleoecological data from Asia are very restricted. A proximal femur from Shuitangba, found in close proximity and associated with the mandible of *Mesopithecus*, provides a first opportunity to infer locomotor adaptations of the Chinese representative. Herein, we apply 2D geometric morphometric analysis in order to study the ecomorphological aspects of the fossil femur. The femur from Shuitangba is compared against a group of extinct and extant femora from Africa, Asia and Europe. The results show a semi-arboreal locomotion with terrestrial features for the Shuitangba femur. Compared to the rest of *Mesopithecus* samples from Europe, the studied femur appears to represent a more arboreal species, but it is not clustering well with any other group of extinct or extant monkeys. From a taxonomic point of view, we cannot rule out the case of the femur belonging into *M. pentelicus* but we cannot also exclude the possibility it belongs into *M. monspessulanus* or some other entirely different species.

1. Introduction

A) The Colobinae family

The living monkeys of Africa and Asia are included in a single family, the Cercopithecidae Gray 1821, divided into two subfamilies, Cercopithecinae Gray 1821 and Colobinae Jerdon 1867. Nowdays, the colobines are more arboreal than the cercopithecines, but the fossil record shows that this was not always the case. The fundamental niche of the colobines would appear to have been a diet on leaves and other immature tree parts in the middle and upper canopy, a habitat now occupied by many living colobines (Nakatsukasa, et al., 2010).

Molecular studies suggest that Cercopithecinae diverged from Colobinae during the Early Miocene (ca. 19 Ma) (Pozzi , et al., 2014), nevertheless their Middle-Late Miocene fossil record remains sparse (Nakatsukasa, et al., 2010). The earliest known cercopithecid, which is also considered as the earliest representative of colobines, is *Microcolobus tugenensis* (Colobinae), which is known by a single mandible and associated canines discovered from the ca. 10 Ma-old Ngeringerwa beds in Tugen Hills, Kenya (Nakatsukasa, et al., 2010).

The Colobinae or leaf-eating monkeys include 61 species in 11 genera (Koufos, 2009). Some classifications split the colobine monkeys into two tribes, while others into three groups. Both classifications put the three African genera *Colobus*, *Piliocolobus*, and *Procolobus* in one tribe, the Colobini. The other tribe, of Asian radiation, the Presbytini, currently comprises of *Trachypithecus, Presbytis, Semnopithecus, Pygathrix, Rhinopithecus, Nasalis* and *Simias*. The first occurrence of Colobinae in the fossil record dates to the Middle Miocene of Kenya (12.5–10 Ma). During the Late Miocene, an unnamed colobine tooth dated around 8 Ma is recorded in Marceau (Algeria) (Nakatsukasa, et al., 2010) and at the same time colobine firstly occurred in Europe with *Mesopithecus*, whose first occurence is recorded in the early Turolian (8.7–8.2 Ma) faunas of northern Greece (Koufos, 2019, 2009). The genus expanded during the Late Miocene from Italy to China. During the Early Pliocene, the colobine *Dolichopithecus* also appears in the European fossil record along with *Mesopithecus* which coexisted temporally and occurred sympatrically in several sites of France (Montpellier, Perpignan), Bulgaria (Dorkovo), and Romania (Măluşteni) (Eronen & Rook, 2004; Delson, et al., 2005). Both *Dolichopithecus* and *Mesopithecus* disappear from Europe at the Ruscinian, whereas, after the Early Pleistocene, colobines became fully extinct from Europe, though they persist in Asia, with some extinct species possibly being related to the living Asian species (Eronen & Rook, 2004). While the phylogenetic relationships of *Mesopithecus* and *Dolichopithecus* with extant Asian colobines remain unclear, the numerous modern representatives combined with fossil evidence in Africa and Eurasia attest to the evolutionary success of this subfamily.

B) The genus *Mesopithecus*

The extinct genus *Mesopithecus* is widely known from the Late Miocene and Early Pliocene of Eurasia recorded from MN11 to MN16 (Fig. 1) (Eronen & Rook, 2004). The oldest unequivocal occurrences of *Mesopithecus* are from the sites of Nikiti-2 and Ravin des Zouaves-5 in northern Greece that bear faunas of MN11 (early Turolian) age, dated to around 8,7-8,2 Ma. *Mesopithecus* was recently found in southwestern China (Jablonski, et al., 2020). This extends the geographic range of the genus suggesting its ability to adapt to different habitats. The current taxonomy of the taxon is as follows:

Order Primates Linnaeus, 1758
Infraorder Catarrhini E. Geoffroy Saint-Hilaire, 1812
Superfamily Cercopithecoidea Gray, 1821
Family Cercopithecidae Gray, 1821
Subfamily Colobinae Blyth, 1863
Genus *Mesopithecus* Wagner, 1839

Mesopithecus emergence timing overlaps with the divergence date of the crown African and Asian colobine monophyletic clades. *Mesopithecus* itself is most likely related to the odd-nosed Asian subclade (Alba, et al., 2015). However its phylogenetic relationships are still unclear (Alba, et al., 2015). In its cranium and dentition *Mesopithecus* reveals mostly ancestral colobine features and could well be representative of early members of the subfamily. The long bones are rather robust most like the larger macaques. It would appear that *Mesopithecus* was a colobine which had begun to converge toward a more terrestrial macaque-like way of life (Alba, et al., 2015).

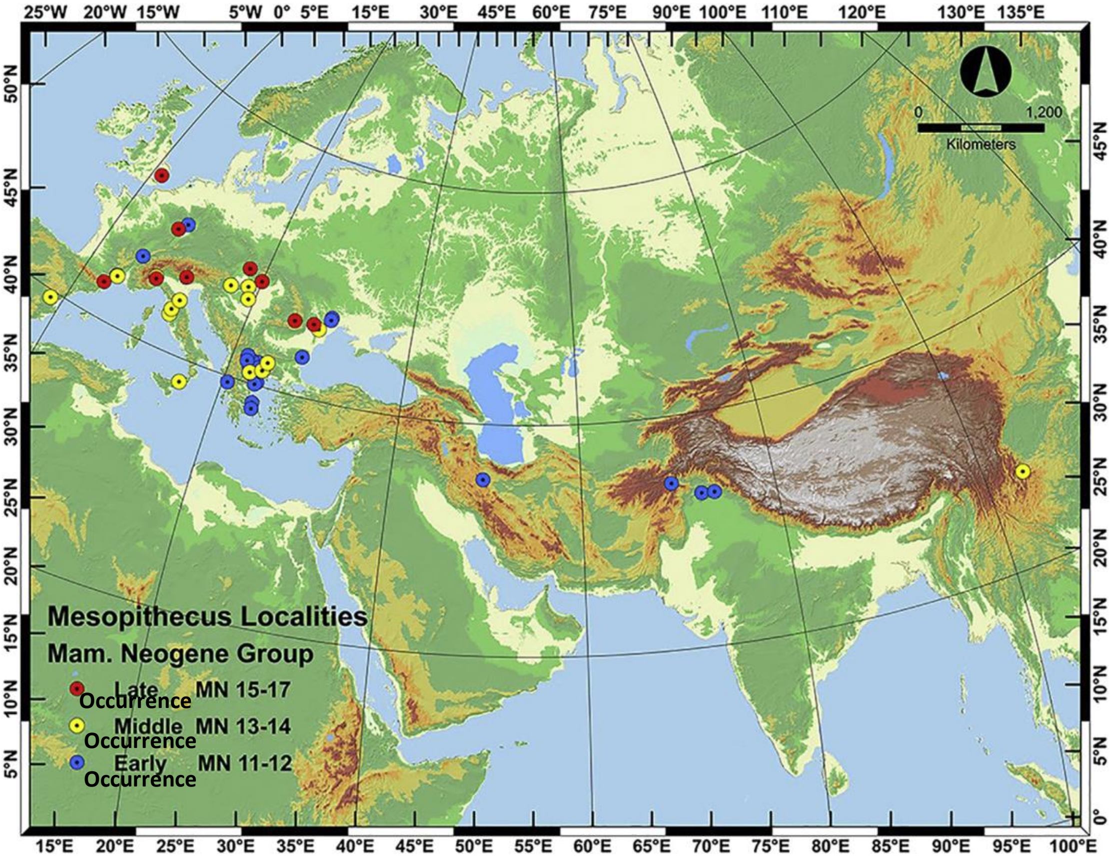

Figure 1. Localities of *Mesopithecus* in order of occurrence. (Jablonski, et al., 2020)

Based mostly on dental and postcranial size and morphology, three species of European *Mesopithecus* have been recognized: *M. delsoni* Bonis et al., 1990 from MN11 originally from Ravin des Zouaves-5, Axios Valley, Greece, *M. pentelicus* from MN12 originally from Pikermi, Greece and *M. monspessulanus* from MN13 originally from Montpellier, France (Alba, et al., 2013). All three species are succedent and recorded in the stratigraphic levels of

Axios Valley, N. Greece. The last two were considered to be chronospecies until recently, but their coexistence in the fossil site of Dytiko-2, Axios Valley, rather suggests that they are probably distinct biospecies that briefly coexisted (Delson, et al., 2005). *M. monspessulanus* is mostly different from the other two by its smaller size and narrower molars (Pradella & Rook, 2007). The taxonomic status of the earliest taxon, *M. desloni*, was in debate because differences from *M. pentelicus* have been considered by some authors as rather subtle. Recent work (Bogdanova, et al., 2023) revealed morphological differences that confirm the species status of *M. delsoni*. In this study we follow Koufos (2009) in recognizing three different species of European *Mesopithecus*.

Mesopithecus distribution remains within humid environments until its last appearance in the Pliocene (MN16) (Eronen & Rook, 2004). The environment in late Miocene is considered open and dry with seasonal climates (Lazaridis, et al., 2018). *Mesopithecus* probably occurred in wooded landscapes with grassy layers (Lazaridis, et al., 2018). *Mesopithecus* in general is described as a semi-terrestrial primate living in open habitats such as wooded savannah (Thiery, et al., 2017). The older and larger form, *Mesopithecus delsoni* from Greece and Bulgaria, has been reconstructed as a semiterrestrial monkey with some terrestrial postcranial features (Delson, 1992; Youlatos, et al., 2012; Bogdanova, et al., 2023). The most widespread species, *Mesopithecus pentelicus*, was also presumably a semiterrestrial monkey, exhibiting variable rates of arboreality-terrestriality (Youlatos, 2003; Youlatos & Koufos, 2010; Youlatos, et al., 2012; Ji, et al., 2020) whereas the more recent and smaller species, *Mesopithecus monpsessulanus* displayed more arboreal postcranial features (Youlatos, et al., 2012).

The diet of *Mesopithecus* was based on seeds (Thiery, et al., 2017). *Mesopithecus* is not a leaf eater like extant colobines. It is mostly an opportunistic feeder consuming seeds, fruits and nuts (Thiery, et al., 2017). Its feeding habits are consistent with woodlands and forest savannah (Lazaridis, et al., 2018) and it may be supposed that it lived in troops in gallery forest and savannah fringe, spending a good part of the day feeding terrestrially or moving between arboreal feeding sites. On the other hand, the younger species, *M. monspensulanus* inhabited a more wooded and well-watered environment and appears to have been adapted to a more arboreal habitus, perhaps under the influence of competition (Szalay & Delson, 1979).

C) Ecomorphology

Ecomorphology or ecological morphology is a discipline that bridges conceptual and analytical aspects of both functional and evolutionary fields. The main goal of ecomorphological analyses is to take advantage of the outcomes of functional anatomy and to draw relationships between particular anatomical arrangements and ecologically relevant functions (Pallas, 2020). Locomotion is important to ecology as it allows animals to move into environments that can be further defined by physical and mechanical properties (*e.g.*, substrates). Ultimately, the range of locomotor abilities of an individual affects its capabilities to *e.g.*, access food, access and interact with mates, or to escape from predators (Pallas, 2020).

