Calcaneal proportions in primates and locomotor inferences in *Anchomomys* and other Palaeogene Euprimates

Salvador Moyà-Solà · Meike Köhler · David M. Alba · Imma Roig

Abstract Foot proportions, and in particular the lengthening of the tarsal elements, play a fundamental role in the discussion on the locomotor adaptations of Palaeogene primates. The elongation of the distal portion of the tarsus, particularly the anterior part of the calcaneus, is frequently interpreted as an adaptation to leaping and has played a fundamental role in the reconstruction of the locomotor adaptations of the earliest primates. Here, we report an allometric analysis of calcaneal proportions in primates and other mammals, in order to determine the actual differences in calcaneal proportions. This analysis reveals that primates as a group display a relatively longer distal calcaneus, relative to both total calcaneal length and body mass, when compared with other mammals. Contrary to current expectations, morphofunctional analysis indicates that a moderate degree of calcaneal elongation is not an adaptation to leaping, but it is merely a compensatory mechanism to recover the lost load arm (metatarsal length) when the foot adopts a grasping function, in order to maintain the same locomotor efficiency. Leaping can be inferred only when anterior calcaneal length departs from the scaling of non-specialized primate groups. The role of leaping on the inferred locomotor repertoire of earliest primates needs to be revised considering the results of this work.

Keywords Fossil and extant primates · Foot · Calcaneal proportions · Allometry · Grasping · Leaping · *Anchomomys*

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Introduction

The origin of primates of modern aspect (euprimates) was characterized by a profound reorganization of the postcranial anatomy apparently related to arboreal locomotion (Dagosto 1988). The belief that leaping played an essential role in euprimate origins stems, in great measure, from the distinctive proportions of the euprimate foot, characterised by elongation of the tarsal elements—including the navicular, the neck of the talus and the cuboid, and in particular the distal portion of the calcaneus. These euprimate traits, more accentuated in prosimians than in anthropoids (Ford 1988; Gebo 1986), are considered to be a biomechanical innovation in the lever system of the foot that enables to increase the effective length of the hind limbs, so that a more powerful leap can be produced (Dagosto 1988; Hall-Craggs 1965). On the basis of these considerations, calcaneal length is thought to vary within euprimates according to the habitual mode of locomotion of each species (Dagosto 1983; Ford 1988; Langdon 1986). Hence, the degree of distal calcaneal elongation is commonly used to assess the amount of leaping in the locomotor behaviour of fossil primates.

Preliminary analyses (Martin 1990; Roig et al. 2009) have suggested that calcaneal proportions in primates have an important allometric component. In this paper, we extend this analysis and evaluate the actual functional significance of tarsal elongation in primates. This analysis, together with morphofunctional considerations, are employed to test the actual functional significance of tarsal elongation in primates and the real inferential capability of these traits for inferring the locomotor repertoire of fossil primates and of the last common euprimate ancestor. As a special case study, we analyse the recently discovered calcanei of the smallest known adapoid, *Anchomomys frontanyensis* Marigó et al. 2011, in order to evaluate the locomotor significance of its apparently unusual calcaneal proportions. The *A. frontanyensis* calcanei display a narrow and distally elongated appearance that superficially resembles those of omomyoids instead of adapoids. Accordingly, we apply our allometric analysis to two complete *A. frontanyensis* calcanei from Spain, in order to determine whether they reflect particular locomotor adaptations to leaping or whether they simply display the expected proportions on the basis of size-scaling effects.

In order to quantify the relative length of tarsal elements in primates, some authors (Hall-Craggs 1965) employed a ratio between the heel portion of the calcaneus and the combined length of the distal portion of the calcaneus and the cuboid. However, considering the scarcity and fragmentary nature of fossil specimens, this measurement is of limited applicability. Walker (1967) and subsequent authors (like Dagosto 1983, 1988; Gebo 1985; Martin 1990) have relied instead on the calcaneus alone as a proxy for tarsal proportions in primates. The relative abundance of this bone in the fossil record makes it particularly useful to this regard. The relative length of the distal portion of the calcaneus has been therefore employed as one of the most informative pedal features for inferring the locomotor capabilities of fossil primates, thus playing a fundamental role in the debate on the reconstruction of the locomotor adaptations of the last euprimate common ancestor.

Materials and methods

Selection of measurements with biomechanical significance

In order to analyze calcaneal proportions from a morphofunctional perspective, it is essential to select those variables that are most meaningful from a biomechanical viewpoint. Several authors (Gebo and Dagosto 1988; Godinot 1991) have divided the calcaneus into three distinct parts: the heel, the facet for the astragalus, and the distal part (to the articulation with the cuboid). Even though this subdivision provides a good description of calcaneal proportions, the resulting segments lack a clear biomechanical meaning. Other authors have opted instead for selecting a divisory point on the mid-tarsal area: the distal end of the dorsal talar facet on the calcaneus (Hall-Craggs 1965; Berge and Jouffroy 1986); the proximal end of the articular facet on the sustentaculum tali (McArdle 1981); or the junction of the proximal border of the sustentaculum tali and the corpus calcanei (Martin 1972, 1979, 1990). However, none of them corresponds to the actual point where body weight must be counteracted (which defines the proximal end of the load arm); the latter corresponds to the mid-point of the dorsal talar facet of the calcaneus, which can be determined by dividing the length of this facet into two halves (Fig. 1).
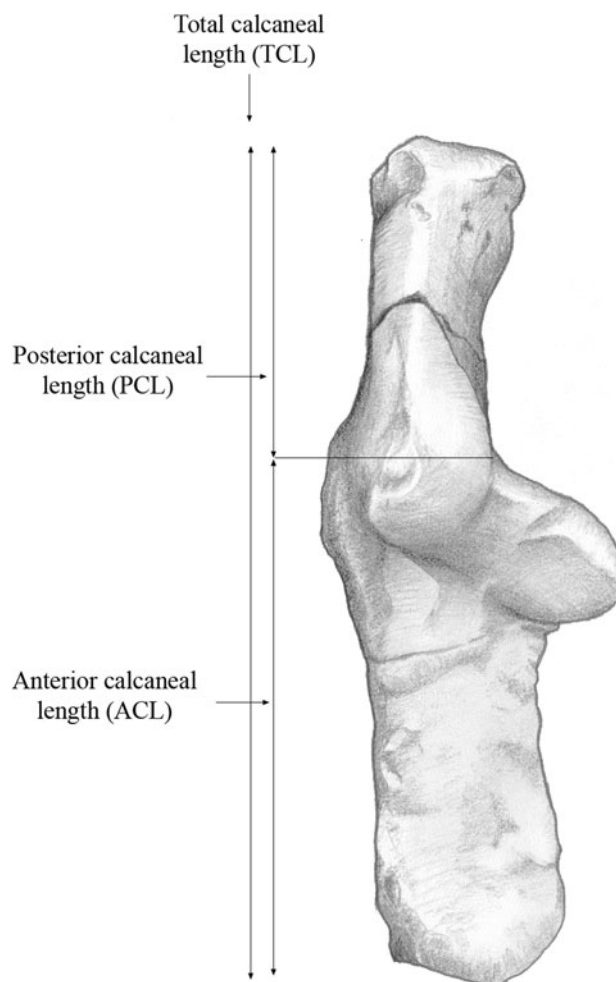

