

Functional anatomy of the calcaneum and talus in Cercopithecinae (Mammalia, Primates, Cercopithecidae)

Anatomía funcional del calcáneo y el astrágalo en Cercopithecinae (Mammalia, Primates, Cercopithecidae)

M. Pina¹, M.J. Salesa², M. Antón², J.F. Pastor³

ABSTRACT

Among the species of the order Primates exist a huge variety of forms and habitats. This heterogeneity has encouraged the evolution and development of a great number of locomotor adaptations to different environments. Thus, nowadays there are both arboreal and terrestrial groups within the order. The subfamily Cercopithecinae present taxa with both kinds of locomotor behaviours, although the most of them are adapted to a ground life-style. This group probably has an arboreal ancestor and its radiation is relatively recent. Consequently, species belonged to this group present mixed features or sometimes not too much derived ones. Likewise, it is important the fact that the evolutionary history and phylogeny of the group could influence in some characteristics. Both the calcaneum and the talus are two of the largest bones of the foot and are good for inferring the kind of locomotion. For this reason, it has been used these two tarsal bones to study the morphology of eight species of cercopithecines and then deduce functional implications of the kind of locomotion.

Key words: Primates, Cercopithecinae, calcaneum, talus, functional anatomy

RESUMEN

Dentro del orden Primates existe una gran variedad de especies distribuidas a lo largo de hábitats muy diversos. Dicha heterogeneidad ha fomentado la evolución y desarrollo de un gran número de adaptaciones locomotoras a los diferentes ambientes en los que habitan. Así, existen en la actualidad tanto grupos arborícolas como terrestres. La subfamilia Cercopithecinae agrupa una serie de taxones que representan ambos comportamientos locomotores, aunque la mayoría de las especies están adaptadas a una vida en el suelo. Se supone que este grupo desciende de un ancestro arborícola y que su radiación es relativamente reciente. En consecuencia, las especies de este grupo presentan características mixtas o poco derivadas en algunas ocasiones. Asimismo, es importante tener en cuenta la influencia que la herencia filogenética puede tener sobre alguno de estos rasgos. El calcáneo y el astrágalo son dos de los huesos más grandes del pie y ambos son buenos indicadores del tipo de locomoción. Por este motivo, se han utilizado estos dos tarsales para llevar a cabo el estudio de la morfología de ocho especies de cercopitecoideos, de tal manera que luego se ha podido hacer una serie de inferencias funcionales en cuanto al tipo de locomoción de las mismas.

Palabras clave: Primates, Cercopithecinae, calcáneo, astrágalo, anatomía funcional

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Introduction

The order Primates includes more than 200 extant species with a great variety of body sizes, appearances and habitat preferences (MacDonald, 1991; Campbell, 1998). Consequently, the group exhibits a significant variety of locomotor behaviours, which imply differences in bone structure and morphology, and both calcaneum and talus reflect such different types of locomotion (Gebo, 1993; Ankel-Simons, 2007). A postcranial skeleton adapted to a climbing and leaping life, as well as hands and feet evolved for an effective grasping, are features allowing primates to be regular arboreal dwellers (Campbell, 1998; Ankel-Simons, 2007). In consequence, most of the extant species present primitive features related to locomotion, such as a five-fingered hands and feet, or a great mobility of forelimbs and hind limbs (Napier & Napier, 1967; Campbell, 1998).

It has been proposed that the ancestral condition in anthropoid Primates from Eocene was arboreality (Gebo, 1986; Fleagle, 1999; Kay *et al.*, 1997). Some authors propose that these first anthropoids practiced a kind of locomotion similar to the current vertical clinging and leaping species (Napier & Walker, 1967). However, others (e.g., Rollinson & Martin, 1981, Kay *et al.*, 1997 or Campbell, 1998) suggest that the anthropoid ancestor presented a hind limb dominated arboreal quadrupedalism, based mainly on postcranial evidences and body size estimations (Gebo, 1986; Rollinson & Martin, 1981; Jablonski *et al.*, 2002). Onward on time, some primitive cercopithecines developed more terrestrial habits, coming down to the ground, and adapting their anatomy to a new lifestyle (Kay *et al.*, 1997; Jablonski, 2002). As expected, they increased their size and the length of the forelimbs, and thus they tended to stabilize their movements (i.e., cercopithecoids) (Campbell, 1998). Most of the Old World monkeys, belonging to the superfamily Cercopithecoidea, are adapted to a terrestrial life (Groves, 2001). The distribution area of cercopithecoids spreads to both sides of the equatorial zone, mainly middle-south Africa, India and southeastern of Asia. Throughout this territory, it is possible to find this type of primates in a wide range of latitudes, climates and habitats, from tropical rainforest to mountains, savannahs or even shrublands (Napier & Napier, 1967; MacDonald, 1991; Fleagle, 1999). This diversity has encouraged species to develop different adaptations to

the habitats according to the specific necessities of the area in which they live. Among these specializations, those related to locomotion are especially important since they enable the animal to move efficiently when foraging or escaping predators (Campbell, 1998; Fleagle, 1999). The direct consequence of this fact is the possibility to find species of cercopithecoids adapted to a wide range of modes of life; from arboreal to terrestrial life, and even intermediate, or semi-terrestrial, species whose life happens between both the ground and the trees (Patel, 2010). Among these taxa, there are some arboreal quadrupeds (which secondarily came back to the trees) (Jablonski, 2002), such as the genus *Macaca*, which share several features with typical arboreal species, like a long tail. Also, there are terrestrial quadruped species, such as those belonging to the *Papio* genus, that are larger and have developed adaptations for a higher stability of the forelimb (Napier & Napier, 1967; MacDonald, 1991; Campbell, 1998). It is important to underline that each adaptation for a new environment is constrained by the genetic legacy of the group (Campbell, 1998). In this case, cercopithecoids were terrestrial forms during a long time in their evolution and lost many of the arboreal features that their ancestors probably had (Gebo, 1993; Hartwig, 2002). All the extant arboreal cercopithecoid species live on trees as a consequence of a secondary process of adaptation to this substrate from terrestrial forms (Gebo, 1993; Hartwig, 2002). They are supposed to have had an arboreal ancestor, but, during their first radiation (dated at the beginning of the late Miocene), several terrestrial forms evolved, developing a set of adaptations for this new locomotor style (Campbell, 1998; Jablonski, 2002). In recent times, a second radiation occurred, and several arboreal species evolved from terrestrial ancestors, which produced the development of secondary adaptations for arboreality. This new adaptation was relatively recent, and that is the reason why the arboreal species do not show extreme specializations for arboreal locomotion (Gebo, 1993; Benefit, 1999), and the anatomical and morphological differences between arboreal and terrestrial species of the group are really scarce. Thus, phylogenetic relationships among cercopithecoids are often controversial and, as related species could be adapted to extremely different habitats or substrates (Fleagle, 1999; Groves, 2001). Likewise, species belonging to the same genus can differ in their anatomy and bear