Locomotor behavior is highly correlated with potential for movement at joint articular surfaces (Ciochon & Corruccini, 1974). Joint surfaces transmit only compressive loads, and perhaps even more importantly, determine range of motion and joint stability during motion. Thus, animals with locomotor patterns that emphasize more cautious movement, and thus lower bending and torsional limb loadings, and/or more varied limb positions, and thus greater joint excursions, should have larger joint surfaces relative to crosssectional diaphyseal strength, and vice versa (Ruff, 2002). Many studies link primate proximal femoral morphology with the role of the hindlimb in locomotion, indicating that a strong functional signal underlies the configuration of this element (Harmon, 2007).

D) Goals

This research focuses on the functional anatomical (ecomorphological) study of the proximal part of the femur of the Shuitangba specimen. As part of the hip joint, the proximal femur contains plenty of functional information related to locomotion. For these purposes we used

2D geometric morphometrics on the proximal femora of fossil and extant cercopethicids in order to:

i) To investigate the taxonomic validity of the preserved femur and

ii) To assess the locomotor habits as reflected on selected characters of the preserved femur in comparison with the European representatives of *Mesopithecus*.

2. Materials and Methods

A) Locality, material and age

Shuitangba is an open-pit lignite mine located in the Zhaotong Basin of northeastern Yunnan, southwestern China (Figs. 2, 3). The fossil-bearing Neogene Zhaotong Formation of Shuitangba accumulated at a margin of a sub-basin within the Zhaotong Basin (Jablonski, et al., 2020). Vertebrate fossils are found for the most part, as isolated elements scattered throughout the stratigraphic horizons; they occur in bone layers in the water-lain silty and peaty clays between the lignite beds. The fauna includes an ape, tapirs, diverse insectivores, flying squirrels, and bamboo rat, and indicates a densely vegetated, moist forest paleoenvironment (Jablonski, et al., 2020). Plentiful remains of large tree trunks and branches provide further direct evidence of a heavily wooded habitat. The dominance and diversity of freshwater birds, the abundance of fish, frog, turtle, and crocodile remains, the presence of two aquatic beavers and an otter-like mustelid all indicate a depositional environment at the margin of standing water (Jablonski, et al., 2020). Interbedded gastropod layers suggest periods of quiescence during deposition. Combined with the results of preliminary taphonomic and sedimentological analyses, it is likely that the bones were deposited in a swampy environment. The fossiliferous deposits in the Yuanmou area consist mostly of alluvial sediments that may have been deposited under warm and humid, but seasonal, conditions. Taphonomic and paleoecological analyses of the fauna suggest forest habitats in the vicinity of Yuanmou, but more open habitats, such as bush and grassland, were proximal to the site of deposition (Jablonski, et al., 2014, 2020).

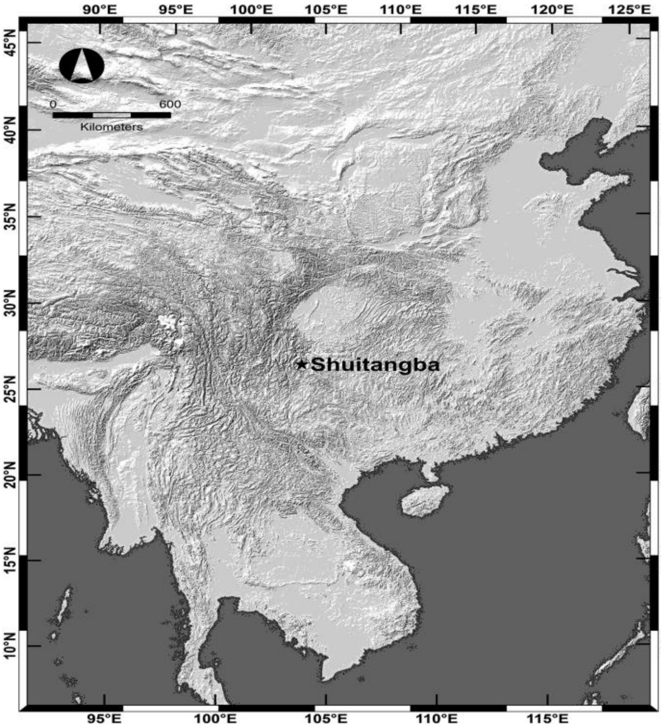

Figure 2. The locality of Shuitangba. (Jablonski, et al., 2020)

The colobine fossil elements from the locality of Shuitangba comprise a mandible with lower dentition, a proximal femur and a complete calcaneus and they likely represent the oldest known colobines from East Asia and one of the few sites of co-occurrence of a hominoid with a colobine (Ji, et al., 2020). The stratigraphic position of the colobine fossils in the Shuitangba stratigraphic succession and the estimated rate of sediment accumulation, imply an age of ~6.4 Ma for the mandible and the proximal femur (Jablonski, et al., 2020). Jablonski et al. (2020) and Ji et al. (2020) attribute the specimens to *Mesopithecus* expanding the dispersal of the genus to southwestern China, at the same time when it was diversifying within Europe. Its presence here underscores its close affinities and potential ancestry to the extant oddnosed colobines. Ji et al. (2020) recognized close resemblance between the Shuitangba and Pikermi, Greece *Mesopithecus* and therefore they refer to the Chinese taxon to as *M.* cf. *pentelicus*. The estimated age of the Shuitangba findings also falls within the range of most European occurrences of *Mesopithecus*, and especially *M. pentelicus*, that is, in MN 12-13, ca. 7.0 and 5.3 Ma (Jablonski, et al., 2020).

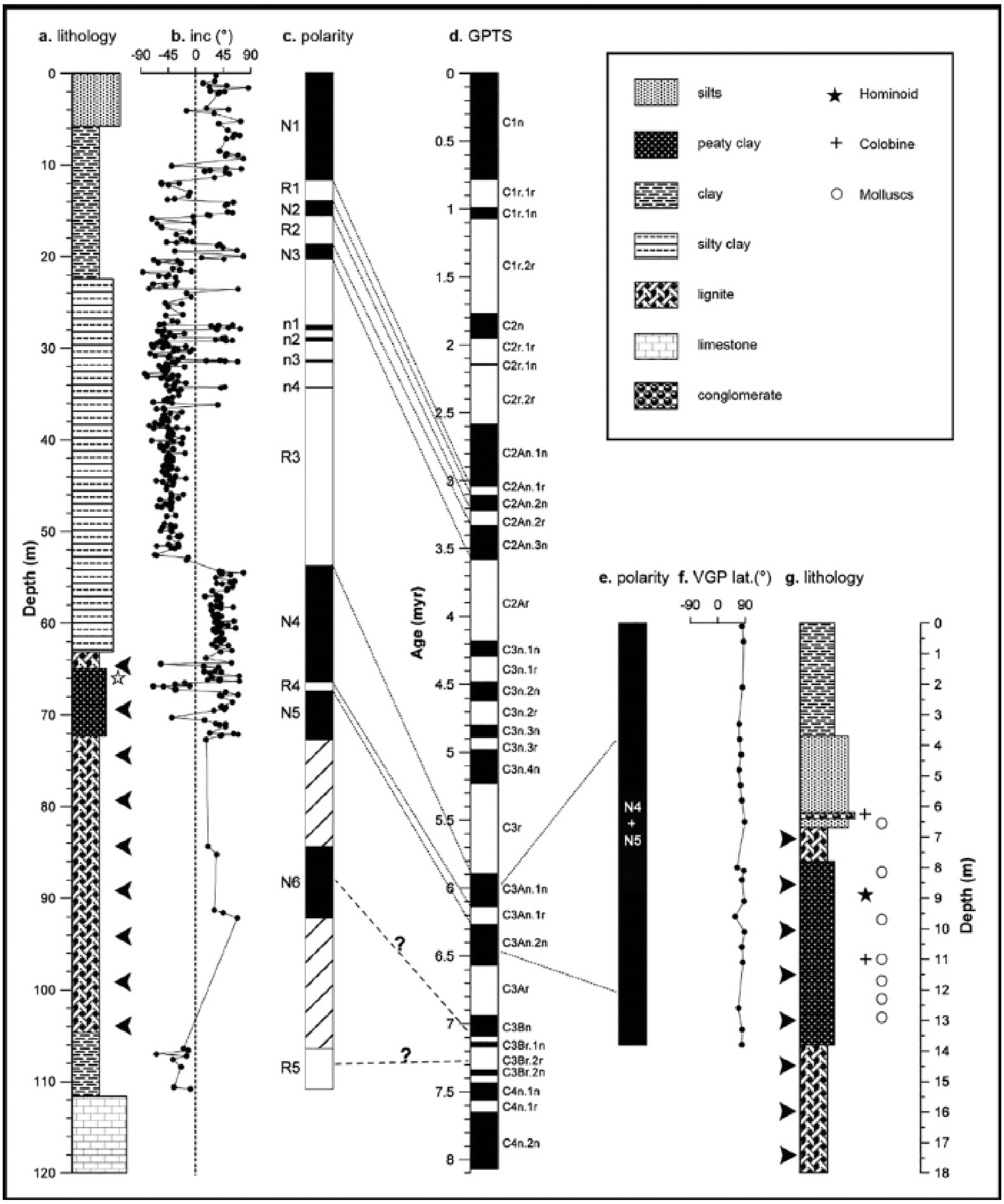

Figure 3. The location of the *Mesopithecus* colobine fossils in the lithostratigraphic and magnetostratigraphic context of Shuitangba (Jablonski, et al., 2020).

B) Comparative sample

The fossil femur from Shuitangba is originally compared with the following fossil femora: two *Mesopithecus* femora from Dytiko-2, Axios Valley, Greece, three of *M. pentelicus* from

Pikermi and one of *M. delsoni* from Hajdidimovo, Bulgaria. The fossil sample also included the following extinct cercopithecids: *Cercopithecus* (n=5), *Theropithecus* (n=12) and *Rhinocolobus* (n=1). The comparative sample was completed with photographs of femora of the following extant primate taxa: *Colobus* (n=14), *Erythrocebus* (n=1), *Hylobates* (n=1), *Lophocebus* (n=1), *Macaca* (n=2), *Papio* (n=6), *Piliocolobus* (n=2) and *Rhinopithecus* (n=17).

C) Proximal femur morphology

The anatomical terminology of the proximal femur follows Polly (2007). Morphologically the femur is a long bone (Fig. 4). At the proximal end there is a round-shaped head which connects to the shaft through the neck. The head faces medially. At the centre of the head there is the fovea capitis, a non-articular depression that receives the ligamentum teres. The neck is surrounded by two processes known as trochanters. The greater trochanter faces laterally and is at the opposite side of the head and represent the insertion site for mm. gluteus medius, gluteus profundus and piriformis. The lesser trochanter is located below the neck at the caudal (posterior) side of the shaft and is the insertion site of m. iliopsoas. All together they control the movement of the hip, the former three are the extensors and the latter is the flexor. In the middle of the triangle formed by the head, the greater and lesser trochanter, there is the trochanteric fossa, a posterior pit whereupon inserts the tendon of obturator externus responsible for the lateral rotation of the thigh. The long, rounded shaft between the proximal and the distal ends (epiphyses) of the bone is called the diaphysis. At the posterior surface of the shaft there is the linea aspera, a long, wide, elevated ridge, origin of the vastus muscles. Between the base of the greater trochanter and the lip of the linea aspera there is a long, wide feature called the gluteal line, often referred to as the third trochanter, where the m. gluteus maximus inserts.

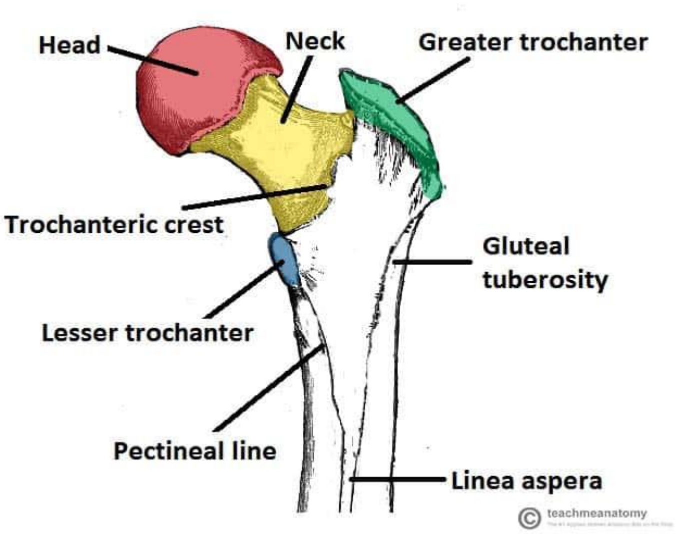

Figure 4. Basic anatomical features of the femur (posterior view) (https://teachmeanatomy.info/lower-limb/bones/femur/).