Fig. 1 Measures of the calcaneus used in this work. Original art by Marta Palmero

Allometry and statistical methods

Two different calcaneal proportions were investigated: extrinsic proportions, i.e. distal calcaneal length (ACL, in millimetres) relative to body mass (BM, in grams); and intrinsic proportions, i.e. ACL relative to total calcaneal length (TCL, in millimetres). We followed an allometric approach for removing size-scaling effects, in order to ensure that the proportional differences observed between several taxa were not merely attributable to size-scaling effects. The variables where log-transformed by using natural logarithms (ln), in order to employ the logarithmic version of the allometric formula: $\ln y = b \cdot \ln x + a$; where b is the allometric slope and a is the intercept. Least-squares regression was employed to derive allometric best-fit lines on the basis of extant taxa, while fossil taxa were included in order to compute allometric residuals. In order to compute separate allometric regressions, we employed four different groups: specialized prosimian leapers (galagids and tarsiids), which are well known for their extreme degree of calcaneal elongation, other prosimians, anthropoids and non-primate mammals; a primate regression line (by excluding specialized leapers, which are clear outliers) was also derived in order to compute allometric residuals. Allometric differences between several regression lines (equality of slopes and equality of intercepts) were tested by means of analysis of covariance (ANCOVA), whereas differences between more specific groups were tested by comparing the allometric residuals computed on the basis of the primate regression. Statistical computations were carried out with SPSS v. 16.0.

The extant and fossil comparative sample

The comparative samples employed in this study include 75 extant primate species, 35 extinct primate species and 57 living species from several other mammalian orders (Scadentia, Insectivora, Carnivora, Rodentia); artiodactyls and perissodactyls were excluded from the analysis due to their particular calcaneal morphology, which makes it difficult to homologise the two distinguished segments with those of primates. Data on calcaneal variables for living species were taken from the literature (modified from Dagosto and Terranova 1992; Gebo et al. 2000a) or measured by the authors 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). Data on calcaneal variables for fossil primates were measured by the authors from original specimens or good quality casts, or taken from the literature (Anemone and Covert 2000; Ciochon et al. 2001;

Gebo 1986, 1987; Gebo and Simons 1987; Gebo et al. 1991, 2000b; Walker 1970). Body mass (BM) data were taken from the literature for all extant taxa (Nowak 1999; Silva and Downing 1995; Smith and Jungers 1997).

