LOCOMOTOR INFERENCES IN *ANCHOMOMYS* STEHLIN, 1916 (PRIMATES, ADAPIDAE) ON THE BASIS OF CALCANEAL PROPORTIONS

Inferencias locomotoras en *Anchomomys* Stehlin, 1916 (Primates, Adapidae) en base a las proporciones del calcáneo

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ABSTRACT

Anchomomys is a small adapid primate that has been recorded in Middle Eocene deposits of Spain from the localities of Sant Jaume de Frontanyà 3C (Barcelona) and Caenes (Salamanca). Here we report the results of an allometric analysis of calcaneal proportions in primates and other mammals, in order to interpret the unusual calcaneal proportions to *Anchomomys*. This analysis confirms that calcaneal elongation in primates, as compared to other mammals, is a consequence of adaptation to grasping. Several primate groups differ in their respective degrees of distal calcaneal elongation due to differences in their degree of grasping behaviors and types of support. It is concluded that calcaneal elongation in *Anchomomys* cannot be interpreted as a leaping adaptation; on the contrary, this taxon displays the calcaneal proportion expected for a small-bodied primate with a grasping foot adapted to vertical climbing.

Kewyords: Calcaneus, Paleobiology, Locomotion, Adapiformes, Fossil primates.

RESUMEN

Anchomomys es un pequeño primate adápido que, en España, se ha registrado en los yacimientos del Eoceno Medio de Sant Jaume de Frontanyà 3C (Barcelona) y Caenes (Salamanca). Damos a conocer aquí los resultados de un análisis alométrico de las proporciones del calcáneo en primates y otros mamíferos, para interpretar las inusuales proporciones del calcáneo de *Anchomomys*. Este análisis confirma que la elongación del calcáneo en los primates, en comparación con otros mamíferos, es consecuencia de la adaptación a la prensión. Varios grupos de primates difieren en sus respectivos grados de elongación distal del calcáneo debido a diferencias en sus comportamientos prensores y tipos de apoyo. Se concluye que la elongación del calcáneo en *Anchomomys* no puede ser interpretada como una adaptación al salto; por el contrario, este taxón presenta las proporciones del calcáneo que cabría esperar en un primate de pequeño tamaño con un pie prensor adaptado a trepar verticalmente.

Palabras clave: Calcáneo, Paleobiología, Locomoción, Adapiformes, Primates fósiles.

INTRODUCTION

Primates tend to display a higher degree of distal calcaneal elongation than other mammals (Morton, 1924; Martin, 1972, 1990; Martin & Bearder, 1979; Dagosto, 1988; Hall-Graggs, 1965). Distal calcaneal length among euprimates is thought to be related to the habitual mode of locomotion of each species (Langdon, 1986; Ford, 1988; Dagosto, 1983, 1986; Gebo, 1986, 1988; Russell L. Ciochon *et al*., 2001). Accordingly, the degree of distal elongation of the calcaneus is commonly used to infer the amount of leaping behaviour in the locomotor repertoire of fossil primates, and even employed as a phylogenetically informative character.

The calcaneus of the small-bodied adapid *Anchomomys*, previously recorded in several Spanish sites (Moyà-Solà & Köhler, 1993), displays several features (such as elongated distal calcaneal length and narrow shape) that more closely resemble the calcanei of omomyids, rather than those of other adapid primates. The small size of this taxon, however, should be taken into account when trying to make functional interpretations on the basis of calcaneal proportions. In this communication, we report the results of an allometric analysis of calcaneal proportions among euprimates and other mammals, in order to remove body mass scaling effects and be able to test whether the particular proportions of the *Anchomomys* calcaneus indicate specific locomotor adaptations or merely result from the small body size of this taxon.

MATERIALS AND METHODS

The fossil sample employed in this study includes a complete (IPS7748) and ten partial (IPS7752, 7751, 7749, 7984, 7985, 7986, 7987, 7988, 7989, 7745) calcanei of *Anchomomys* sp. from the Middle Bartonian locality of Sant Jaume de Frontanyà 3C (MP 14 or MP 15; Bellmunt Formation, Barcelona, Spain) as well a complete calcaneus (IPS7769) of the same taxon from the similarly-aged (MP 15 or 16) locality of Caenes (Duero Basin, Salamanca, Spain). The attribution of these calcanei to *Anchomomys* sp. is grounded on the association with dental and other postcranial remains of this taxon. Moreover, neither an omomyid nor another primate of comparable size has been found in either of these sites.