Most of these features have significant functional importance. The greater trochanter functions as a primary lever for extension of the hip. Consequently, it is often long and robust in cursorial mammals (Polly, 2007). The muscles that insert on the greater trochanter run caudally from the anterior pelvis, pulling the trochanter forward, which helps extend the limb by pivoting it around the head. The longer the trochanter, the more efficient the moment arm for extension (Polly, 2007). The third trochanter is well developed in cursorial mammals because it is also the insertion point of hip extensors. These muscles run in the opposite direction from the posterior part of the pelvis, from where they pull the distal femur caudally by tugging on the third trochanter (Polly, 2007). The head of the femur is broader and more proximally directed in species that significantly abduct the femur during locomotion, such as ambulatory mammals (Polly, 2007). The relative neck length, neck diameter and neck-shaft angle affect the mobility of the hip joint (flexion-extension, abduction-adduction, axial rotation) and the structural strength of the femoral neck.

D) Geometric morphometrics and analyses

Morphological - morphofunctional information can also be quantified using geometric morphometrics (GM). GM is an approach to study shape using Cartesian landmark and semilandmark coordinates that can capture morphologically distinct shape variables (Harmon, 2007). Strategically selected spots are used as landmarks providing us with a two-dimensional (2D) visual representation of the bone. The landmarks should be numerous enough to accurately capture the shape of the bone as well as to contain all the crucial functional information. The landmarks may not be demonstrably homologous, but they must be geometrically equivalent across study specimens (Harmon, 2007). The landmarks can be located repeatedly based on some spatial property, in this case, points of maximum curvature and anatomical boundaries (Harmon, 2007). In the present study, the choice of the landmarks was made by the author.

2D coordinates were used to represent the shape of the proximal femur in order to ascertain shape variation and its relationship to locomotion among cercopithecids. The hypothesis was that phenetic affinities in the shape of the proximal femur reflect the degree of similarity in locomotor behaviour. Geometric morphometric analyses of multidimensional shape data are used widely in studies of bony morphology of primate crania and postcrania (Harmon, 2007). The proximal femur is an appropriate candidate for 2D analysis because its complex convex and concave morphology is not easily partitioned into discrete linear segments (Harmon, 2007)

Using 2D illustration to study 3D specimens has its own difficulties. Four different sides (views) were chosen for this study in an effort to give a better estimation of reality. The sides are the anterior (dorsal), the posterior (plantar), the proximal and the medial (Fig. 5). For each side, two different analyses were conducted. One including the *Theropithecus* group and one excluding it. This was because the group was represented by many specimens that could significantly modify the result of the analyses. This provided a verification to the original analysis and also a much clearer and detailed view of the remaining groups. Three more approaches were explored, one containing fewer landmarks and two containing more. The chosen approach was the one which provided the entirety of the important information without any unnecessary data.

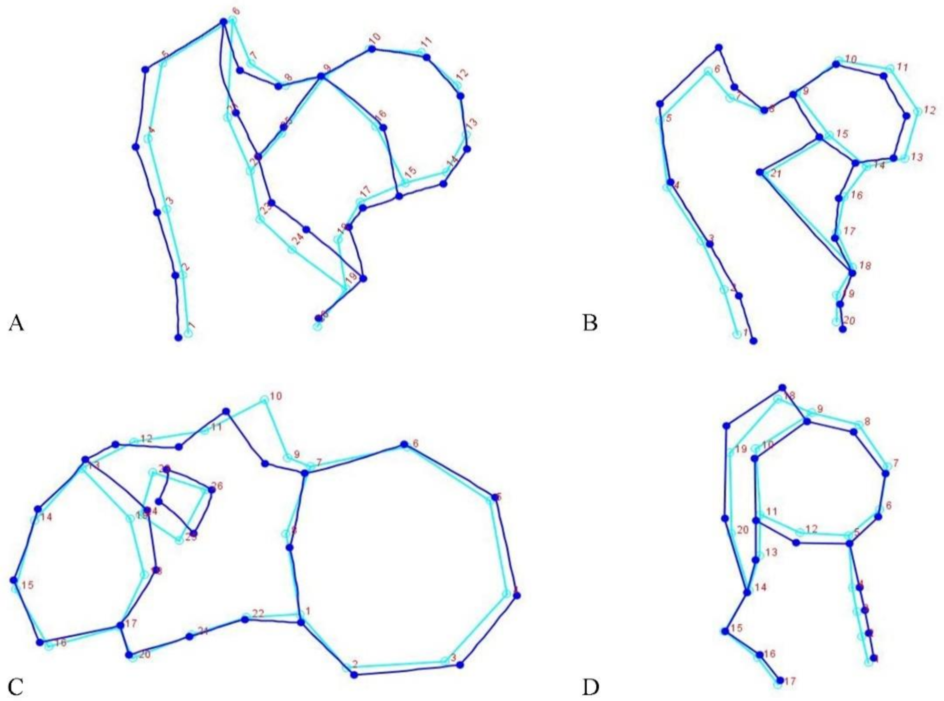

Figure 5. Landmarks used in the present study. A) Landmarks in the posterior side. B) Landmarks in the anterior side. C) Landmarks in the proximal side. D) Landmarks in the medial side.

After the 2D data were obtained, the main analysis performed was the Canonical Variate Analysis (CVA) (Campbell & Atchley, 1981). CVA is a widely used method for analysing group structure in multivariate data. It is mathematically equivalent to a one-way multivariate analysis of variance and often goes by the name of canonical discriminant analysis. Generalized Procrustes analysis (GPA) is used to adjust for position, orientation and scale among landmark configurations (Gower, 1975).

Regression Analysis (RA) was used to verify the correlation between them. Regression analysis is a powerful statistical method that allows to examine the relationship between two or more variables of interest (Anon., 2008). While there are many types of regression analysis, at their core they all examine the influence of one or more independent variables on a dependent variable. All the analyses were performed using MorhoJ (1.07a), an integrated software package for doing geometric morphometrics (https://morphometrics.uk/MorphoJ_page.html).

Discriminant Analysis (DA) was applied as a multivariate technique used to separate two or more groups of observations (individuals) based on k variables measured on each experimental unit (sample) and find the contribution of each variable in separating the groups (Huberty, 1975). Paleontological Statistics (PAST) (https://www.nhm.uio.no/english/research/resources/past/) was used for the DA.

3. Results

A) Qualitive morphological comparisons

The specimen from Shuitangba is a partial right femur, broken before fossilization just above the midshaft (Fig. 6, Fig. 7). The femoral head is large and round and protrudes from the central axis. The fovea capitis is wide, deep and oval-shaped, and it is slightly placed posteriorly. The femoral neck is wide, thick and short. The trochanter major is large, kind of flat at the top, and extends only a little above the head. The trochanteric ridge is very evident and leads to an enlarged trochanter minor, which is relatively low but very well developed. The trochanteric fossa between them is extremely deep and long. The trochanter tertius is not visible. The shaft is slim and not very wide. It is round in cross-section in the front and flat at the back.

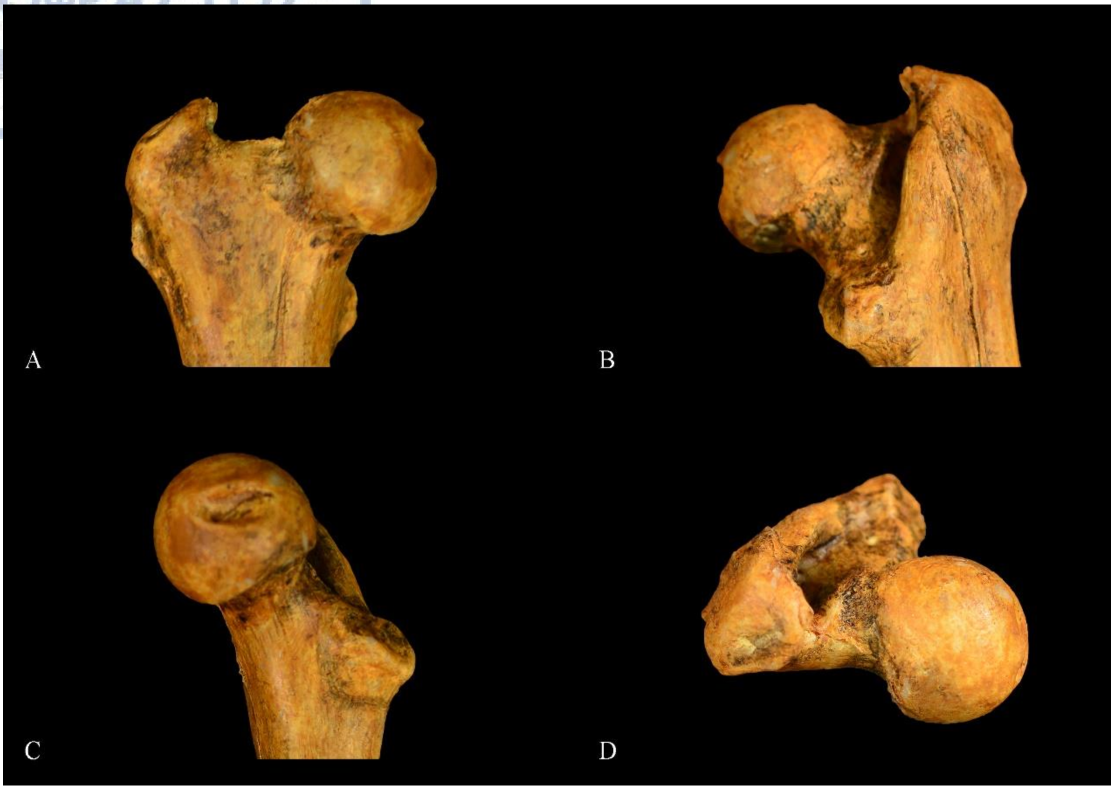

Figure 6. Views of the Shuitangba proximal femur. A) Anterior, B) Posterior, C) Medial, D) Proximal.

Figure 7. 3D representation of the fossil femur from Shuitangba.

A morphological comparison of the Shuitangba femur with those of *Mesopithecus* from Greece indicates important differences, especially at the crest connecting the greater and lesser trochanter. The Chinese specimen is also different from the *Colobus* and *Rhinopithecus* femora and completely different from that of *Papio* (Fig. 8).

Figure 8. The posterior side of femur in the main studied specimens. A. The Shuitangba colobine, B. *Mesopithecus* from Pikermi, C. *Mesopithecus petelicus* from Dytiko-2, D. *Mesopithecus delsoni* from Bulgaria, E. *Colobus guereza* from Kenya, F. *Rhinopithecus roxellana* from China, G. *Papio cynocephalus* from Kenya

In the posterior side, the Shuitangba femur appears similar to the femora of *Mesopithecus* from Pikermi, as well as to that of *Colobus*, especially in the shape of the neck and the femoral head. These features appear quite different when compared with the other species (Fig. 9). In the proximal side the Shuitangba femur is more similar with *Mesopithecus* from Dytiko-2 and *Colobus*, mainly in the shape and size of the greater and lesser trochanter. The rest of the examined *Mesopithecus* specimens are closer to *Rhinopithecus*, whereas *Papio* femur is completely different in this view (Fig. 10).