The case study: *Anchomomys* calcanei from Spain

Two complete calcanei of *Anchomomys* were employed: IPS7748 (Fig. 2a–d) from the Middle Bartonian (MP14 or MP15) locality of Sant Jaume de Frontanyà 3C (Bellmunt Formation, Barcelona, Spain), attributed to *A. frontanyensis*; and IPS7769 (Fig. 2e–h) from the similarly aged (MP15 or MP16) locality of Caenes (Duero Basin, Salamanca, Spain), attributed to *Anchomomys* sp. The taxonomic attribution to *Anchomomys* of this postcranial material is based on the taxa previously identified in these sites (Moyà-Solà and Köhler 1992, 1993), their relative abundance and size congruence. In particular, the site of Sant Jaume de Frontanyà is extensively sampled and more than two tones of sediments have been washed (Moyà-Solà and Köhler 1993). Only three primate species have been recovered and *A. frontanyensis* is the most abundant taxon, representing more than the 80% of the primate fauna. Using the criterion of relative abundance and size congruence, most of the postcranial specimens recovered in this site can be attributed to *Anchomomys*. Furthermore, the postcranial bones attributed to *Anchomomys*, in particular the talus and other tarsal bones, show the typical adapiform pattern and cannot be attributed to an omomyoid primate (Moyà-Solà and Köhler 1993). An alternative attribution of the studied calcanei to *Adapis* (in Sant Jaume de Frontanyà) or *Microadapis* (in Caenes) can be discarded on the basis of the small size of the studied specimens, whereas the microchoerid (*Pseudoloris pyrenaicus*) from Sant Jaume de Frontanyà (Minwer-Barakat et al. 2010) is even much smaller and its postcranial bones have been identified. Finally, no dental or postcranial specimen of any omomyoid of comparable size to *A. frontanyensis* has been found in any of these sites. Calcaneal measurements were taken on both *A. frontanyensis* calcanei, whereas BM estimates were derived on the basis of dental material only from Sant Jaume de Frontanyà (because the available sample from Caenes is comparatively too small). This dental sample includes 10 p4, 11 m1, 8 m2, 7 m3, 1 P4 and 3 M3. Both mesiodistal length (MD) and buccolingual (BL) width of *A. frontanyensis* molars were measured, and employed to compute premolar and molar areas as $MD \times BL$ (in mm²). The tooth-specific average value of crown area was then employed to derive BM estimates by using the 'prosimian' regression equations published by Egi et al. (2004); the average of the several BM estimates derived separately for each tooth was employed in the allometric
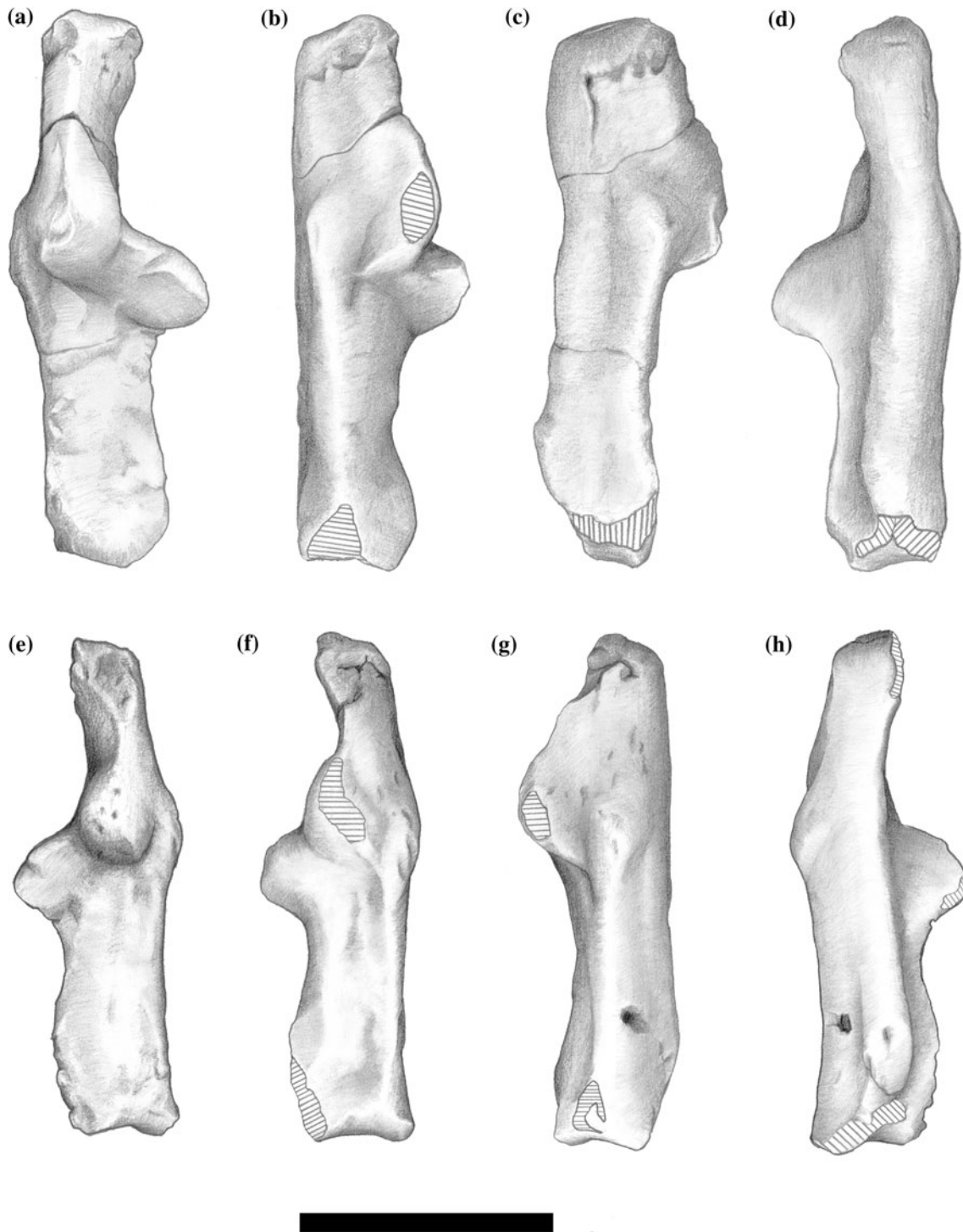
Fig. 2 Drawings of the two complete calcanei of *Anchomomys* studied in this paper. **a–d** Right calcaneum IPS7748 from Sant Jaume de Frontanyà 3C; and **e–h** left calcaneum IPS7769 from Caenes.

a, **e** In laterodorsal, **b**, **f** lateral, **c**, **g** lateroplantar and **d**, **h** medioplantar views. *Scale bar* equals 5 mm. Original art by Marta Palmero

analyses. On the basis of dental material, the BM estimates for *Anchomomys* from Sant Jaumè de Frontanyà are the following: 216 g (p4), 139 g (m1), 103 g (m2), 107 g (m3), 187 g (P4) and 93 g (M3). This yields a estimated BM of 141 g for *Anchomomys* from Sant Jaume de Frontanyà.

Results

Allometry

The allometric regressions derived in this paper have been reported in Fig. 3 and Tables 2, 3. All the regressions are significant at $p < 0.001$ and display a good correlation coefficient (>0.9 regarding intrinsic proportions, and >0.8 relative to body mass), except for the leaper regression against BM, which fails to be significant due to considerable dispersion coupled with small sample size. All the regressions are negatively allometric (slope <1), indicating that within the several groups investigated, larger-bodied species tend to display a lower degree of distal calcaneal elongation.

A visual inspection of these regression lines further indicates that there are allometric grade relationships between the several groups. Albeit the correlation is better when intrinsic calcaneal proportions (ACL vs. TCL; Fig. 3a) are computed, the degree of calcaneal elongation relative to BM (Fig. 3b) roughly shows the same allometric grade differences. Thus, primates as a group tend to display a more elongated distal portion of the calcaneus than other mammals. This can be unambiguously shown regarding intrinsic calcaneal proportions, since ANCOVA results show that equality of slopes cannot be discounted ($p = 0.304$), whereas equality of intercepts can be rejected at $p < 0.001$. Given that equality of slopes can be rejected regarding extrinsic calcaneal proportions, the existence of a comparable allometric grade shift in ACL versus BM cannot be tested by means of ANCOVA. Further statistical differences can be shown between anthropoids and prosimians (when specialized leapers are excluded): equality of slopes cannot be discarded either regarding intrinsic ($p = 0.181$) or extrinsic ($p = 0.657$) proportions, whereas equality of intercepts can be discarded in both instances at $p < 0.001$. This confirms that prosimians as a group, and not merely specialized prosimian leapers, tend to display a higher degree of distal calcaneal elongation than anthropoids.