The comparative sample employed in this study includes 74 extant primate species, as well as 62 living species from other mammalian orders (Scadentia, Insectivora, Carnivora, Rodentia and Proboscidea). Measurements were taken at the Anthropologisches Institut und Museum der Universität Zürich (Switzerland), the Zoologisches Museum Hamburg (Germany), the Museu de Ciències Naturals de la Ciutadella (Barcelona, Spain), and the Institut Català de Paleontologia Miquel Crusafont (Barcelona, Spain), or taken from literature. Measurements for 32 fossil primate species were also taken from the original specimens, from good quality casts or from the literature.

In order to reliably analyze calcaneal proportions from a functional viewpoint, it is important to rely on biologically meaningful measurements from a mechanical viewpoint (functional measurements). In particular, we divide the calcaneus in two distinct segments with biomechanical significance, which are delimited by the mid-point of the dorsal talar facet on the calcaneus. Accordingly, three different calcaneal measurements were employed: total calcaneal length (TCL); posterior calcaneal length (PCL), as measured from this point until the distal portion of the heel; and anterior calcaneal length (ACL), as measured from this point until the center of the cuboid facet on the calcaneus. From a mechanical viewpoint, ACL represents the level arm, while PCL represents the power arm.

With regard to statistical techniques, we relied on the logarithmically transformed version of the allometric formula: $\ln y = b \cdot \ln x + a$; where b is the allometric slope and a is the intercept. The data were log-transformed by employing natural logarithms (ln). Least-squares regression was employed to derive allometric best-fist lines. In order to remove size-scaling effects, we separately regressed ACL and PCL against body mass (BM). We also regressed ACL against TCL, in order to investigate intrinsic calcaneal proportions (index of calcaneal elongation).

RESULTS

Allometric comparisons of several calcaneal measurements with respect to BM confirm that primates as a group have longer distal calcanei than other mammals (Morton, 1924; Martin, 1972,

1990; Martin & Bearder, 1979; Dagosto, 1988; Hall-Grags, 1965). On the contrary, all primates (including specialized leapers) show the same allometric relationship between PCL and BM than other mammals, with only some minor differences between groups. This suggests that heel length is highly constrained by BM, further confirming that ACL (instead of TCL) is the parameter that has been elongated in primates (fig.1).

With regard to intrinsic calcaneal proportions, our results indicate again that primates have a relatively longer distal portion of the calcaneus than other mammals. This indicates that distal calcaneal elongation is the ancestral euprimate condition, as previously suggested by some other authors (Martin, 1972; Dagosto, 1988, 1990).

Both allometric analyses, however, permit to distinguish three primate groups on the basis of their respective degrees of distal calcaneal elongation. Anthropoids, in particular, display the lowest degree, while prosimians can be further divided into two distinct groups: lemurids and cheirogaleids, showing a somewhat higher degree than anthropoids; and galagos and tarsiers (which can be qualified as small vertical clinging and leaping primates), with the highest degree of anterior calcaneal elongation. Lorisids, on the contrary, display a low degree of anterior calcaneal elongation, overlapping with the lower anthropoid values.

DISCUSSION

The degree of distal calcaneal elongation has been functionally related to locomotor adaptations, so that an index of calcaneal elongation has been interpreted in terms of preference for leaping (Gebo, 1988; Dagosto, 1988). This is obvious in the case of specialized leapers such as galagos and tarsiers, but much less evident in other primates with less extreme degrees of distal calcaneal elongation. Morton (1924), for example, proposed that distal calcaneal elongation in primates might be merely an adaptation related to the possession of a grasping foot (see also Martin & Bearder, 1979; Martin, 1993, 1990). This implies a more proximal position of the fulcrum in primates, i.e. a reduction of the lever arm of the foot, which has been partially compensated by the lengthening of the distal portion of the calcaneus. Biomechanically, the length of the distal