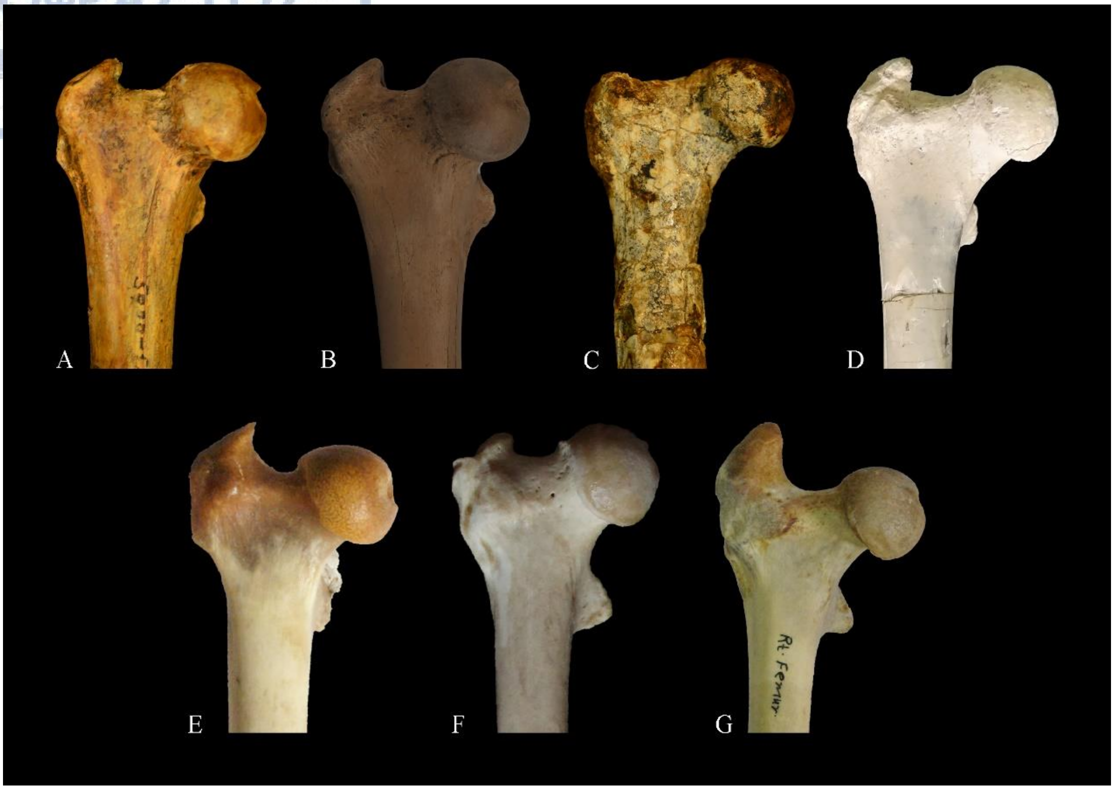

Figure 9. The anterior side of femur in the main studied specimens. A. The Shuitangba colobine, B. *Mesopithecus* from Pikermi, C. *M. petelicus* from Dytiko-2, D. *M. delsoni* from Bulgaria, E. *Colobus guereza* from Kenya, F. *Rhinopithecus roxellana* from China, G. *Papio cynocephalus* from Kenya

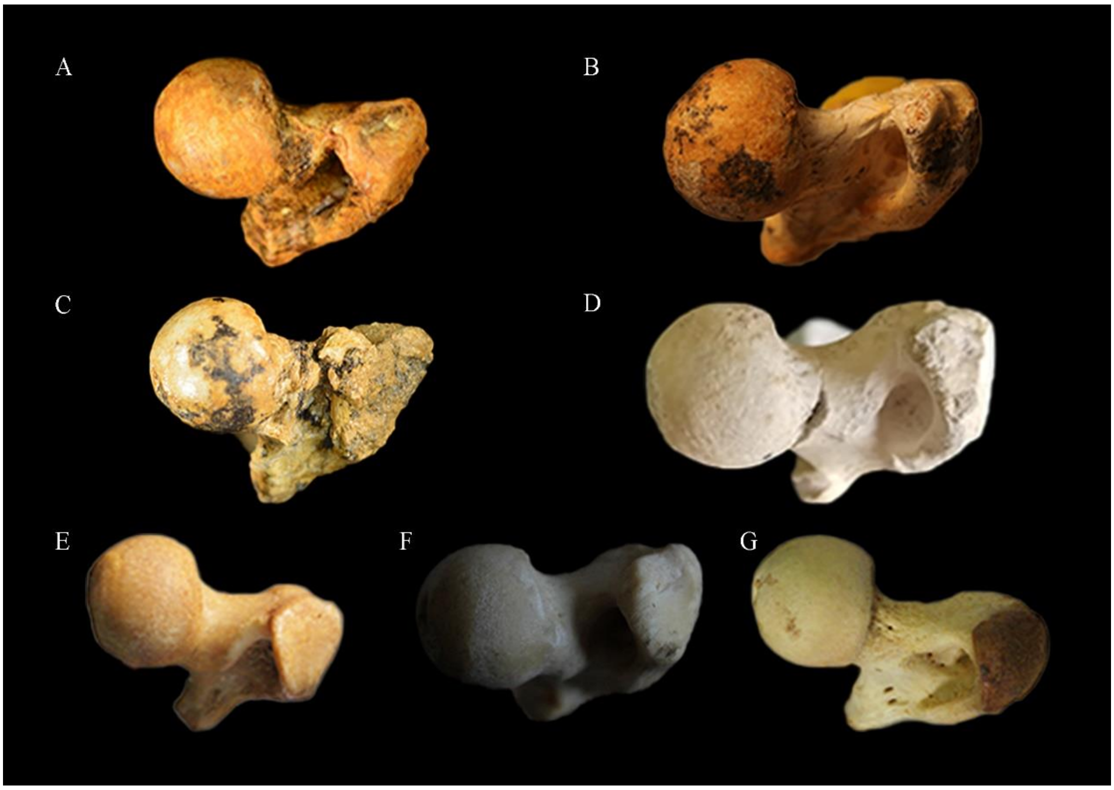

Figure 10. The proximal side of femur in the main studied specimens. A. The Shuitangba colobine, B. *Mesopithecus* from Pikermi, C. *M. petelicus* from Dytiko-2, D. *M. delsoni* from Bulgaria, E. *Colobus guereza* from Kenya, F. *Rhinopithecus roxellana* from China, G. *Papio cynocephalus* from Kenya

B) Quantitative morphological comparisons

Canonical Variates Analysis (CVA)

The specimen from Shuitangba is symbolized with the use of the letters Mss. The letters Mes are used for the other *Mesopithecus* specimens from Greece and Bulgaria. The entirety of the abbreviations are shown in Table 11.

Table 11. Abbreviations used in the canonical variates analyses (CVA) with the behavioural (locomotor) characterization of the taxa.

Abbr.	Taxon	Locomotor behaviour
Cer	*Cercopithecus*	Terrestrial
Col	*Colobus*	Semi-arboreal
Ery	*Erythrocebus*	Semi-terrestrial
Hyl	*Hylobates*	Arboreal
Lop	*Lophocebus*	Semi-terrestrial
Mac	*Macaca*	Semi-arboreal
Mes	*Mesopithecus*	Semi-terrestrial
Mss	*Mesopithecus* (Shuitangba)	Semi-arboreal
Pap	*Papio*	Terrestrial
Pil	*Piliocolobus*	Semi-arboreal
Rhi	*Rhinopithecus*	Semi-arboreal
Rin	*Rhinocolobus*	Semi-terrstrial
The	*Theropithecus*	Terrestrial

Posterior side

The results from the posterior side clearly demonstrate a cline from the most arboreal species to the most terrestrial (Fig. 12). The Shuitangba femur falls somewhere in the middle, close to the other *Mesopithecus* samples and very close to the *Colobus* specimens.

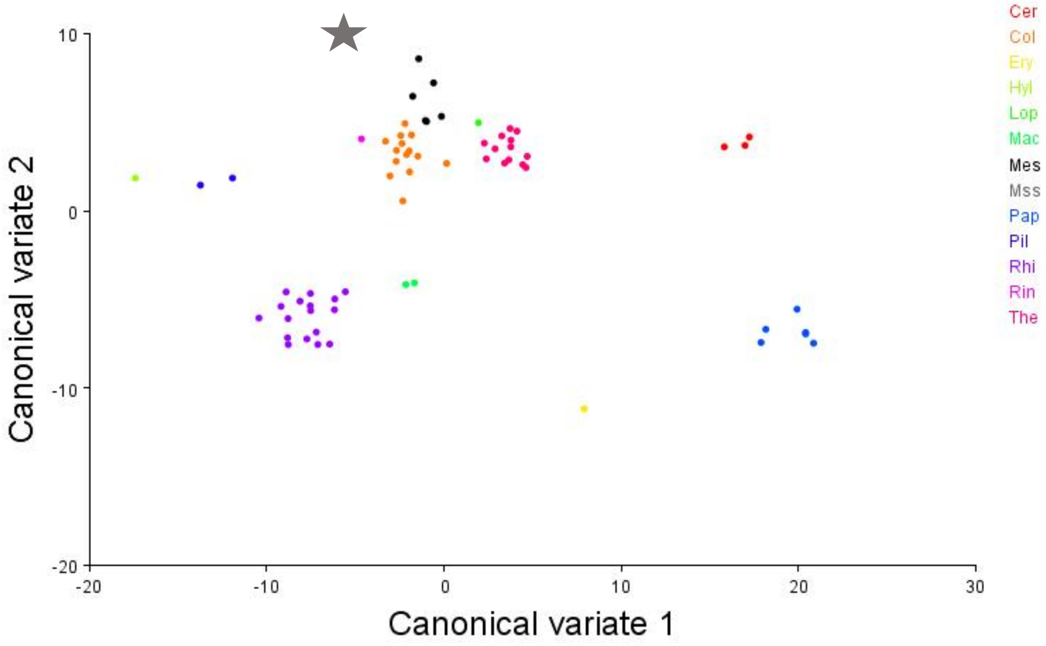

Figure 12. Canonical variation analysis of the posterior side landmarks. Cer: red dots, Col: orange dots, Ery: yellow dots, Hyl: light green dots, Lop: green dots, Mac: tirquaz dots, Mes: black dots, Mss: grey dots, Pap: blue dots, Pil: dark blue dots, Rhi: purple dots, Rin: light purple dots, The: fuchsia dots

The CVA of the posterior side landmarks is shown in Fig. 12. In the far most left side there is *Hylobates* representing the most arboreal species and at the other side there is *Papio* representing the most terrestrial. The rest of the specimens are located in between based on their variable degree of arboreality and terrestriality. Hence CV1 of proximal femur from the posterior side clearly demonstrates a cline from the most arboreal species (left) to the most terrestrial ones (right). The Shuitangba femur falls somewhere in between, near the arboreal side, close to the other *Mesopithecus* samples and very close to the Colobus specimens. We obtain a similar arrangement of the specimens in the morphospace when the analysis is run excluding *Theropithecus* (Fig. 13). However, the discrimination of the different groups is clear in the intermediate section of the morphospace.

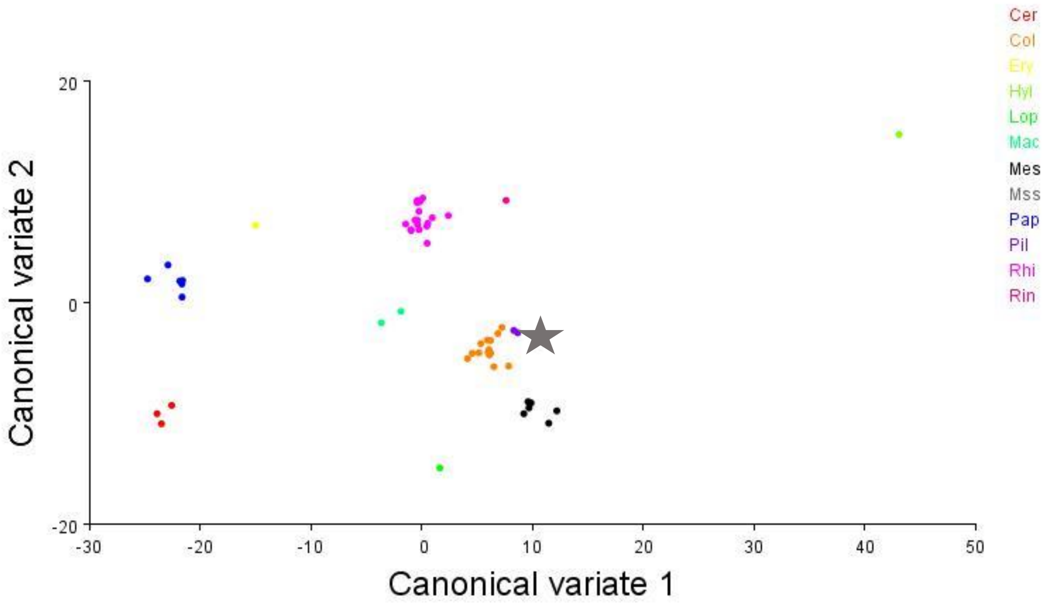

Figure 13. Canonical variety analysis of the posterior side landmarks excluding *Theropithecus*. See Fig. 12.