Nevertheless, an extreme degree of distal calcaneal elongation is only found in prosimian specialized leapers (tarsiids and galagos). This is confirmed by the analysis of allometric residuals (Fig. 4; Table 3). Neither the maximum–minimum range nor the 95% confidence interval for the mean of leapers' residuals overlaps those of other primates (either extant or fossil), irrespective of whether intrinsic or extrinsic distal calcaneal proportions are taken into account (Table 3). On the contrary, the residuals for *Anchomomys* fall closer to other prosimians (both living and extinct; see Table 3 and Fig. 4). *Anchomomys* thus differs from specialized leapers by displaying an absolutely shorter calcaneus (in spite of a comparable body size), a shorter distal portion when compared with total calcaneal length,
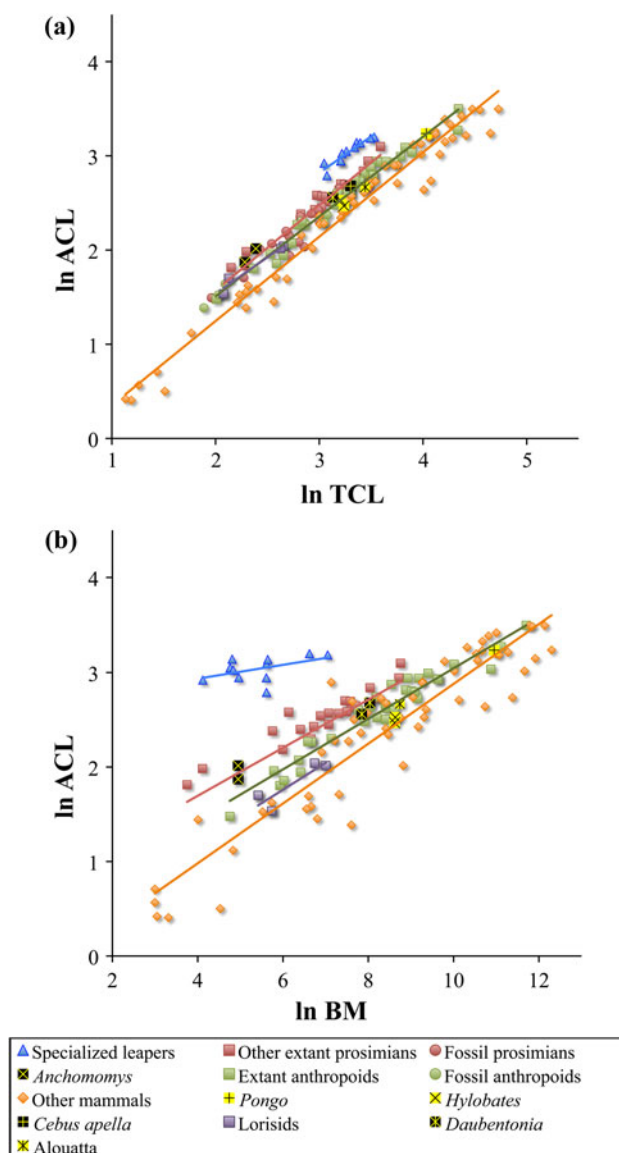

Fig. 3 Allometric bivariate plots showing calcaneal proportions in primates and other mammals. **a** Distal calcaneal length (ACL) versus total calcaneal length (TCL); **b** ACL versus body mass (BM). In each case, five separate allometric regressions have been depicted: prosimian specialized leapers (*blue*), lorisids (*violet*), other extant prosimians (*red*; including lorisids but excluding specialized leapers), extant anthropoids (*green*) and other mammals (*orange*; perissodactyls, artiodactyls and proboscideans excluded). Note that there are allometric grade shifts between these several groups regarding the degree of distal calcaneal elongation, and that this trend is highly expressed in specialized prosimian leapers. Note also that the two *Anchomomys frontanyensis* calcanei fall very close to the generalized prosimian regression

and a lower degree of distal calcaneal elongation relative to body mass. No fossil prosimians fall close to the specialized leaper regression (Fig. 2a), including not only adapids, but also omomyids, whereas *Anchomomys* falls very close to the regressions of generalized prosimians regarding both intrinsic (Figs. 3a, 4a) and extrinsic (Figs. 3b, 4b)
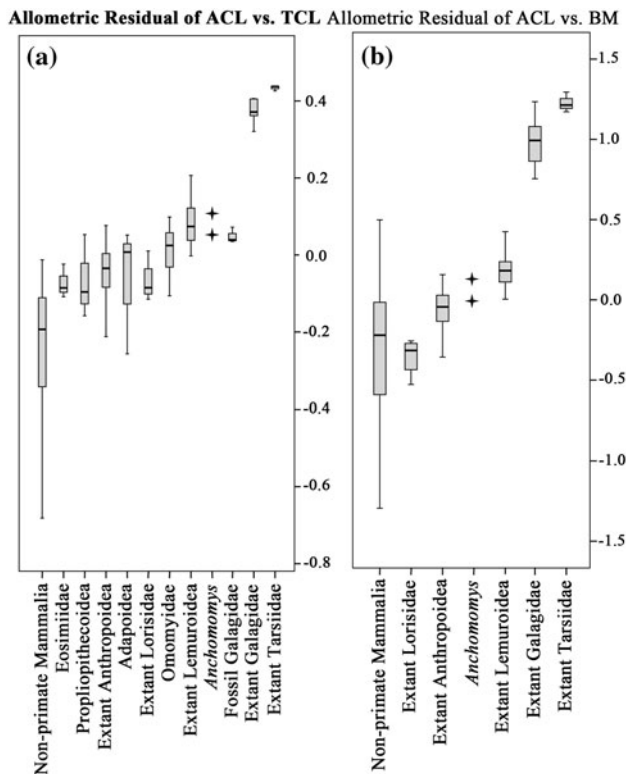
Fig. 4 Boxplots showing the degree of distal calcaneal elongation by taking into account **a** intrinsic, and **b** extrinsic proportions on the basis of allometric residuals computed from the primate regression line. *Horizontal lines* represent the median values, whereas the *boxes* represent the 25 and 75% percentiles, and the *whiskers* the maximum–minimum ranges (excluding outliers)

Table 1 Measurements (in mm) of the calcaneal specimens of *Anchomomys* analyzed in this paper

Record no.	Locality	ACL	PCL	TCL
IPS7748	Caenes	6.5	3.3	9.8
IPS7769	Sant Jaume de Frontanyà	7.5	3.4	10.9

ACL distal calcaneal length, *PCL* proximal calcaneal length, *TCL* total calcaneal length

proportions. These results indicate that this taxon does not display the typical calcaneal proportions of a specialized leaper, but rather the expected proportion for a small-bodied prosimian with a more generalized locomotor repertoire.