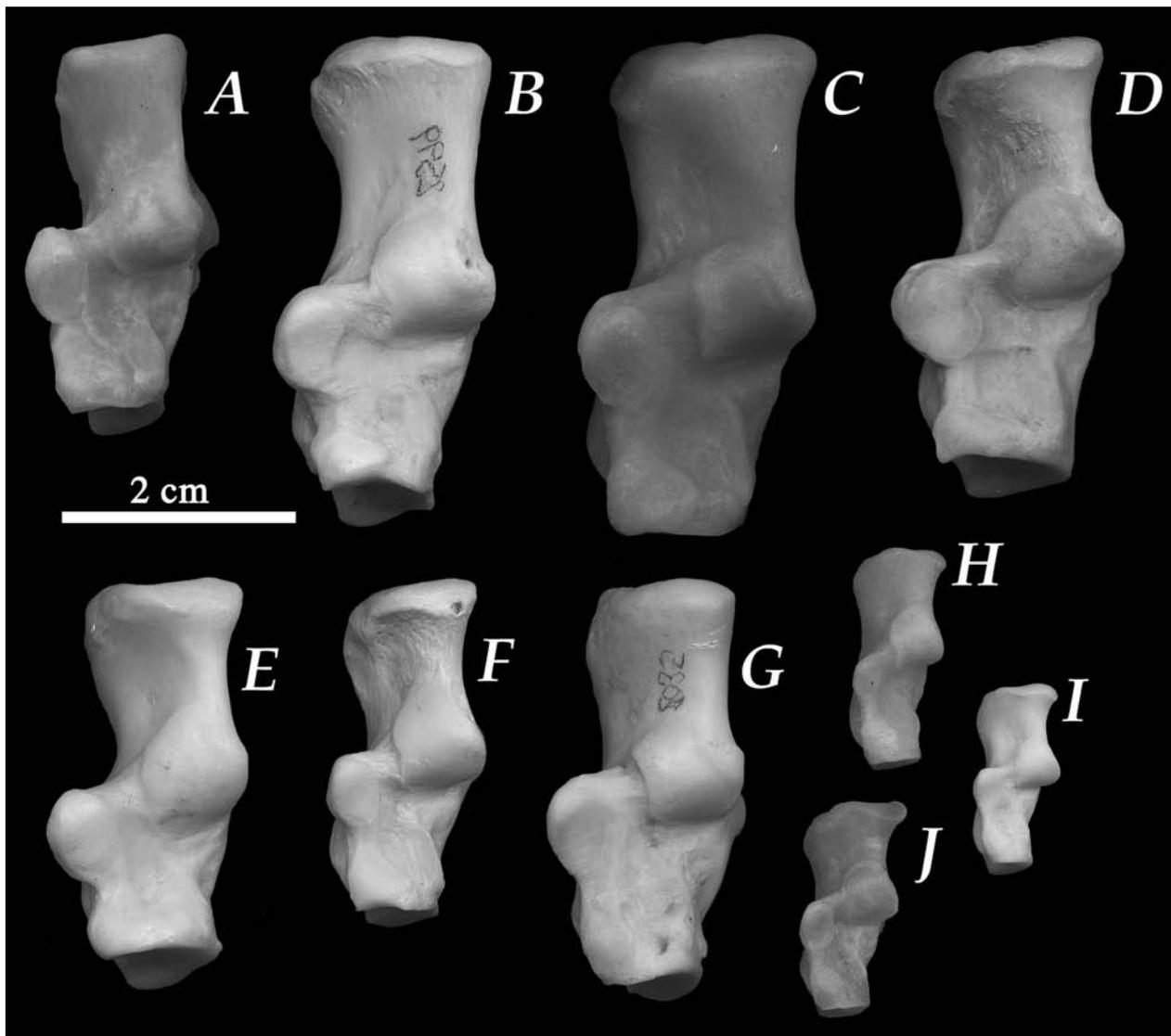


Fig. 1.—Dorsal view of the calcaneum of *M. nigra* (A), *M. sylvanus* (B), *P. hamadryas* (C: male, D: female), *M. tonkeana* (E), *M. fascicularis* (F), *L. albigena* (G) and *Mi. talapoin* (H, I and J).

more resemblance to other genera. In contrast, non-related species can be highly similar in appearance (Gebo, 1993). This makes difficult to tell which anatomical features are consequence of locomotor adaptations, and which are derived from the evolutionary history of the group.

In view of this, the main aim of this work is to perform a functional analysis of both the calcaneum and the talus among several species of Cercopithecinae, to better understand the morphological correlates of different postural behaviours and types of locomotion between arboreal and terrestrial species.

Material and Methods

The calcaneum and talus of eight extant species of the subfamily Cercopithecinae were analyzed in this study. They represent all the types of locomotion of this group: one terrestrial species, *Papio hamadryas* (MAV-5426, female, and MAV-3097, male); two semi-terrestrial species, *Macaca nigra*, (MAV-3520, female) and *Macaca sylvanus* (MAV-2599, male); and four arboreal species, *Macaca fascicularis* (MAV-2887, male), *Macaca tonkeana* (MAV-3251, female), *Lophocebus albigena* (MAV-2035, male), and *Miopithecus talapoin* (MAV-2004, female, MAV-223, male, and MAV-5443, male). These specimens belong to the collections of the Museo Anatómico of the Universidad de Valladolid (Valladolid, Spain).