In this analysis, in which *Theropithecus* specimens are excluded, (Fig. 13) it is evident that the Shuitangba femur is closer to *Colobus* and *Piliocolobus* than the *Mesopithecus* samples. The regression on the CV1 ascertains these results (Fig. 14, Fig. 15).

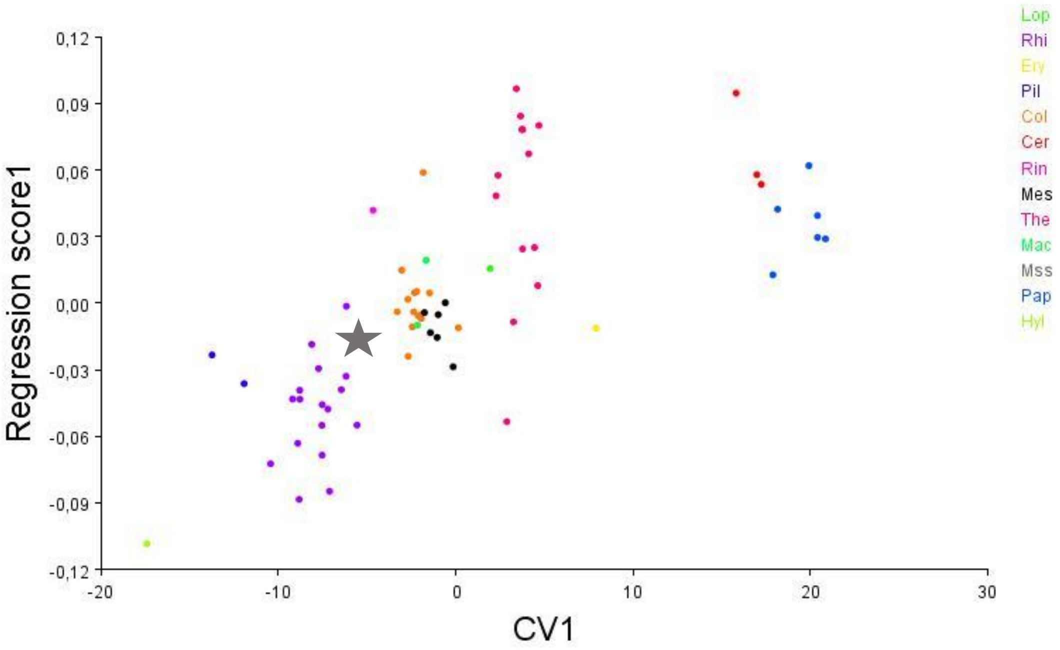

Figure 14. Regression on CV1 of the posterior landmarks on proximal femoral side. See Fig. 12.

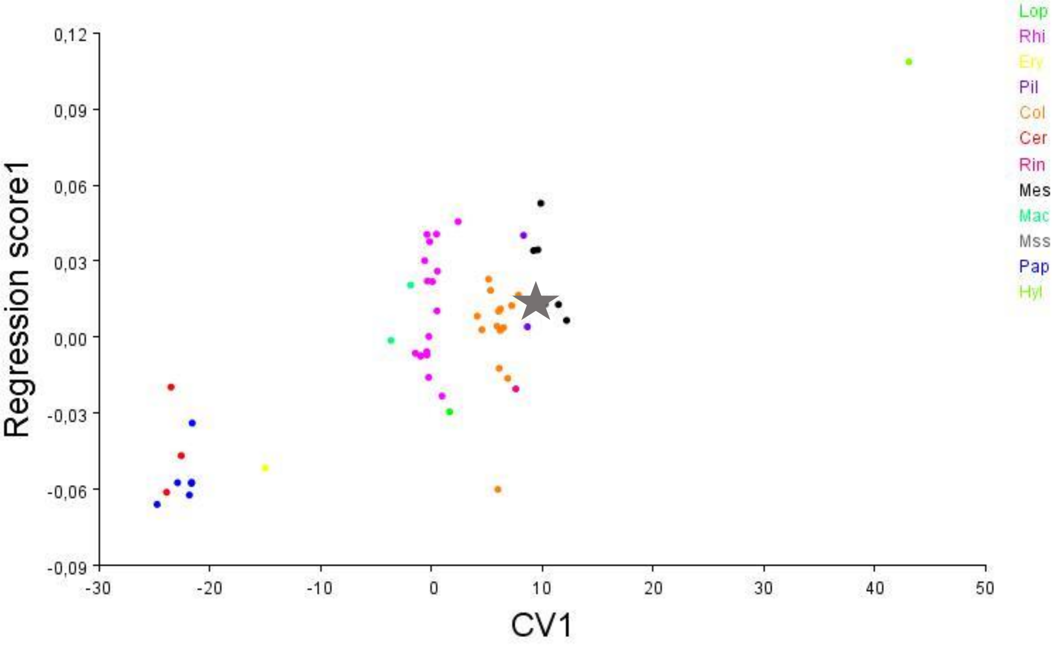

Figure 15. Regression on CV1 of the posterior landmarks on proximal femoral side, excluding *Theropithecus*. See Fig. 12.

It is important to notice that when *Theropithecus* is excluded, then the analysis place the Shuitangba femur closer to *Colobus*, *Piliocolobus* and *Mesopithecus*, while, in every analysis of the posterior side, the Chinese fossil seems to be closer to the arboreal end of the graphs rather than to the terrestrial.

Anterior side

The analysis of the anterior side produced more or less similar results (Fig. 16).

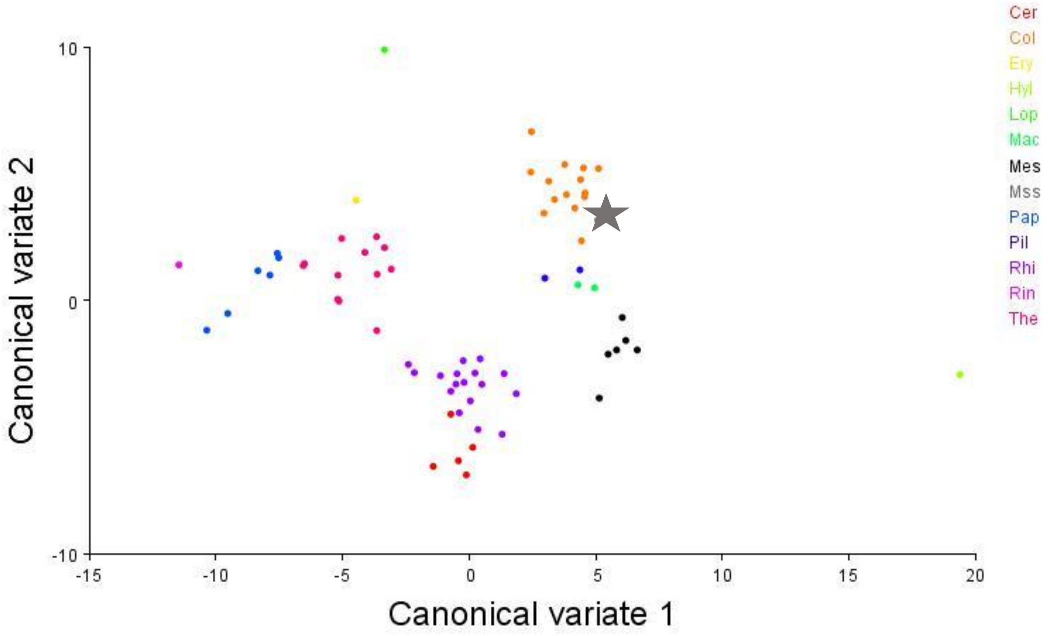

Figure 16. Canonical variety of the anterior side landmarks on proximal femoral side. See Fig. 12.

The *Colobus*, *Piliocolobus*, Shuitangba and *Mesopithecus* specimens are clustered all together and closer to the arboreal side. Excluding the *Theropithecus* group the same patterns emerges (Fig. 17). The Shuitangba femur is placed in between the *Colobus* and *Mesopithecus*.

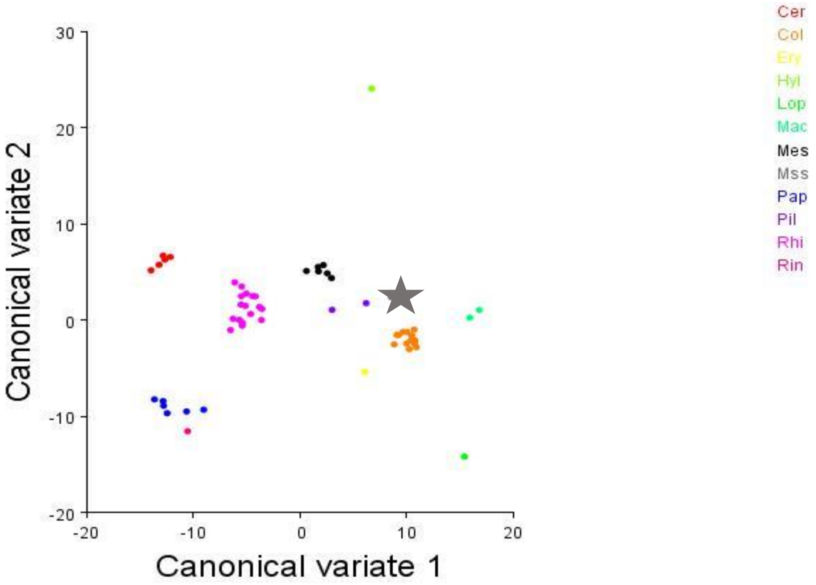

Figure 17. Canonical variety analysis of the anterior landmarks on the proximal femur, excluding *Theropithecus*. See Fig. 12.

Regression analysis appears to verify the results in both cases (Figs. 18, 19).

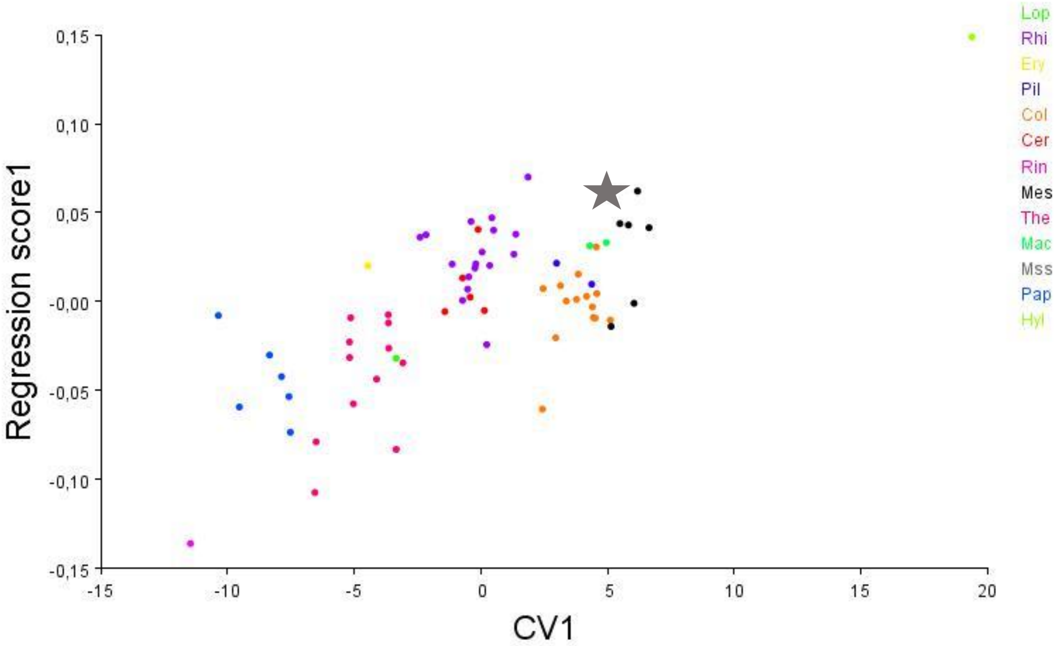

Figure 18. Regression analysis on CV1 of the anterior landmarks. See Fig. 12.