Calcaneal proportions in primates

The results of the allometric analysis (Figs. 3, 4; text and Tables 2, 3) confirm previous suggestions that primates as a group have a longer distal portion of the calcaneus than other mammals (Covert 1988; Dagosto 1988, 1990; Hall-Craggs 1965; Morton 1924; Martin 1972, 1979, 1990). This supports the contention that some degree of distal calcaneal

elongation characterises the ancestral euprimate condition (Dagosto 1988, 1990; Martin 1990), instead of being a derived prosimian feature (Ford 1988; Gebo 1986). Our results, however, further indicate that different calcaneal proportions can be distinguished among several primate groups. Prosimians tend to display a higher degree of distal calcaneal elongation than anthropoids, both relative to total calcaneal length and body mass. However, only the highly specialized, small vertical-clinging-and-leaping prosimians (galagos and tarsiers) clearly depart by displaying an extreme degree of distal calcaneal elongation (Figs. 3, 4; Table 3). Furthermore, the strongly negative allometric relationship between ACL and BM determines that small-bodied species tend to display a higher ratio of ACL versus TCL, as pointed out by Martin (1990).

Discussion

Functional significance of distal calcaneal elongation in primates

The functional significance of distal calcaneal elongation in particular groups when compared with others, when size-scaling effects are taken into account, is a controversial question. However, distal calcaneal elongation has been related to locomotor adaptations by interpreting it in terms of preference for leaping (Anemone and Covert 2000; Covert 1988; Dagosto 1986, 1988, 1990; Gebo 1986, 1993; Gebo et al. 2000a; Martin 1972, 1979, 1990). However, this explanation is unlikely because extant primates as a group display a distal calcaneus relatively elongated to some degree compared to non-primate mammals, in spite of the fact that primates as a whole show variable degrees of commitment to leaping and some do not leap at all (Ford 1988; Gebo 1987).

The fact that distal calcaneal elongation cannot be merely interpreted in the light of leaping abilities alone is further illustrated by additional sources of evidence: the distally elongated calcanei of lorisids and orangutans (Fig. 3), even though they never leap; or the situation close to the strepsirrhine regression of taxa with a low incidence of leaping (Fig. 3), such as the quadrupedal aye-aye and *Cebus apella* (Curtis and Feistner 1994; Gebo 1989a, b, respectively), or the suspensory *Ateles* and *Hylobates*; the similar degree of distal calcaneal elongation displayed by groups with different leaping frequencies, such as lemurids when compared with indriids and lepilemurids (Gebo and Dagosto 1988); and the wide spectrum of leaping frequencies displayed among closely related taxa with similar calcaneal proportions, such as cheirogaleids (Martin 1979). On the other hand, the marked degree of distal calcaneal elongation displayed by galagos and tarsiers clearly differs

Table 2 Allometric regressions employed in this paper

Group	N	r	SEE	p	Slope	95% CI	Intercept	95% CI
ln ACL vs. ln TCL								
Leapers	11	0.939	0.046	<0.001	0.773	0.560, 0987	0.500	−0.202, 1.202
Primates	64	0.977	0.092	<0.001	0.821	0.775, 0.866	−0.054	−0.199, 0.092
Mammals	56	0.985	0.153	<0.001	0.895	0.852, 0.939	−0.544	−0.693, -0.396
Prosimians	27	0.983	0.072	<0.001	0.904	0.835, 0.973	−0.235	−0.438, -0.033
Anthropoids	37	0.986	0.073	<0.001	0.847	0.798, 0.895	−0.185	−0.347, -0.023
ln ACL vs. ln BM								
Leapers	11	0.487	0.118	0.129	0.073	−0.026, 0.172	2.643	2.102, 3.185
Primates	63	0.893	0.192	<0.001	0.233	0.203, 0.263	0.726	0.487, 0.964
Mammals	56	0.930	0.321	<0.001	0.316	0.282, 0.351	−0.285	−0.587, 0.017
Prosimians	26	0.816	0.225	<0.001	0.254	0.178, 0.330	0.678	0.150, 1.206
Anthropoids	37	0.963	0.119	<0.001	0.267	0.242, 0.293	0.371	0.153, 0.589

'Leapers' include small, vertical-clinging-and-leaping prosimians (galagos and tarsiers); 'Prosimians' and 'Primates' exclude galagos and tarsiers; 'Mammals' refer to non-primate eutherians (artiodactyls, perissodactyls and proboscideans excluded). Only extant species have been included in the regressions

BM body mass (in g), *ACL* distal calcaneal length (in mm), *TCL* total calcaneal length (in mm), N = sample size, r = correlation coefficient, *SEE* standard error of estimate, *p* significance, *CI* confidence interval

from the generalized proportions displayed by indriids, in spite of the fact that both groups are equally committed to leaping (>40% of their locomotor behaviours; Gebo 1987, 1988; Gebo and Dagosto 1988). These differences are attributable to a compromise with other types of locomotion (especially climbing), a biomechanically different type of leaping (thigh-powered instead of foot-powered), and differences in body size (Demes et al. 1996; Gebo 1988; Rollinson and Martin 1981). Considering these facts, it is highly unlikely that a moderate lengthening of the distal portion of the calcaneus can be interpreted as reflecting a higher emphasis on leaping, as argued by previous authors (Dagosto 1988, 1990; Gebo 1986; Covert 1988; Gebo et al. 2000a; Martin 1972, 1979, 1990).

Morton (1924) described two types of foot in primates, on the basis of the habitual position of the fulcrum: the 'metatarsi-fulcrumating' foot, typical of anthropoids and many non-primate mammals, with the fulcrum situated on the metarsal heads; and the 'tarsi-fulcrumating' foot, typical of prosimians, with the fulcrum situated on the distal tarsal bones, with the hallux and the other digits performing a tightly clasping action, while the metatarsals act passively as a span (Fig. 5). For our analysis of calcaneal proportions, the 'tarsi-fulcrumating' model of Morton (1924) is important because it allows identifying an important effect of the grasping adaptation of the foot: the posterior shifting of the fulcrum and its locomotor consequences.