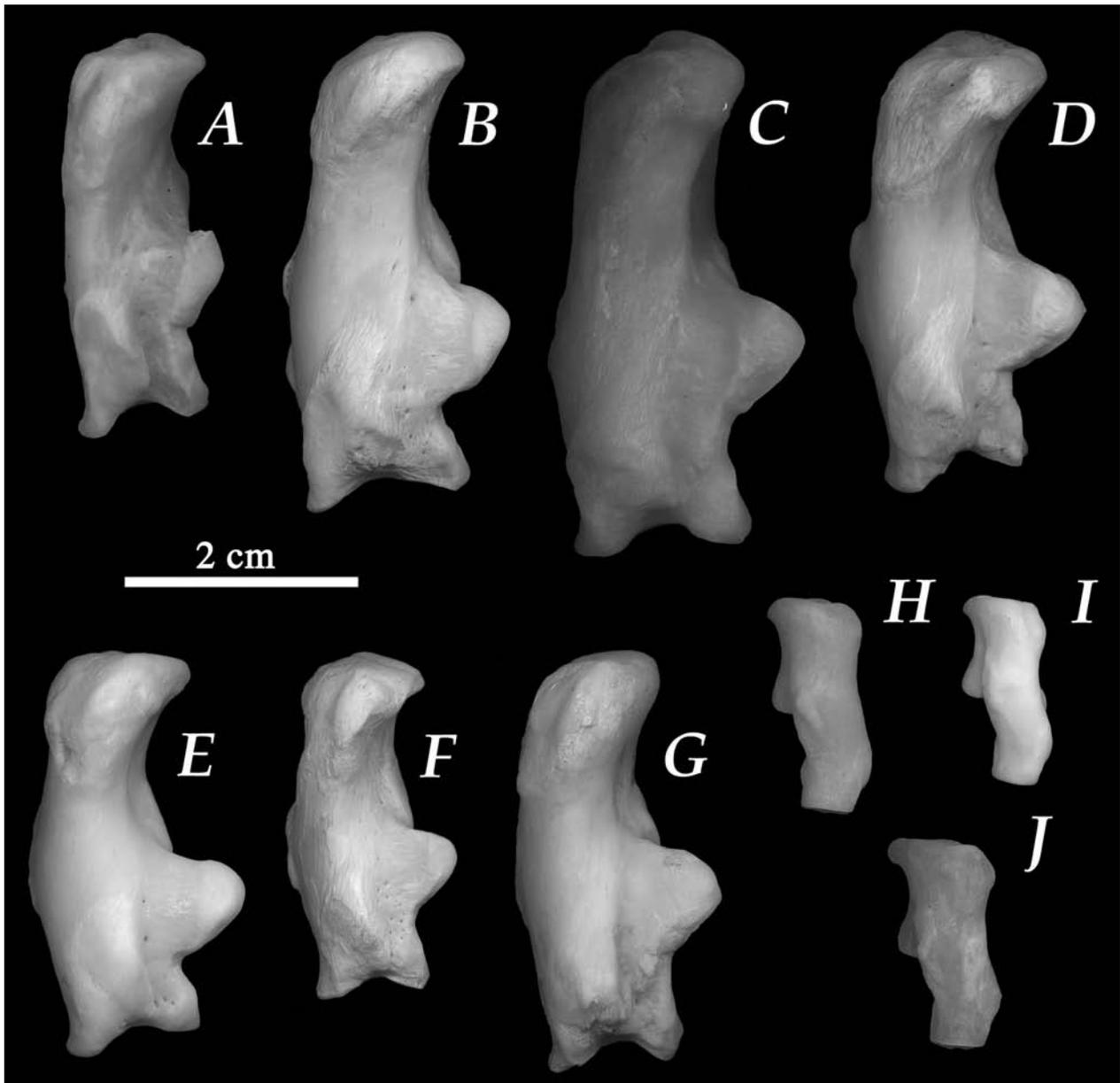


Fig. 2.—Plantar view of the calcaneum of *M. nigra* (A), *M. sylvanus* (B), *P. hamadryas* (C: male, D: female), *M. tonkeana* (E), *M. fascicularis* (F), *L. albigena* (G) and *Mi. talapoin* (H, I and J).

For the anatomical descriptions, we have followed the terminology used by Barone (1999, 2000), and the *Nomina Anatomica Veterinaria* (2005).

Morphological Observations

The following section consists in a brief anatomical description of both calcaneum and talus, in order to point out the differences among the analyzed species.

Calcaneum

The calcaneum is one of the largest bones of the ankle; dorsally it articulates with the talus, and distally with the cuboid. The body of the bone is relatively short, but develops a large proximal projection, the *tuber calcanei*, where the calcaneal tendon, a common tendon for the muscles *soleus*, *gastrocnemius* and *plantaris*, is attached. The attachment area is larger in arboreal cercopithecines than in terrestrials, and it turns towards the distal margin in these species (fig. 1).