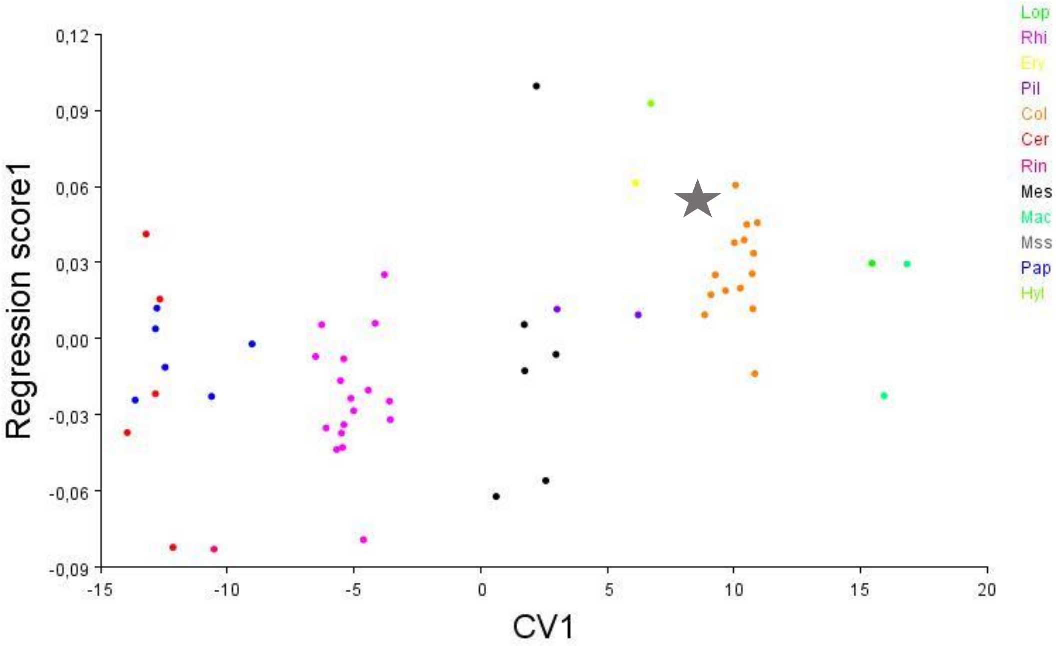

Figure 19. Regression analysis on CV1 of the anterior landmarks excluding *Theropithecus*. See Fig. 12.

Proximal side

In the proximal side there were no available specimens for *Theropithecus*. Thus, the analysis was done without considering the genus (Fig. 20). We still observe the same transitional pattern from arboreal to terrestrial forms. Once again we notice that the Shuitangba femur is found between *Colobus* and *Mesopithecus*.

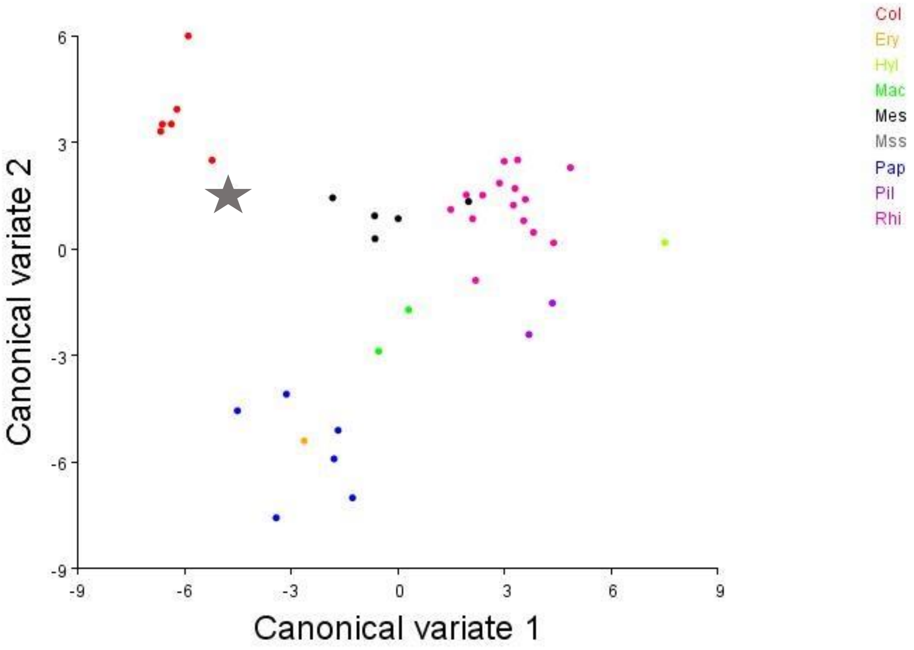

Figure 20. Canonical variety of the proximal side landmarks. See Fig. 12.

Interestingly, in this case the regression analysis places the *Colobus* group next to the *Papio* one, and this is probably due to the lack of specimens. However, the Shuitangba femur is once more placed next to the *Colobus* group, as in the previous analyses (Fig. 21).

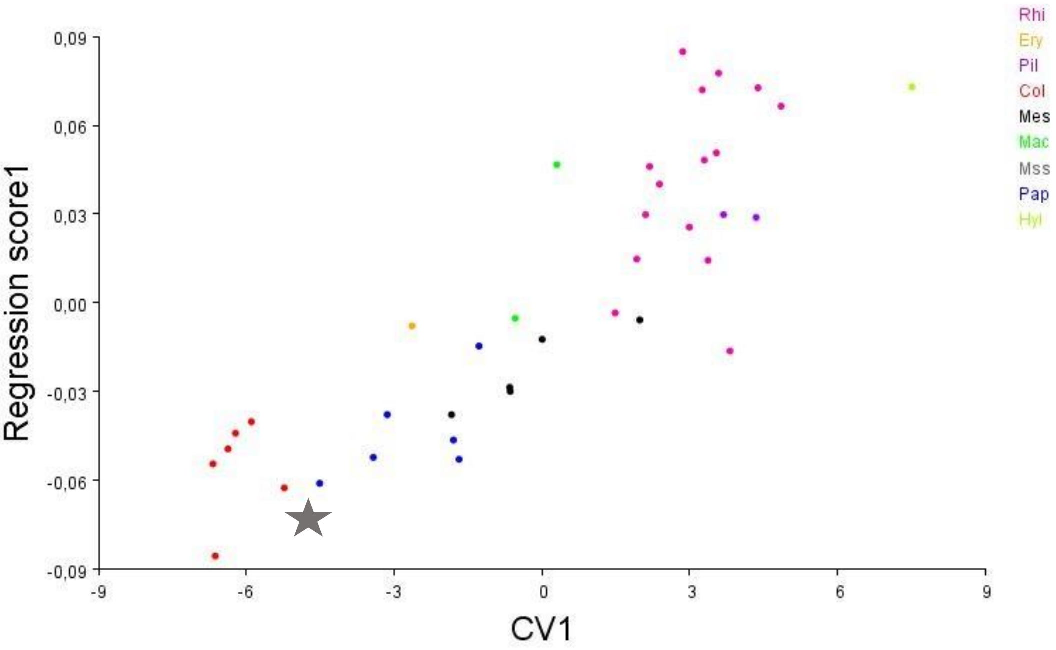

Figure 21. Regression analysis on the CV1 of the proximal landmarks. See Fig. 12.

Medial side

The last analysis concerned the medial side of the proximal femur (Figs. 22, 23). Unfortunately, we did not possess many specimens for this analysis due to lack of enough photos of this view. The results are slightly confusing, but it is still interesting to see that the Shuitangba femur falls mostly next to the same groups as in the previous analyses (Figs. 9, 13, 17).

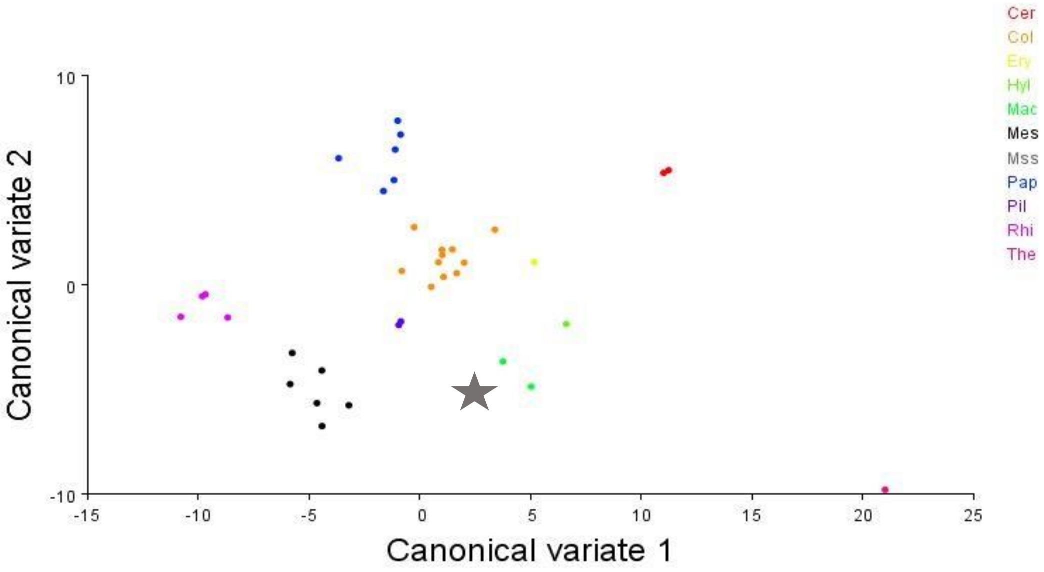

Figure 22. Canonical variety analysis of the medial side landmarks. See Fig. 12.

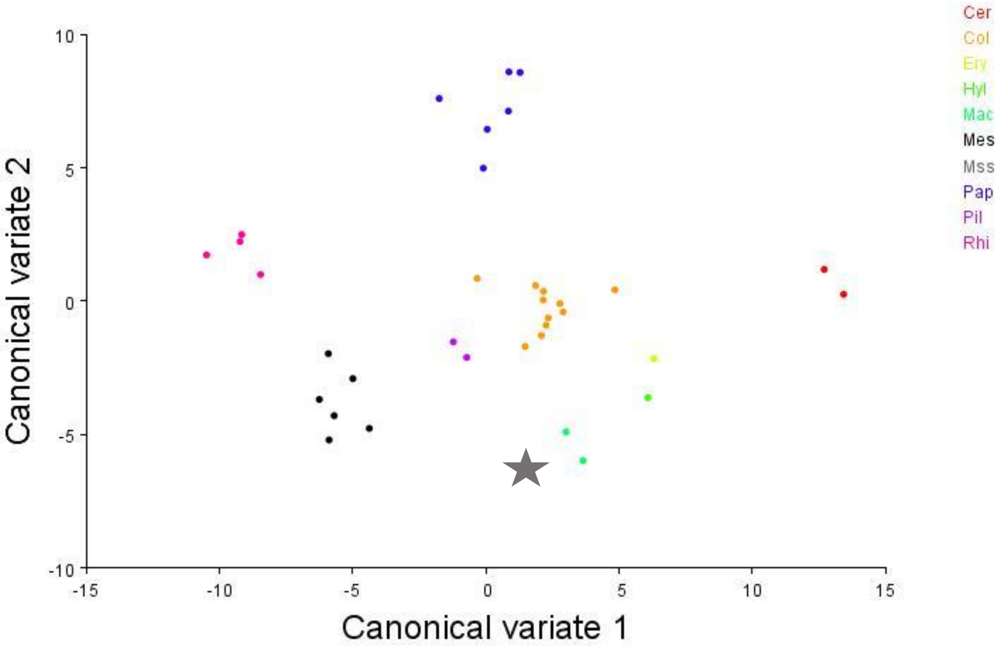

Figure 23. Canonical variety analysis of the medial side landmarks excluding *Theropithecus.* See Fig. 12.