The foot works as a second-class lever, in which the muscular force is applied to the tuber calcis (gastrocnemius, in-force), raising the load (partial body mass, out-force) at the ankle joint through rotation at the fulcrum (metatarsals or phalanges in generalized mammals and tarsus in most primates) (Fig. 5). Biomechanically, the distal calcaneus and consecutive segments such as the distal tarsals and metatarsals (depending on the species) are the load arm and their length permit the leverage action necessary to move the body. The degree of lengthening determines velocity (space covered by unit of time) (Hall-Craggs 1965; Demes and Günther 1989). The grasping adaptation of the primate foot implies, as an immediate biomechanical consequence, that the load arm is dramatically reduced, because the weight is transmitted to the branch by means of the webbing between digits one and two. The more proximal position of the fulcrum on this type of foot would imply an increase in the mechanical advantage of the muscle force, but a concomitant reduction in velocity. In a tarsi-fulcrumating foot, the leverage action that non-primate mammals accomplish with the metatarsals must necessarily be carried out by the tarsal segment of the foot, posterior to the new fulcrum position. Thus, the reduction of the load arm of the foot needs to be compensated by a lengthening of the tarsus (mainly the calcaneus) in all grasping primates, but particularly in the tarsi-fulcrumating prosimians, where the metatarsals are not involved in propulsion at all. In fact, this interpretation of Morton's model contrasts with other views that admit that "the lengthening of the tarsus is an adaptation to increase the effective length of the hind limb so that a more powerful leap can be produced" (Dagosto 1988). The current belief that the lengthening of the tarsus indicates leaping adaptations largely stems from the latter interpretation.

Table 3 Descriptive statistics of allometric residuals for evaluating intrinsic and extrinsic calcaneal proportions in several groups of primates and in the two *Anchomomys* calcaneal specimens (by using the body mass estimate derived in this paper)

	N	Mean	SD	95% CI	Range
Allometric residuals of ACL versus TCL					
Extant Tarsiidae	3	0.43	0.01	0.42, 0.45	0.43, 0.44
Extant Galagidae	8	0.38	0.05	0.35, 0.42	0.32, 0.47
Anchomomys (SJF)	1	0.11	–	–	–
Extant Lemuroidea	23	0.08	0.06	0.06, 0.11	0.00, 0.21
Anchomomys (Caenes)	1	0.05	–	–	–
Fossil Galagidae	3	0.05	0.02	0.00, 0.10	0.04, 0.07
Omomyidae	7	0.01	0.07	−0.06, 0.08	−0.11, 0.10
Adapoidea	16	−0.04	0.11	−0.10, 0.01	−0.26, 0.05
Extant Anthropoidea	37	−0.04	0.07	−0.07, −0.02	−0.23, 0.08
Extant Lorisidae	4	−0.07	0.05	−0.16, 0.02	−0.11, 0.01
Eosimiidae	3	−0.07	0.04	−0.18, 0.04	−0.11, −0.02
Propliopithecoidea	3	−0.07	0.11	−0.34, 0.20	−0.16, 0.05
Non-primate Mammalia	56	−0.24	0.17	−0.29, −0.20	−0.69, −0.13
Allometric residuals of ACL versus BM					
Extant Tarsiidae	3	1.23	0.06	1.07, 1.38	1.17, 1.29
Extant Galagidae	8	0.98	0.16	0.85, 1.12	0.76, 1.23
Extant Lemuroidea	22	0.18	0.10	0.13, 0.23	0.00, 0.42
Anchomomys (SJF)	1	0.14	–	–	–
Anchomomys (Caenes)	1	−0.01	–	–	–
Extant Anthropoidea	37	−0.07	0.13	−0.11, −0.03	−0.36, 0.16
Non-primate Mammalia	56	−0.30	0.38	−0.40, −0.20	−1.28, 0.51
Extant Lorisidae	4	−0.35	0.12	−0.55, −0.16	−0.53, −0.26

N sample size, *SD* standard deviation, *CI* confidence interval, *SJF* Sant Jaume de Frontanyà
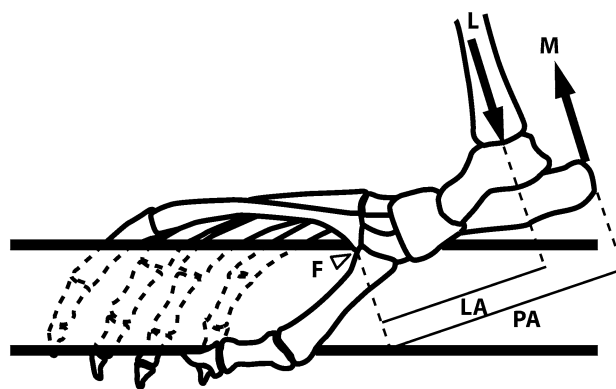

Fig. 5 Schematic depiction of the tarsi-fulcrumating foot of a lemuriform, conceptualized as a second-class lever. *F* fulcrum, *M* muscular force, *L* load (portion of body mass), *LA* load arm and *PA* power arm

when compared with the more cursorial anthropoids. In spite of using their foot in grasping postures during locomotion, anthropoids frequently employ their metacarpal heads as a fulcrum during horizontal quadrupedalism. On the contrary, the foot of most prosimians is adapted to vertical clinging, therefore implying that the distal tarsal bones are much more frequently employed as a fulcrum when compared with anthropoids.

To sum up, the widely accepted hypothesis that distal calcaneal elongation, irrespective of its extent, is related to leaping improvement (Dagosto 1988; Martin 1993) is rejected by our analysis. Instead, grasping would act as a functional constraint determining that the tarsal segment must accomplish the leverage action of the foot. The moderate degree of distal calcaneal elongation displayed by primates as a whole when compared with other mammals might be simply related to the need to compensate for the reduction of the load arm due to grasping adaptations. The differences in calcaneal elongation between anthropoids and prosimians could be related to the different foot postures habitually employed by both groups. In this context, the anthropoid-like moderate elongation present in lorises might be explained by their adaptation to slow-cautious climbing, which does not require the same degree of lengthening than in other primates with more active locomotion. Our allometric analysis of calcaneal proportions in primates and other mammals thus clearly indicates that a moderate degree of calcaneal elongation cannot be interpreted as indicating a higher emphasis on leaping, but is merely a biomechanical compensatory remodelling required by the acquisition of a grasping foot. Under this perspective, only when the calcaneal proportions depart from the size-scaling relationships of non-specialized primate groups (prosimians and anthropoids), can leaping locomotion be inferred on the basis of distal calcaneal length.