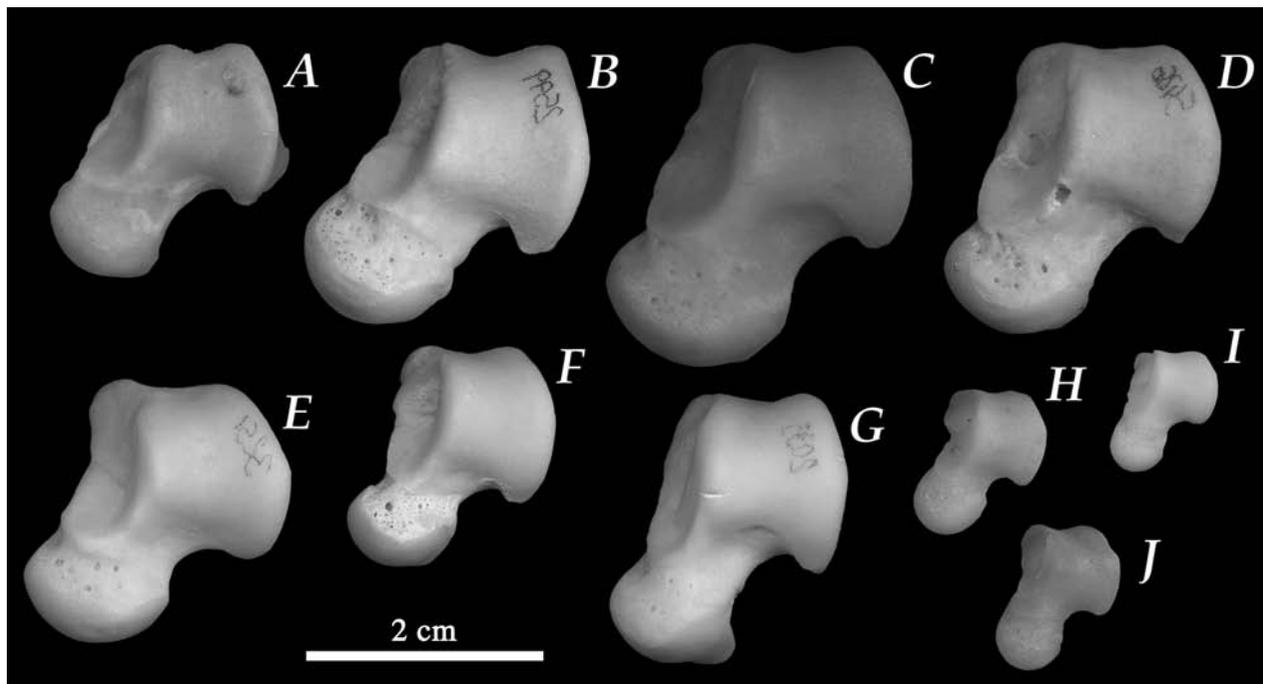


Fig. 3.—Dorsal view of the talus of *M. nigra* (A), *M. sylvanus* (B), *P. hamadryas* (C: male, D: female), *M. tonkeana* (E), *M. fascicularis* (F), *L. albigena* (G) and *Mi. talapoin* (H, I and J).

In general, the *tuber calcanei* is more developed in the arboreal species.

The articulation facet for the cuboid, on the distal part of the calcaneum, shows a lateral orientation, particularly in *M. tonkeana* and *M. fascicularis*. However, the calcaneum of terrestrial cercopithecoids is straighter than that of the other species (fig. 2). Furthermore, the articular surface for the cuboid is more concave in the four species of the genus *Macaca*. The dorso-proximal half is characterized for the presence of the articular surfaces (proximal, middle and distal) for the talus. The *sulcus calcanei* is found among the three articular surfaces of the calcaneum, and is deeper in the terrestrial cercopithecines (mainly in *M. nigra*). The proximal articular surface is approximately located in the middle of the bone and is dorso-distally oriented. It creates a visible step, less marked in *P. hamadryas*, *M. nigra* and *M. tonkeana*, and showing a sharper shape in *M. sylvanus*, *M. fascicularis*, *L. albigena* and *Mi. talapoin*.

The coracoid process, in the lateral side of the articular surface, is more developed in *P. hamadryas* and *L. albigena*. The middle articular surface has a lateral orientation and is located in the proximal zone of the *sustentaculum tali*. This articular surface is situated relatively close to the distal one in *Macaca*, *L. albigena* and *Mi. talapoin* (in *M. fascicularis* they are even together), and the distance between them is higher in *P. hamadryas*. The distal articular surface is placed in the distal margin of the calcaneum and is dorso-proximally oriented. *Lophocebus albigena* and *Mi. talapoin* have a small articular surface, medially oriented, while in *M. nigra* and *M. tonkeana* the orientation is almost proximal.

There is a groove for the tendon of the muscle *fibularis longus* located between the coracoid process and the trochlear

process, throughout the lateral side. This groove is especially deep in *M. nigra* and *M. fascicularis*. The scar for the attachment of the muscle *quadratus plantae*, on the lateral surface of the calcaneum, shows different development and roughness depending on the species, this structure is larger and more marked in the arboreal species than in the terrestrial ones (as is evident in *M. fascicularis*).

Talus

The talus of the studied sample retains a primitive morphology. Three parts can be distinguished: the body, the distal neck and the talus head. The head articulates with the navicular, whereas the dorsal surface articulates with the distal epiphysis of the tibia. The articular surface for the tibia or trochlea is well-developed, and shows a smooth surface with a subtle valley in the middle. The lateral edge of the trochlea expands dorsally and distally (more than the medial one) (fig. 3). There are several differences in the medial side of the trochlea. In *M. fascicularis*, *L. albigena* and *Mi. talapoin* the articular surface is larger and spreads by the medial margin of the trochlea. These three species present a longer neck, in contrast to the rest of the taxa, in which it is well developed, and with a dorso-proximal orientation. In the proximal border, the two tubercles of the talar process (lateral and medial) are visible, and also the groove for the passage of the tendon of the muscle *flexor digitorum lateralis*, deeper in the *Macaca* species than in the rest of the studied specimens.

The neck of the talus is short and robust, and this is more evident in the terrestrial cercopithecines than in the arboreal