The Shuitangba femur is still closer to the arboreal side, regardless of the lack of adequate data. This side presented many difficulties in its discriminative power, probably due to lack of adequate data and to differences in the view angle of the pictures used for the analysis.

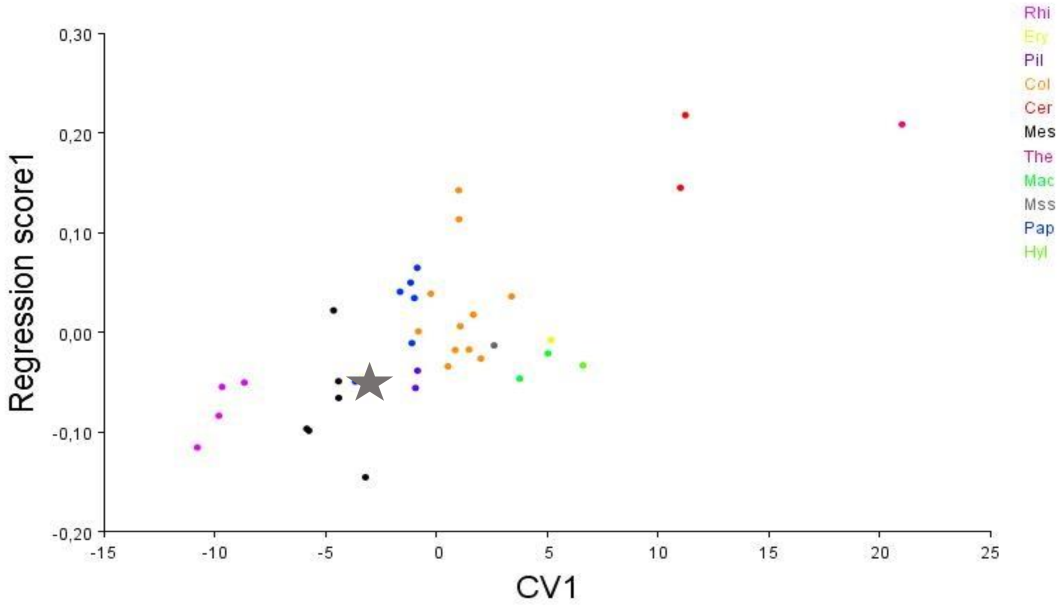

Figure 24. Regression analysis on CV1 of the medial landmarks. See Fig. 12.

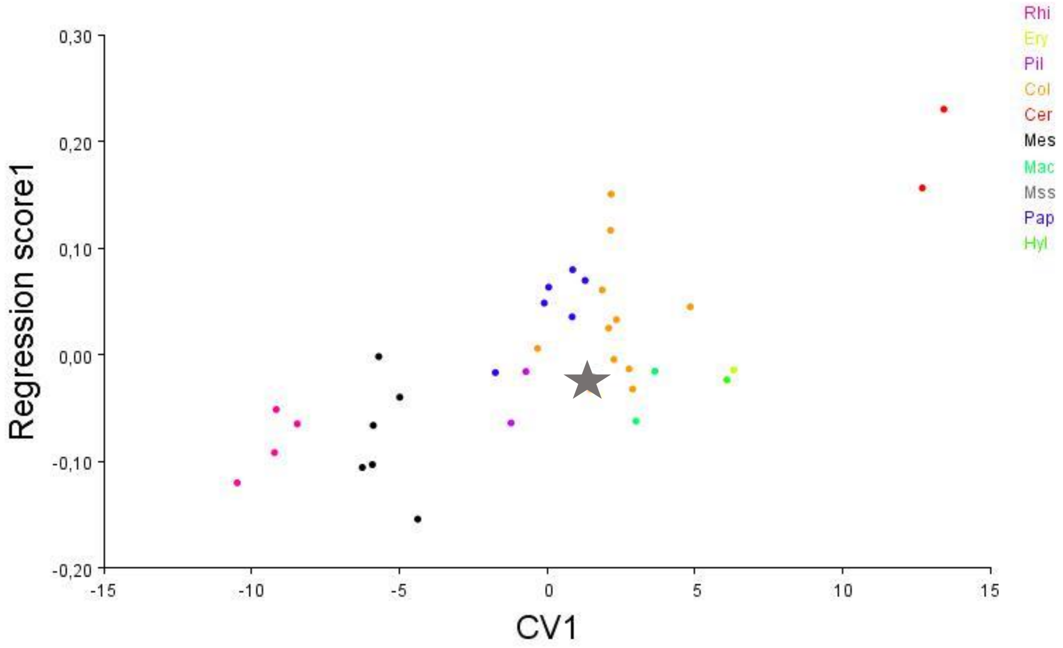

Figure 25. Canonical variety analysis of the medial side landmarks excluding *Theropithecus*. See Fig. 12.

The regression analysis for this side does not provide any discriminative results (Figs. 24, 25). However, the Shuitangba femur is always placed next to the *Colobus* group.

Discriminant Analysis (DA)

Discriminant analysis was also performed for the anterior and posterior side with some interesting findings.

In the posterior view analysis, a grading from the most terrestrial species (*Papio*) to the most arboreal (*Hylobates*) is noticed (Fig. 26). The *Mesopithecus* group lies in the middle, but the femur from China is somewhat closer to the arboreal side. Both are also near the *Colobus* group. When *Theropithecus* is excluded, the results are still similar (Fig. 27). The only noticeable difference is that the Shuitangba femur is now placed closer to the middle of the terrestrial/arboreal grading and closer to the group of *Macaca*.

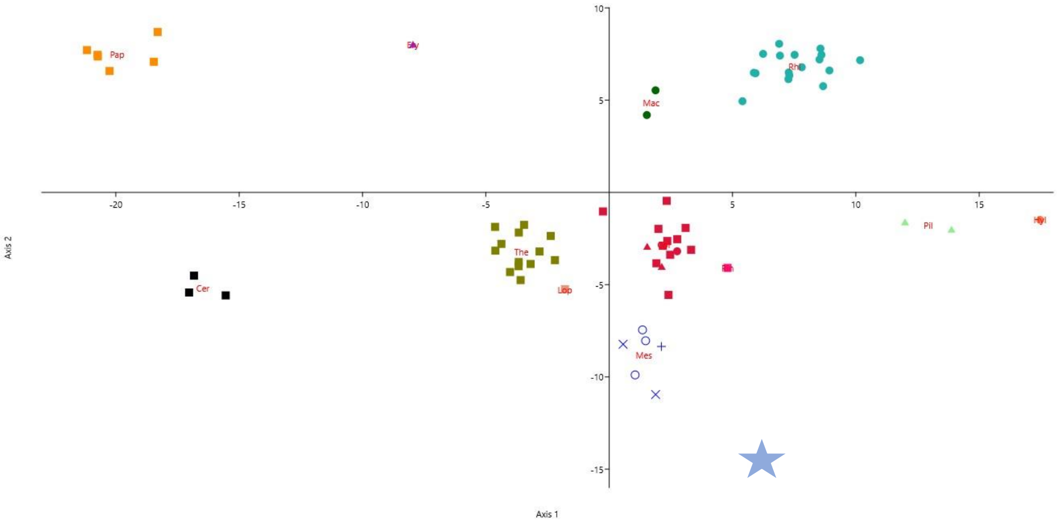

Figure 26. Discriminant analysis of the posterior side landmarks. Cer: black, Pap: orange, Ery: purple, The: oil, Lop: pink, Mes: blue, Mss: light blue, Col: fuchsia, Rin: dark pink, Mac: green, Rhi: light blue, Pil: light green, Hyl: light orange.

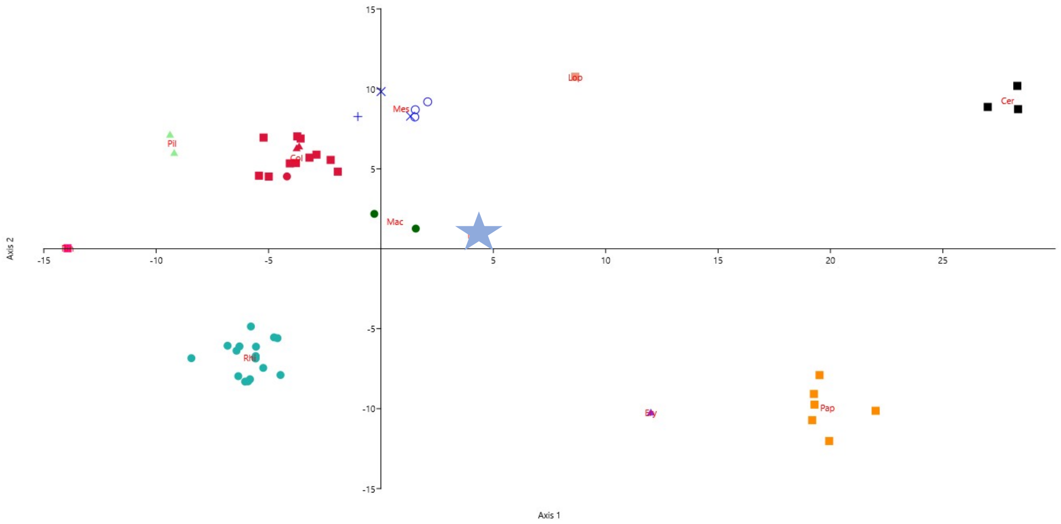

Figure 27. Discriminant analysis of the posterior side landmarks excluding *Theropithecus*. See Fig. 26.

In the anterior view the terrestrial/arboreal grading is also apparent (Fig. 28). The *Mesopithecus* group is placed in the arboreal part of the grading, but the Shuitangba femur is not close to the rest of this group. It seems to be closer to *Colobus*, *Piliocolobus* and *Macaca*. When *Theropithecus* is excluded, the grading does not change greatly (Fig. 29). The difference is that the *Mesopithecus* group is closer to the *Rhinopithecus* one, but the Shuitangba femur is located between *Colobus* and *Piliocolobus*.

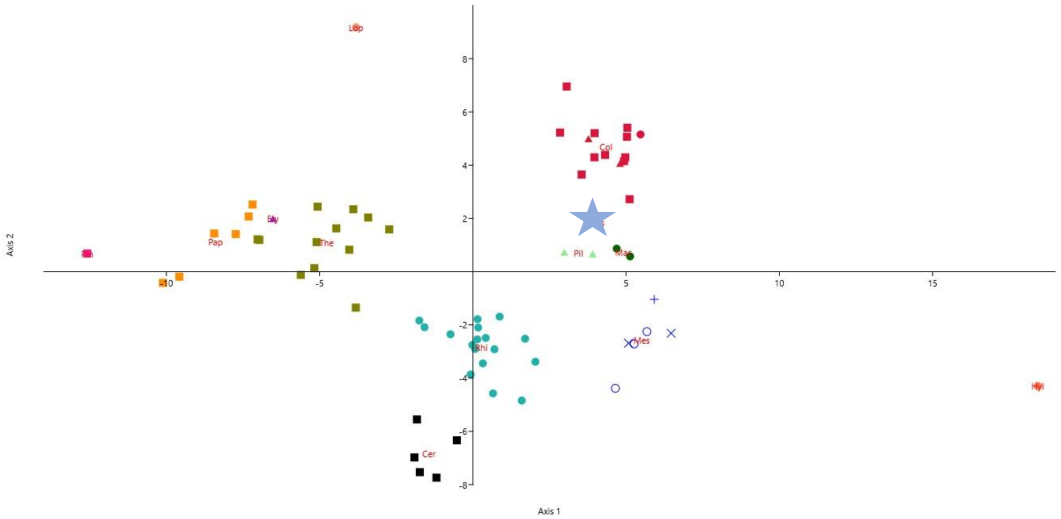

Figure 28. Discriminant analysis of the anterior side landmarks. See Fig. 26.