However, our allometric analysis clearly reveals, in agreement with some views (Dagosto 1990; Martin 1990) but in strong contrast to others (Gebo 1986; Gebo et al. 2000a; Morton 1924), that the 'metatarsi-fulcrumating' primates (anthropoids) also display a relatively elongated distal portion of the calcaneus, although to a lesser degree than prosimians. The adaptation of the foot to grasping in both prosimians and anthropoids therefore explains the higher relative distal calcaneal length of primates as a whole when compared with other mammals, whereas the greater emphasis on grasping and the associated 'tarsi-fulcrumating' foot of prosimians explains their higher degree of distal calcaneal elongation (except in the slow-climbing lorisids)

Calcaneal proportions in *Anchomomys* and other fossil primates

The measurements of the *Anchomomys* calcaneal specimens analyzed in this paper (Fig. 2) have been reported in Table 1, whereas a succinct description is provided below. The calcanei from both localities are quite similar to one another, although that from Sant Jaume de Frontanyà is slightly larger than the one from Caenes, potentially reflecting interspecific differences. Morphologically, these calcanei are narrow and elongated, with a proportionally long distal portion and a short heel process. The posterior calcaneal facet is relatively long and proportionally narrow, especially in the specimens from Sant Jaume de Frontanyà. The section of the heel process is ovoid (mediolaterall compressed), and the section of the anterior part is triangular. The peroneal tubercle is moderately sized, while the calcaneocuboid joint is broad, fan-like, deep and plantarly open where the pivot is situated. There is a large distal plantar tubercle for the calcaneocuboid ligament. This association of features is somewhat peculiar, because in spite of the omomyoid-like appearance and proportions, the adapid affinities of the material can be readily recognized on the basis of the long and narrow posterior calcaneal facet, as well as the morphology of other postcranial elements from Sant Jaume de Frontanyà (Moyà-Solà and Köhler 1993).

Somewhat surprisingly, the calcaneus of *A. frontanyensis* has, in spite of being an adapoid, omomyoid-like overall proportions. However, the allometric analysis reported in this paper clearly shows that, when size-scaling considerations are taken into account, the calcaneal proportions of *A. frontanyensis* (Fig. 2; Table 1) are the expected ones for a primate with a 'tarsi-fulcrumating' foot of its small size (Figs. 3, 4). Omomyoids are customarily considered more specialized leapers, whereas adapoids are usually interpreted as more generalized quadrupedal animals with more restricted leaping adaptations. We show here, however, that the apparently peculiar calcaneal proportions of *A. frontanyensis* merely result from size-scaling effects, so that they do not indicate any particular emphasis on leaping behaviours. This agrees with other postcranial features of this taxon, such as the long and narrow (adapoid-like) proximal calcaneal facet, the general morphology of the talus—including the talofibular joint that gently slopes laterally and the lateral position of the groove for the tendon of the flexor hallucis longus (Moyà-Solà and Köhler 1993)—and even the femoral anatomy, which shows a generalized quadrupedal pattern without specific leaping features (SMS, unpublished data). This does not mean that *A. frontanyensis* never leaped, but merely that this taxon lacks the high degree of leaping specialization that is displayed by extant tarsiers and galagos. This is confirmed by

the overall postcranial anatomy of the former, which fits well the pattern of a quadrupeal and climbing prosimian with low incidence of leaping. Hence, when size-scaling effects are taken into account, the calcaneal proportions of *A. frontanyensis*, apparently unusual for an adapoid, are best interpreted as the expected proportions for a small-bodied primate with a grasping and a prosimian-like foot with a proximally-placed fulcrum, adapted to vertical clinging, but with no particular emphasis towards leaping.

With regard to other fossil primates, no significant departure from the expected calcaneal proportions for a primate with a 'tarsi-fulcrumating' foot of their size are found in fossil galagids (*Komba* and *Progalago* from the Miocene of East Africa), omomyids or eosimiids, contrary to what would be expected if they were committed leapers (Figs. 3, 4). This fact does not imply that leaping adaptations cannot be confidently inferred from of other skeletal features in these taxa (Dagosto 1988; Walker 1970; Gebo 1987, 1988, 1989a, b; Gingerich 1981). Rather, it merely means that, on the basis of calcaneal proportions, no special adaptations to leaping can be inferred. Eosimiids, which are considered putative stem anthropoids (Beard et al. 1994, 1996), display anthropoid-like calcaneal proportions, which contradicts previous inferences of leaping adaptations on the basis of a moderate calcaneal elongation (Gebo et al. 2000a, b), but agrees with the frequent use of horizontal foot postures that has been inferred from several pedal elements (Gebo et al. 2000b), as in extant anthropoids. In this regard, eosimiids resemble the larger-bodied, stem anthropoids from Africa (propliopithecoids). To sum up, the previous interpretation of calcaneal elongation in omomyoids and eosimiids as a leaping adaptation is not supported by our analysis. On the contrary, the high ACL/TCL length ratio in *Eosimias* is merely a consequence of its small body size, as in *A. frontanyensis*.

On the other hand, some adapines (*Adapis* and *Leptadapis*) from the Eocene of Europe display a shorter ACL than expected on the basis of BM (even shorter than in lorisids), displaying an intermediate condition between anthropoids and non-primate mammals. Their calcaneal proportions are unusual for a primate with a grasping foot (Martin 1979, 1990), particularly as judged on the basis of the long, robust and abductable hallux (Dagosto 1983). This led to different interpretations, suggesting either that these calcanei had been misidentified as primate (Martin 1979), that they represent a secondary reversal to the ancestral euprimate condition (Dagosto 1983), and/or that they reflect an adaptation to slow arboreal locomotion (Martin 1993). The proportions of the adapine calcaneum, with very short ACL, together with other morphological similarities to lorisids (Dagosto 1983), suggest that, like the latter group, adapines probably never leaped and had a very slow-moving locomotion, therefore confirming previous

suggestions (Dagosto 1983; Martin 1993) that fossil European adapines were specialized slow-quadrumanous climbers similar to the extant *Nycticebus* (Dagosto 1983, 1993).