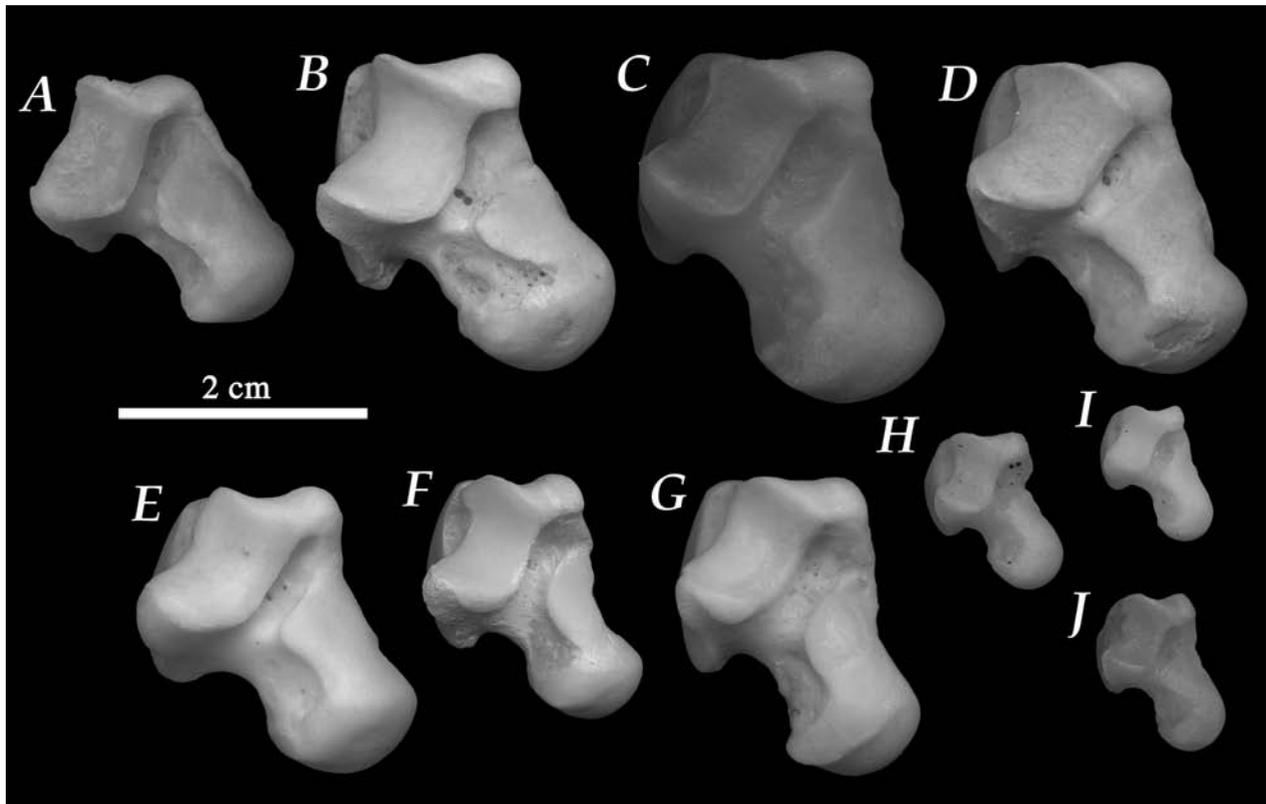


Fig. 4.—Plantar view of the talus of *M. nigra* (A), *M. sylvanus* (B), *P. hamadryas* (C: male, D: female), *M. tonkeana* (E), *M. fascicularis* (F), *L. albigena* (G) and *Mi. talapoin* (H, I and J).

species. Likewise, the neck of the terrestrial species is oriented medially, whereas that of the arboreal species is distally oriented (*M. tonkeana* shares the same morphology as terrestrial species).

In plantar view, the three articular surfaces for the calcaneum can be observed. The largest facet is the proximal one, which shows a smooth and concave surface; it is deeper in *M. sylvanus*, *M. fascicularis* and *L. albigena*. In these species, the proximal and distal borders are more developed (fig. 4). The middle articular surface for the calcaneum is wide and starts in the body of the talus, continuing along the neck (it only contacts with the *sustentaculum tali* of the calcaneum); this articular surface is well marked in arboreal cercopithecines, with the exception of *M. tonkeana*, whose morphology is closer to that of the terrestrial species. And finally, the third articular facet for the calcaneum, the distal one, is small and laterally oriented, with *M. fascicularis*, *L. albigena* and *Mi. talapoin* showing a relatively larger facet than that of other species.

Functional Implications

Calcaneum

Development of the *tuber calcanei* and the attachment of the calcaneal tendon.

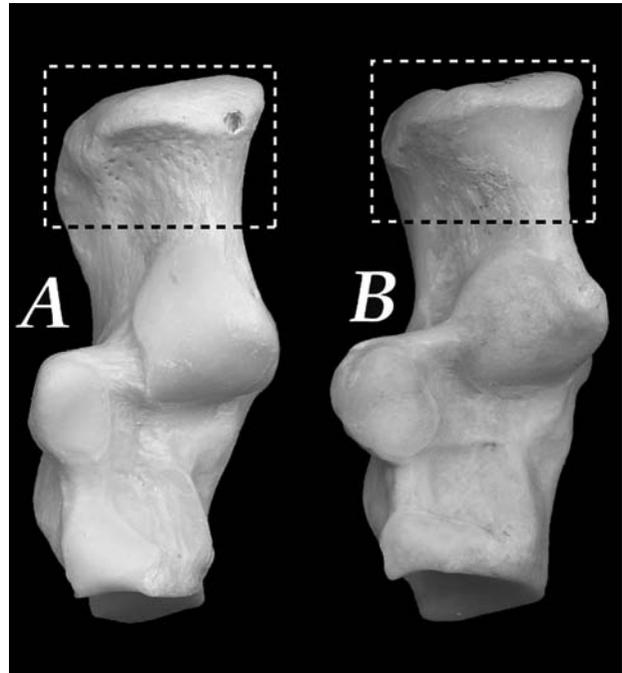


Fig. 5.—Differences of the *tuber calcanei* between terrestrial (A: *P. hamadryas*) and arboreal species (B: *M. fascicularis*).

The calcaneal tendon is a thick and strong structure composed by the distal tendons of the three extrinsic muscles of the leg: *gastrocnemius*, *soleus* and *plantaris* (Swindler & Wood, 1973; Gebo, 1993). These three muscles play an essential role in the plantar flexion of the foot, an important movement in propulsion (Gebo, 1993; Barone, 2000; Platzer, 2008). The arboreal species exhibit a greater use of these movements, since leaping is a significant component of their locomotion (Fleagle, 1999). Therefore, the increase in the development of these structures is higher in arboreal cercopithecines, especially the *tuber calcanei*, since it acts as an attachment area for the calcaneal tendon (fig. 5). Likewise, the calcaneum is relatively large in all cercopithecines. This fact allows the lever of propulsion to be increased and, consequently, the power of the *triceps surae* package of muscles (*gastrocnemius*, *soleus* and *plantaris*) (Strasser, 1988; Platzer, 2008).