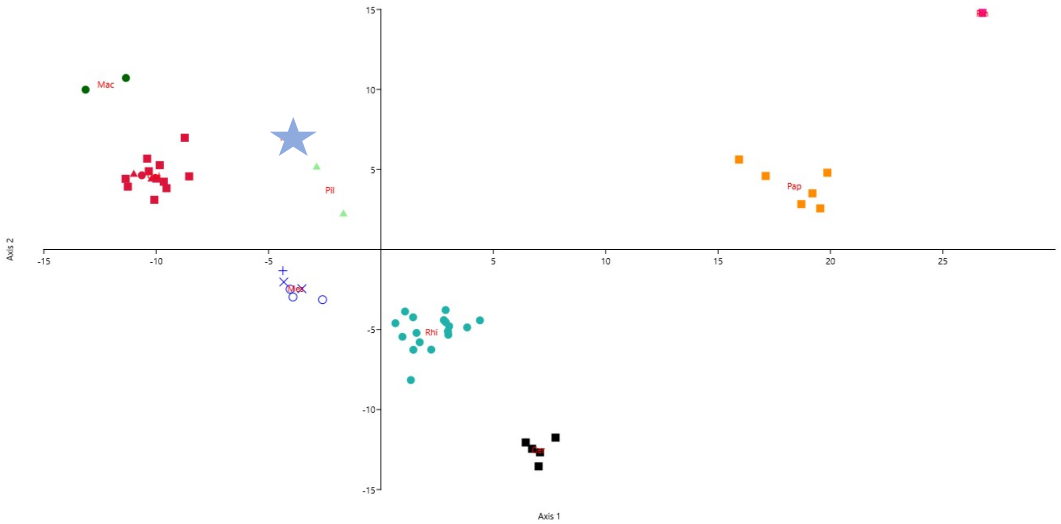

Figure 29. Discriminant analysis of the anterior side landmarks excluding *Theropithecus*. See Fig. 26.

4. Discussion

A) Taxonomic Validity and Affinities

Ji et al. (2020) studied the calcaneus found in Shuitangba and Jablonski et al. (2020) the mandible and teeth from the same site. They both concluded that the specimens belonged to *M. pentelicus* based on morphological features and biometric analyses. Since the proximal femur was found near the mandible, it was also considered to belong to *M. pentelicus* too. In this thesis, the anatomical comparison between the Shuitangba colobine femur and European *Mesopithecus* specimens revealed however some notable differences, particularly in the crest connecting the greater and lesser trochanters. While the Shuitangba femur shares some similarities with *Mesopithecus* from Greece and Bulgaria, such as the shape and size of the greater and lesser trochanter, it also exhibits distinct features, such as the shape of the trochanteric crest and the placement of fovea capitis, indicating potential taxonomic differences or evolutionary divergence. Moreover, the morphological dissimilarities between the Shuitangba femur and other femora, such as those of *Colobus* and *Papio*, like the shape of the trochanteric crest and the width of the trochanteric fossa, further underline its unique characteristics. These findings suggest that the Shuitangba specimen may represent a distinct taxon within the colobine lineage, possibly related to *Mesopithecus* but exhibiting different adaptations than *M. pentelicus*. Overall, this study shows that there are not enough data supporting the placement of the Shuitangba femur to *Mesopithecus pentelicus* and suggests it should be referred to as *Mesopithecus* sp. with ecological affinities to the African colobines, until more thorough studies are conducted.

B) Ecological Implications

Research on the morphology of the femur has garnered considerable attention due to its significance in the locomotor adaptations of mammals. Numerous studies have focused on the relationship between femoral morphology and the diverse locomotor strategies employed by mammals in various environments. The study by Frost and Bartels (2020) examined the relationship between femoral neck-shaft angle and locomotor performance in primates, providing valuable insights into how femoral morphology influences mammalian movement. Ciochon & Corruccini (1974), McHenry (1975), MacLatchy & Bossert (1996), DeSilva, et al. (2006), Harmon (2006, 2007 and 2009), Nakatsukasa, et al. (2012), Pina, et al. (2019), and Rein (2020) have also contributed significantly to our understanding of femoral morphology and its functional associations with mammalian locomotion. These studies collectively highlight the importance of femoral morphology in relation to locomotor behaviour and ecological adaptations in mammals.

The present ecomorphological analysis, particularly through the Canonical Variates Analysis (CVA), provides insights into the functional morphology of the Shuitangba femur and the locomotor behaviour, and ecological niche of the colobine to which it belongs. The femoral morphology, characterized by a large femoral head, deep trochanteric fossa, and prominent trochanters, indicates adaptations for arboreal locomotion.

In all our analyses, the placement of the Shuitangba femur in the 2D morphospace, suggests a clear clustering with arboreal taxa like the extant *Colobus*. In the environment where Colobus monkeys reside, such as tropical forests and wooded habitats, their locomotion is predominantly characterized by arboreal quadrupedalism (Morbeck, 1977). *Colobus* monkeys are known for their specialized anatomical features that facilitate efficient movement in their arboreal habitats. These features include elongated limbs, reduced thumbs, and a highly mobile shoulder joint, allowing them to navigate complex canopy structures with agility and precision (Fleagle, 2013).

Studies focusing on the locomotion of *Colobus* monkeys, such as those by Morbeck (1977), Rose (1978), Gebo & Chapman (1995), McGraw (1996), Schubert (2011), Dunham & McGraw (2014), have emphasized the adaptations of their skeletal anatomy to their arboreal lifestyle. The long, slender limbs of Colobus monkeys are particularly suited for climbing behaviours and leaping between branches (Strasser & Delson, 1987). The reduced thumb, characteristic of colobines, aids in grasping branches and supports their specialized feeding habits (Andrews, et al., 1996).

Furthermore, research on the musculoskeletal anatomy of *Colobus* monkeys, such as that conducted by Morbeck (1977), has highlighted the adaptations of their limb muscles to facilitate efficient locomotion in the canopy. These studies have revealed the presence of powerful forelimb muscles and robust shoulder joints, enabling *Colobus* monkeys to support their body weight while swinging and climbing (Gebo & Chapman, 1995).

Transitioning to the study of *Mesopithecus*, a genus closely related to colobine monkeys, the locomotor adaptations differ due to ecological and evolutionary factors. *Mesopithecus* exhibits a broader range of locomotor behaviours compared to Colobus monkeys, in the sense that is semiterrestrial using both the ground and the trees, reflecting its occupation of diverse habitats in the Late Miocene Eurasia. Research by de Bonis et al. (1990) and Andrews et al. (1996) has suggested that *Mesopithecus* likely engaged in both arboreal and terrestrial locomotion, similar to some modern colobines like *Semnopithecus*. The skeletal morphology of *Mesopithecus*, as described by Zapfe (1991), reflects a balance between arboreal agility and terrestrial adaptations, indicating a more generalized locomotor repertoire compared to *Colobus* monkeys. *Mesopithecus* likely inhabited various environments ranging from forested areas to open grasslands, influencing its locomotor strategies and anatomical adaptations (Koufos, 2009; Youlatos & Koufos, 2010; Bogdanova, et al., 2023).

The semi-arboreal locomotor strategy of the Shuitangba colobine aligns with the environmental context of the Shuitangba locality. The latter is characterized by densely vegetated, moist forest habitats. In the Late Miocene of SW China, the environment was characterized by a mosaic of subtropical forests, woodlands, and grasslands, and primates most likely faced diverse ecological challenges and opportunities. This habitat diversity likely influenced their locomotor adaptations and behavioural strategies (Li, et al., 2019). The dense canopy structure of subtropical forests in regions like Yunnan Province provided ideal conditions for arboreal locomotion and canopy crossings (Wang, et al., 2016). This environment favoured species capable of efficient leaping between branches, such as *Colobus* monkeys (Harrison & Delson, 2007).

However, the landscape was not uniform, with open grasslands and wooded habitats also present (Zhang, et al., 1989). These varied habitats offered opportunities for terrestrial locomotion and ground-dwelling behaviours, contributing to the ecological complexity of the region (Jablonski, et al., 2014). In response to this heterogeneous environment, *Mesopithecus* likely exhibited a semi-terrestrial locomotor repertoire, combining elements of both arboreal and terrestrial behaviors (Jablonski, 1995). This adaptation allowed *Mesopithecus* to efficiently navigate between forested areas and open landscapes, accessing a wider range of food resources and minimizing competition with other primate species (Karanth, et al., 2010).

Integrating information about the Late Miocene Chinese environment with comparative anatomical studies of *Mesopithecus* and modern colobines enhances our understanding of primate evolution and ecosystem dynamics during this critical period (Delson, 1973). This broader ecological perspective sheds light on the adaptive significance of locomotor morphology and behaviour in response to habitat diversity and ecological pressures (Jablonski & Leakey, 2008).

C) Paleobiogeography

Comparisons with European *Mesopithecus* specimens from Greece and Bulgaria reveal notable differences in femoral morphology, suggesting potential regional variation within the *Mesopithecus* lineage. This finding contributes to ongoing debates about the dispersal and evolution of early colobine primates across Eurasia. The Shuitangba femur exhibits morphological similarities with extant African colobine genera, particularly *Colobus* and *Piliocolobus*. This resemblance supports hypotheses of shared locomotor adaptations among colobine primates, despite geographic and temporal differences. Comparative analyses of femoral morphology between Shuitangba and other cercopithecoids provide insights into locomotor behavior and ecological adaptations. These comparisons corroborate previous studies highlighting the role of functional morphology in understanding primate paleobiology.

Integration of ecomorphological data from the Shuitangba specimen into broader paleoecological frameworks enhances our understanding of primate evolution in southwestern China during the Late Miocene. By synthesizing findings from multiple studies, researchers can refine paleoenvironmental reconstructions and elucidate the ecological dynamics shaping primate diversity in this region.

D) Evolutionary Significance

The presence of colobine fossils in Shuitangba expands the known geographic range of *Mesopithecus* to southwestern China during the Late Miocene, concurrent with its diversification within Europe. The close resemblance between the Shuitangba specimen and European *Mesopithecus* fossils, coupled with their similar geological ages, suggests potential dispersal events and evolutionary connections between Asian and European colobine populations. Furthermore, the ecomorphological differences between the Shuitangba femur and European *Mesopithecus* specimens indicate convergent evolution toward semi-arboreal locomotion in response to comparable environmental pressures (Jablonski, et al., 2020).

E) Limitations and Future Directions

While this study provides valuable insights into the ecomorphology and taxonomic affinities of the Shuitangba colobine femur, several limitations should be acknowledged. The sample size, particularly for comparative extant taxa, could be expanded to enhance the robustness of the analyses. Additionally, the reliance on femoral morphology for inferring locomotor behaviour may overlook other anatomical adaptations relevant to ecological niche occupation. Future research could integrate multiple anatomical features and incorporate biomechanical analyses to further elucidate the locomotor ecology of fossil colobines.

The comparative approach underscores the importance of interdisciplinary research in elucidating primate evolutionary history. By synthesizing data from paleontology, functional morphology, and paleoecology, scholars can construct more comprehensive narratives of primate evolution and ecosystem dynamics over time. The Shuitangba femur serves as a valuable case study in this endeavor, offering insights into the locomotor adaptations and ecological niches of early colobine primates in southwestern China.

5. Conclusion

The ecomorphological analysis of the Shuitangba colobine femur contributes to our understanding of primate evolution, highlighting the complex interplay between anatomical adaptations, ecological dynamics, and biogeographic processes shaping the evolutionary history of colobine monkeys. Our analysis showed that the Shuitangba femur cannot clearly be safely attributed to *Mesopithecus pentelicus*. Further investigations into the paleobiology of fossil primates will continue to unravel the intricate patterns of adaptation and diversification within this diverse group of mammals.

The ecomorphological analysis of the Shuitangba proximal femur offers valuable insights into the locomotor behavior and ecological adaptations of early colobine primates in southwestern China. Its locomotion appears to be a mixture of terrestrial and arboreal characteristics. Through a combination of qualitative and quantitative methods, this research enhances our understanding of primate evolution and underscores the importance of functional morphology in reconstructing paleoenvironments and paleoecology.

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