Implications for reconstructing the ancestral euprimate locomotor repertoire

For more than a half-century, two competing views on the reconstruction of the ancestral locomotor adaptations of earliest euprimates have been under discussion: the vertical clinging and leaping (VCL) (Napier and Walker 1967) and the nocturnal visual predation (NVP) (Cartmill 1972) hypothesis. Napier and Walker (1967) suggested VCL to constitute the ancestral locomotor behaviour of euprimates. Although still a matter of debate (Anemone and Covert 2000; Dagosto 2007; Demes and Günther 1989; Gebo 1986; Gebo et al. 2000a, b; Gingerich 1981; Lemelin and Schnidt 2007; Szalay and Dagosto 1988), this notion has not changed substantially since its initial proposal, and leaping has figured prominently in subsequent refinements of this hypothesis, as shown by definitions such as 'hind limb dominated locomotion' (Rollinson and Martin 1981) or 'grasp-leaping' (GL) (Dagosto 1988, 2007; Szalay and Dagosto 1980). In strong contrast, Cartmill (1972, 1974) proposed a slow moving quadrupedal ancestor with grasping extremities related to NVP as a model for the last common euprimate ancestor. On the basis of different sources of evidence, this hypothesis is supported by other authors (Anemone 1990; Ford 1988; Godinot 2007; Lemelin and Schnidt 2007; Schnidt and Lemelin 2002). In fact, the basic point of disagreement between both views is the role of leaping in earliest primates' locomotion.

The hypothesis that leaping played an essential role in euprimate origins stems mainly (but not exclusively, see Dagosto 2007) from the distinctive elongation of the distal foot elements, such as the navicular, the neck of the talus and the cuboid and specially the calcaneus, in most Palaeogene primates and extant strepsirrhines. These euprimate traits, more accentuated in prosimians than in anthropoids (Ford 1988; Gebo 1986), have been considered a biomechanical innovation in the lever system of the foot enabling to increase the effective length of the hind limbs, so that a more powerful leap can be produced (Hall-Craggs 1965; Dagosto 1988, 2007). According to this hypothesis, euprimates would have resorted to lengthening their tarsal elements for leaping across large gaps within an arboreal environment, because their metatarsals are involved in grasping (Dagosto 1988; Morton 1924). Lengthening of the distal tarsals has been therefore considered a functional alternative to the lengthening of metatarsals, which is the normal condition in other specialised jumpers (e.g.,

Jacculus, kangaroos, rabbits etc.) (Dagosto 1988). This hypothesis played also an important role in the reconstruction of the ancestral morphotype of the Anthropoidea. The apparently somewhat elongated anterior calcaneus of *Eosimias* has been therefore interpreted as a primitive feature shared with omomyoids, a suggested sister-group of anthropoids (Gebo 1988), being interpreted as evidencing a leaping ancestry for anthropoids (Gebo et al. 2000b).

On the contrary, the alternative interpretation is presented here that the moderately elongated distal calcaneus and, by extension, tarsus of primates is a compensatory mechanism to recover the lost load arm (metatarsal length) when the foot adopts the grasping function, instead of a leaping adaptation. This interpretation has important implications for the discussion on earliest euprimates locomotion. Under our point of view, the moderately long tarsus of most primates merely stresses the significance of grasping as the original primate adaptation. The fact that, apart from Morton's (1924) work, no attempt has been made to understand the mechanical consequences of the structural changes in the foot related to grasping (e.g., the posterior shift of the fulcrum) has led to overestimating the leaping signal of tarsal lengthening in primates, particularly because some extant forms showing a very long tarsus are strongly committed to leaping. Of course, an analysis of a single feature in a single bone, such as calcaneal proportions, is insufficient to make general conclusions on the locomotor morphotype of the earliest primates. Moreover, a reappraisal of all the features functionally related to leaping/quadrupedalism in primates is beyond the scope of this work. However, the fact that primates as a group display a relatively longer distal calcaneus when compared with other mammals emphasizes the fundamental role of grasping in primate origins. In particular, our results strongly indicate that the VCL hypothesis needs to be revised by taking into account that a moderate foot elongation cannot be used to infer leaping adaptations in earliest primates.

Summary and conclusions

The study of the foot proportions in primates, and in particular of the calcaneus, has played a crucial role in the study of primate origins and adaptations. On the basis of allometric analyses, calcaneal proportions are investigated in primates and in other mammals in order to determine the actual differences between the different primate groups, as well as between primates as a whole relative to other mammals. The analysis reveals that primates as a group display a relatively longer distal calcaneus, relative to both total calcaneal length and body mass, when compared with other mammals, and also that there are important

differences among several primate groups. Prosimians tend to display a higher degree of distal calcaneal elongation than anthropoids. However, only the highly specialized, small vertical-clinging-and-leaping prosimians (galagos and tarsiers) clearly depart from the scaling relationships of mostly unspecialized primates by displaying an extreme degree of distal calcaneal elongation.

In the past, the functional significance of distal calcaneal elongation in primates has been related to locomotor adaptations by interpreting it in terms of preference for leaping. However, this explanation is unlikely because all extant primates display a relatively elongated distal calcaneus when compared with non-primate mammals, in spite of the fact that primates as a whole show variable degrees of commitment to leaping and some do not leap at all. This, together with morphofunctional considerations, suggests that the reduction of the load arm concomitant with the adoption of the grasping foot by primates needs to be compensated by a lengthening of the tarsus (mainly the calcaneus). The universal adaptation to pedal grasping among primates (with the exception of *Homo*) therefore explains the higher relative distal calcaneal length of primates as a whole when compared with other mammals. In turn, in prosimians the greater emphasis on grasping and the associated tarsi-fulcrumating foot of prosimians explains their higher degree of distal calcaneal elongation (except in the slow-climbing lorisids) when compared with the more cursorial anthropoids. From this perspective, the widely accepted hypothesis that distal calcaneal elongation is an adaptation to leaping is rejected by our analysis. Only when the degree of calcaneal elongation departs from the allometric regressions of anthropoids and non-specialized vertical-clinging-and-leaping prosimians (all prosimians other than galagos and tarsiers), the calcaneal proportions can be interpreted as an adaptation to a specific locomotor mode.

This allometric analysis is applied to the recently discovered calcanei of the smallest adapiform *Anchomomys frontanyensis*, which apparently displays an unusually long distal calcaneus for an adapoid. When size-scaling effects are taken into account, it emerges that the *A. frontanyensis* calcaneal proportions are best interpreted as the expected ones for a small-bodied primate with a grasping and a prosimian-like foot with a proximally placed fulcrum, adapted to vertical clinging, but with no particular emphasis on leaping. The alternative interpretation of the moderate distal calcaneal elongation of most primates presented in this work has important implications for the discussion on the role of leaping in earliest primates. The current lack of models allowing to understand the mechanical consequences of the foot changes related to grasping has led to over-interpreting distal calcaneal elongation as a correlate of leaping in primates. We consider that the VCL hypothesis needs to be revised by considering the fact that moderate foot elongation cannot be used to infer leaping adaptations in earliest primates.

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