Articular surfaces for the talus

As a consequence of the intrinsic morphology of the articulation between the talus and calcaneum, there is a reduction in its mobility, which is more evidenced in those movements, inversion and eversion, which characterize the primates (Hartman & Straus, 1969; Strasser, 1988). This is due to the decrease in the range of the latero-medial movements and the increase of the parasagittal one (Harrison, 1989). This morphology is clearly shown in *P. hamadryas*, especially in the proximal articular surface for the talus in the calcaneum, which is proximo-distally shorter and strongly curved. Both the relatively large body and the articular surface morphology in terrestrial species imply a better spread of the weight to the ground. Furthermore, this morphology prevents the talus from proximally moving during the race and decreases the range of the inversion and eversion movements of the ankle (Strasser, 1988; Harrison, 1989; Gebo, 1993). However, the articular surfaces of the arboreal species are characterized by a higher degree of mobility, as seen in *L. albigena* and *Mi. talapoin* (although they also tend to stabilize the articulations). Rotation movements (lateral and medial) of the ankle are important for locomotion on branches (Strasser, 1988).

Development of the muscle *fibularis longus*

As it has been described above, the muscle *fibularis longus* and other structures of the calcaneum

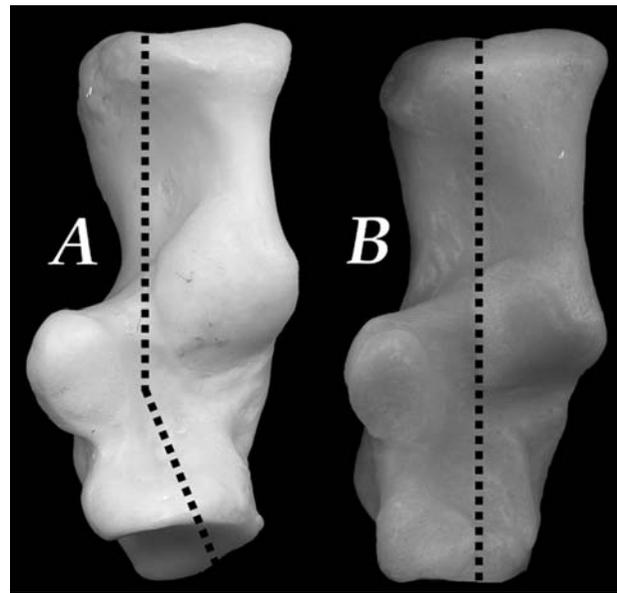


Fig. 6.—It can be seen that arboreal species, such as *M. tonkeana* (A), present a less straight calcaneum than the terrestrial ones, for example *P. hamadryas* (B). In order to this fact, the orientation of the cuboid articulation implies more divergent metatarsals.

(i.e., *sulcus calcanei*) are more developed in arboreal and semi-terrestrial species. This muscle is related to the eversion and plantar flexion of the foot (Barone, 2000; Platzer, 2008), important movements for arboreal locomotion.

Development of the muscle *quadratus plantae*

All the species show a well-developed groove for the muscle *quadratus plantae*, a structure that could be related to locomotion on the trees and the grasping to the branches. This muscle helps the muscles *flexor digitorum medialis* and *flexor digitorum lateralis* in the flexion of both the metatarso-phalangeal and interphalangeal joints of the toes (Barone, 2000; Platzer, 2008), and this fits with a higher development in the arboreal species.

Calcaneo-cuboid articulation

This articulation shows some differences among the studied species. The four species of *Macaca* have a less concave articular surface, while in *L. albigena*, *Mi. talapoin* and *P. hamadryas*, it is deeper. This seems to reflect a higher stability of the joint in the latter species (in principle, more useful for cursorial forms and less for arboreal species). However, it is possible that there is the existence of an

important phylogenetic component in this feature, since among the species of the genus *Macaca* there are different types of locomotion. Furthermore, terrestrial species present a straighter calcaneum and the articular surface for the cuboid is distally oriented (fig. 6B). Other species, such as *M. fascicularis* and *M. tonkeana* show a more lateral orientation of this surface, and in consequence, their metatarsals are more divergent (fig. 6A). For this reason, closer metatarsals are better adapted for running or cursoriality, while the divergence of the toes increases the effectiveness of walking on trees (Harrison, 1989).

Talus

Medial edge of the tibio-talar articulation

The morphology of the trochlea is associated with the degree of medial and lateral stabilization of the ankle articulation (Harrison, 1989). Within the analysed sample, the terrestrial species and *M. tonkeana* display a larger and deeper trochlea, whereas the arboreal species, mainly *L. albigena* and *Mi. talapoin*, show a shallower trochlea, with a medial orientation (fig. 7). Thus, the ankle articulation presents a higher stability in the terrestrial species, a typical feature of animals adapted to running (Strasser, 1988; Harrison, 1989). Likewise, the depth of the trochlea (especially the distal component) facilitates the stability of the movements during the dorsiflexion of the foot, thus increasing the effectiveness in propulsion (Harrison, 1989).

Trochlear asymmetry

When the lateral edge of the trochlea is more developed proximally than the medial one, this increases the abduction capacity in the dorsiflexion of the foot (Strasser, 1988). All the analysed species show this asymmetry, which is more evidenced in arboreal cercopithecines, probably because they need a wide range of movements during the arboreal locomotion (fig. 7). On the other hand, those terrestrial species adapted to cursoriality do not need such movements and they tend to stabilize all the articulations (Harrison, 1989; Nakatsukasa, 1994). A more proximally developed lateral margin of the trochlea produces a higher strength to the ankle joint during the rotational movements and facilitates those realized in a parasagittal plane, that is, the same plane in which the hind limb is moved during the race (Harrison, 1989).