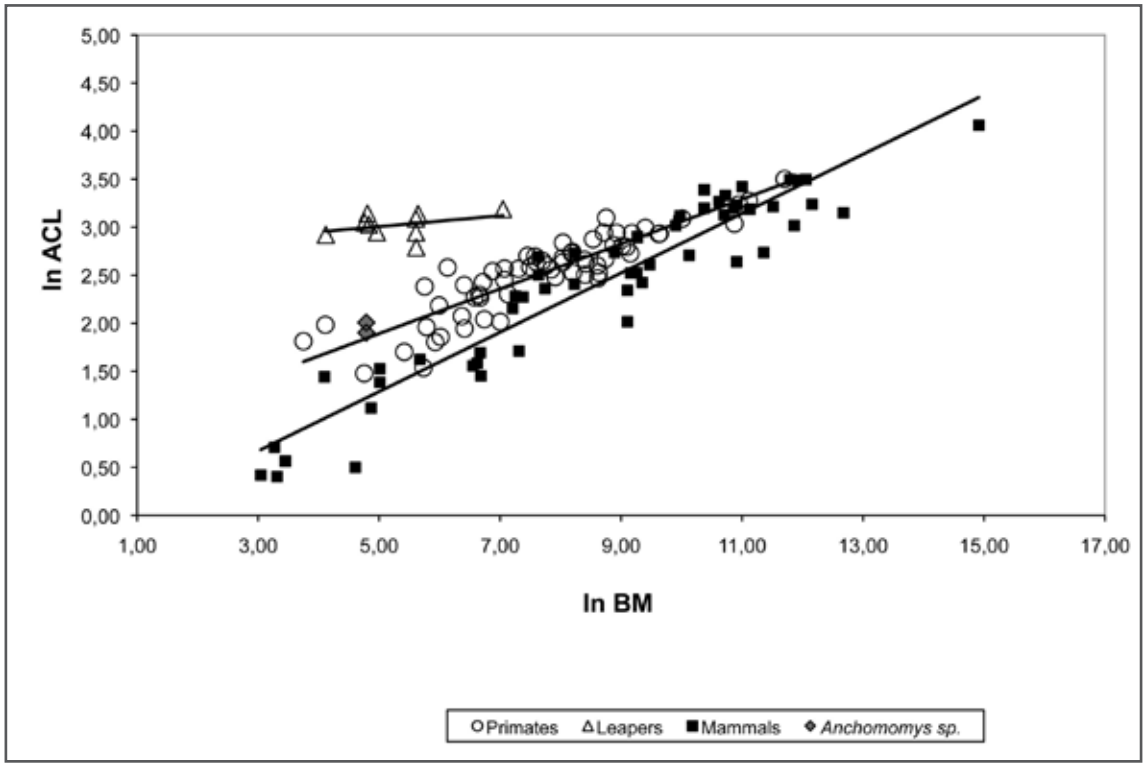

Figure1. Least-square regression of (ln)PCL correlates with (ln)BM showing the allometric correlation with both parameters.

calcaneus and consecutive segments (distal tarsals and metatarsals) determines the acceleration required by take-off velocity (Hall-Craggs, 1964, 1965; Demes & Günter, 1989). Considering the differences in distal calcaneal elongation between generalized prosimians and anthropoids, which include some species with similar ranges of leaping (Gebo, 1985, 1987), it is proposed here that differences between both groups as a whole stem from a different position of the fulcrum during locomotion (see Morton, 1924). The negative allometric relationship between ACL and BM, as reported in this communication, explains why small forms tend to have longer distal portions of the calcaneus than larger species (Martin, 1993), when scaling effects are not taken into account.

When these caveats are taken into account, the calcaneal proportions of *Anchomomys* are the expected ones for a primate with a tarsifulcrumating foot of its small size. When allometric considerations are overlooked, the calcaneal proportions of *Anchomomys* more closely resemble those of omomyids than those of other adapids. The former are customarily considered more specialized leapers, whereas the latter are usually interpreted as more generalized quadrupedal animals with more restricted leaping adaptations. We show here, however, that the apparently peculiar proportions of the *Anchomomys* merely results from size-scaling effects, so that they do not indicate any particular emphasis in leaping behaviors, in agreement with other features of its postcranial skeleton (Moyà-Solà & Köhler, 1993).

CONCLUSIONS

The proportions of the primate calcaneus largely depend on the construction and use of the foot in this group of mammals, as well as on body mass scaling effects. Only in few cases, particular locomotor adaptations departing from a generalized primate condition (such as an extreme reliance on leaping) can be clearly identified on the basis of calcaneal proportions. Moreover, simple bivariate ratios that fail to take into account allometric scaling effects should not be uncritically employed. The allometric analysis reported here shows that moderate calcaneal elongation in primates is a direct consequence of the adaptation to grasping, with some differences resulting from the basic type of locomotion employed by anthropoids (cursorial) or prosimians (vertical clinging). To sum up, when size scaling is taken into account, the calcaneal proportions of *Anchomomys*, apparently unusual for an adapid, are best interpreted as the expected proportions for a small-bodied primate with a grasping and a prosimian-like foot adapted to vertical clinging, but with no particular emphasis towards leaping.

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