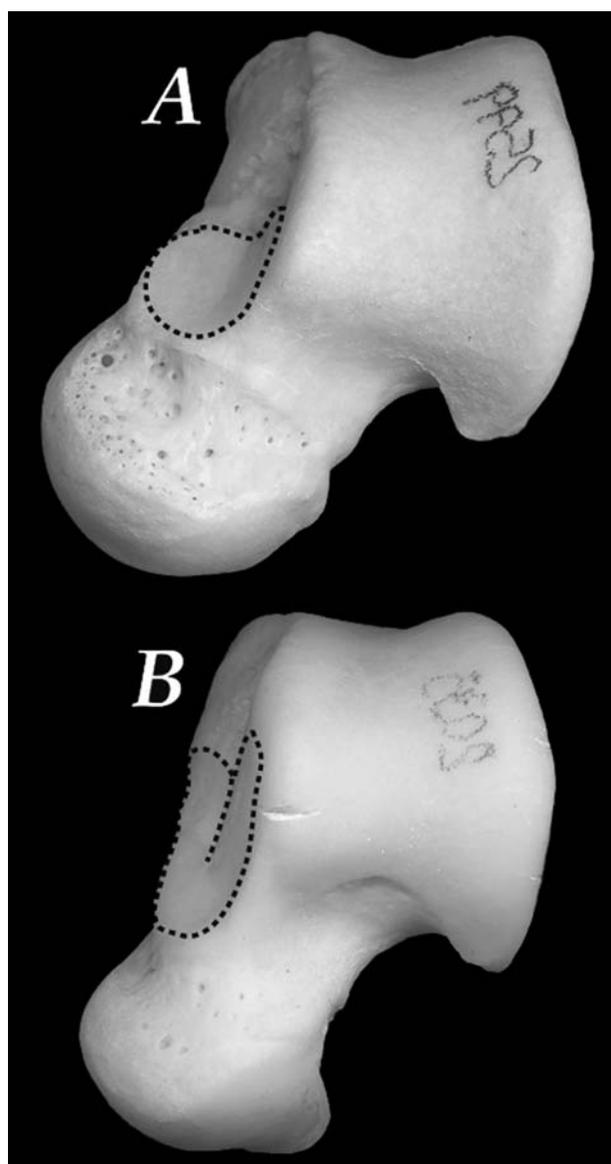


Fig. 7.—Differences of the articular surface between tibia and talus in A: *M. sylvanus* (terrestrial species) and B: *L. albigena* (arboreal species). The area inside the discontinuous line is the medial articular surface with the tibia.

Development of the muscle *flexor digitorum lateralis*

The four species of the genus *Macaca* show a relatively well-marked groove for the muscle *flexor digitorum lateralis*. The talar processes in the other species is less developed and, therefore, the groove is also less marked. This fact has two functional consequences. First, the stabilization of the ankle articulation and, second, the reduction of the muscle *flexor digitorum lateralis*. Both of them are related

to the reduction of the *hallux*, as well as with the grasping ability in the Old World monkeys (Harrison, 1989; Gebo, 1993). Thus, these consequences are relevant in arboreal species, and in a lesser extent in the terrestrial ones, since they do not need grasping for locomotion. In the *Macaca* species, this morphology is probably a primitive feature inherited from a terrestrial ancestor.

Orientation of the talus neck

Traditionally, the medial orientation of the talus neck has been associated with the presence of a prehensile *hallux* and with the capacity to abduct it (Harrison, 1989). However, in our studied sample of cercopithecines, this feature appears in the terrestrial species and *M. tonkeana*, whereas in the arboreal species the talus neck is distally oriented (fig. 7). It would be more expected to find this feature in those species with arboreal locomotion, because it contributes to a better grasping. In contrast, the talus neck is shorter and more robust in arboreal species, which implies a major stability and stiffness for the tarsus. So, our findings do not fit with previous suppositions on the neck morphology, and deeper studies should be done in order to clarify the actual relationship between the talus neck orientation and locomotor adaptations.

Conclusions

Our study shows that both the calcaneum and the talus of the terrestrial species of Cercopithecinae show several features indicating a higher degree of stabilization in the ankle articulation than the arboreal species. The terrestrial mammals have to reduce the lateral movements between the calcaneum and the talus in order to reduce the risk of dislocation during running, and, interestingly, the morphology of the terrestrial species of Cercopithecines reflects it. The morphology of the articular surfaces of both calcaneum and talus allow these bones to made preferential movements in the parasagittal plane, the plane in which the hind limbs move during the running. Likewise, these species present a more efficient spread of the body weight to the ground. A similar fact occurs with the joint between the calcaneum and the cuboid.

Regarding the talus, the terrestrial species present a well-developed lateral border of the trochlea and a deeper articular surface for the tibia. Both features

increase the stability of the articulation, and, by improving the effectiveness of the propulsion, they are helpful for cursorial forms. All the cited features are clearly shown in *P. hamadryas*, the most cursorial of all the studied species and, for this reason, it perfectly reflects adaptations for a life on the ground (MacDonald, 1991; Fleagle, 1999). On the contrary, the arboreal species show a higher mobility of the articulations, mainly in the eversion, dorsiflexion and plantar flexion of the foot. All these movements, in addition to the lever role of the calcaneum and the action of the muscle *triceps surae*, greatly improve the jumping. Also, a well-developed muscle *quadratus plantae*, as seen in the terrestrial species, is important for grasping, a significant character due to the necessity of grasping when moving on branches.

Lophocebus albigena and *Mi. talapoin* are two clearly arboreal species, and they use the ground in rare occasions (Campbell, 1998; Fleagle, 1999). Although some observed features are similar to those exhibited by terrestrial species, these primates still have adaptations for an arboreal life. This is probably related to the retention of primitive morphologies inherited from terrestrial ancestors. A special case is *M. tonkeana*. Although some authors consider this species as being arboreal from direct observations (Groves, 2001; Patel, 2010), others provide data that support a more frequent use of the ground for some of its regular activities (MacDonald, 1991). None of these observations can be confirmed by the characters observed on the calcaneum and talus, since *M. tonkeana* shows terrestrial affinities in a number of features, such as the trend to stabilize articulations (i.e., the joint between the tibia and the talus) or the reduction of its grasping capacity, whereas the morphology of the talus neck shows an evident ambiguity. That is, although *M. tonkeana* presents terrestrial affinities, it also has arboreal characteristics, for example, the medially orientation of the talus neck which is typical of arboreal species.

Likewise, the reduction of the muscle *flexor digitorum longus*, which is observed in most of the species here studied, decreases the grasping ability (although it would be useful for arboreal taxa), which is difficult to explain in the context of adaptation to arboreal life. Thus, this character, and others, would be indicating a conflict between adaptive features and those structures that conform to the genetic legacy, and, unfortunately, distinguishing between both is quite difficult. Such a doubt could

be tentatively solved through the study of the Neogene fossil record of cercopithecines, when the radiation of the group occurred, but postcranial remains are still scarce to establish a sufficiently reliable hypothesis (Jablonski, 2002).

This unsolved question on which structures are part of the evolutionary legacy of Cercopithecinae, and which are adaptive characters could be tackled from the study of the complete anatomy of the group, which could be provided with a better understanding of their postural behaviours and locomotor types, distinguishing adaptation from ancestral inheritance.

ACKNOWLEDGMENTS

We thank the editor of this volume (Jorge Morales) and the reviewer (Martin Pickford) for their reviews and advices, which greatly improved the manuscript. This study is part of the research project CGL2008-00034 (Dirección General de Investigación, MCI). M. J. S. is a contracted researcher within the "Ramón y Cajal" program (Ministerio de Ciencia e Innovación, reference RYC2007-00128), and M. P. has a predoctoral contract in the Institut Català de Paleontologia Miquel Crusafont (ICP).

References

- Ankel-Simons, F. (2007). *Primate anatomy: an introduction*. Elsevier Academic, Amsterdam, 724 pp.
- Barone, R. (1999). *Anatomie Comparée des mammifères domestiques - Tome 1. Ostéologie*. Vigot, París, 761 pp.
- Barone, R. (2000). *Anatomie Comparée des mammifères domestiques - Tome 2. Arthrologie et myologie*. Vigot, París, 1021 pp.
- Benefit, B.R. (1996). The Phylogeny of Old World monkeys. *Evolutionary Anthropology*, 5: 18-24. doi:10.1002/(SICI)1520-6505(1996) 5:1<18::AID-EVAN6>3.0.CO;2-S
- Campbell, B. (1998). *Human Evolution*. Aldine de Gruyter, New York, 523 pp.
- Fleagle, J.G. (1999). *Primate Adaptation and Evolution*. Academic Press, San Diego (California), 596 pp.
- Gebo, D.L. (1986). Anthropoid Origins - the Foot Evidence. *Journal of Human Evolution*, 15: 421-430. doi:10.1016/S0047-2484(86)80025-2
- Gebo, D.L. (1993). *Postcranial adaptation in Nonhuman Primates*. Northern Illinois University Press, Dekalb (Illinois), 281 pp.
- Groves, C. (2001). *Primate Taxonomy*. Smithsonian Institution Press, Washington and London, 350 pp.
- Harrison, T. (1989). New postcranial remains of *Victoriapithecus* from the middle Miocene of Kenya. *Journal of Human Evolution*, 18: 3-54. doi:10.1016/0047-2484(89)90022-5
- Hartman, C.G. & Straus, W.L. (1969). *The anatomy of the Rhesus monkey (Macaca mulatta)*. Hafner Publishing Co., Inc., New York, 383 pp.
- Hartwig, C. (2002). *The Primate Fossil Record*. Cambridge University Press, Cambridge, 530 pp.
- International Committee on Veterinary Gross Anatomical Nomenclature (ICVGAN) (2005). *Nomina Anatomica Veterinaria*. Published by the Editorial Committee of the ICVGAN, Hannover, Columbia, Gent, Sapporo, 166 pp.
- Jablonski, N.G. (2002). Fossil Old World monkeys: the late Neogene radiation. In: *The Primate Fossil Record* (Hartwig, W.C., ed.). Cambridge University Press, Cambridge, 255-299.
- Jablonski, N.G.; Leakey, M.G.; Kiarie, C. & Antón, M. (2002). A new skeleton of *Theropithecus brumpti* (Primates: Cercopithecidae) from Lomekwi, West Turkana, Kenya. *Journal of Human Evolution*, 43: 887-923. doi:10.1006/jhev.2002.0607
- Kay, R.F.; Ross, C. & Williams, B.A. (1997). Anthropoid Origins. *Science*, 275: 797-804. doi:10.1126/science.275.5301.797
- MacDonald, D. (1991). *Primates. Nuestros antepasados*. Ediciones folio, Estella (Navarra), 153 pp.
- Nakatsukasa, M. (1994). Morphology of the humerus and femur in African Mangabeys and Guenons: functional adaptation and implications for the evolution of positional behavior. *African Study Monographs*, Suppl. 21: 1-61.
- Napier, J.R. & Napier, P.H. (1967). *A Handbook of Living Primates*. Academic Press, London, New York, 456 pp.
- Napier, J.R. & Walker, A.C. (1967). Vertical clinging and leaping - a newly recognized category of primate locomotion. *Folia Primatologica*, 6: 204-219. doi:10.1159/000155079
- Patel, B.A. (2010). Functional morphology of cercopithecoid primate metacarpals. *Journal of Human Evolution*, 58: 320-337. doi:10.1016/j.jhev.2010.01.001
- Platzer, W. (2008). *Color Atlas of Human Anatomy. Locomotor System*. Thieme, Stuttgart (Alemania), 468 pp.
- Rollinson, J. & Martin, R.D. (1981). Comparative aspects of primate locomotion with special referente to arboreal cercopithecines. *Symposia of the Zoological Society of London*, 48: 377-427.
- Strasser, E. (1988). Pedal evidence for the origin and diversification of cercopithecoid clades. *Journal of Human Evolution*, 17: 225-245. doi:10.1016/0047-2484(88)90055-3
- Swindler, D.R. & Wood, C.D. (1973). *An atlas of Primate Gross Anatomy. Baboon, Chimpanzee, and Man*. University of Washington Press, United States of America, 362 pp.

Recibido el 16 de febrero de 2011
Aceptado el 23 de agosto de 2011